Phenology of southward migration of shorebirds in the East Asian–Australasian Flyway and inferences about stop-over strategies

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Abstract. The southward migration strategies of shorebirds remain poorly understood in the East Asian–Australasian Flyway, yet understanding such strategies is critical to shorebird conservation. We estimate passage dates of 28 species of shorebird from count data at 15 sites to infer their migration strategies, using Thompson's modelling approach. Our estimates of passage dates were consistent with available tracking data, giving us confidence that the modelled estimates were accurate. For large-bodied shorebirds, modelled departure dates from the northern Yellow Sea were similar to arrival dates throughout Australia, and their arrival dates in different regions in Australia were also similar, suggesting they flew directly from Asian staging areas to Australian non-breeding areas, or stopped only very briefly on the way. In contrast, small-bodied species apparently made multiple stops, especially in northern Australia, during their migration to their final non-breeding destinations. These differing patterns suggest that larger species in this Flyway depend on a small number of staging sites, whereas smaller species migrate in shorter steps and require additional staging sites between the northern Yellow Sea and Australasia. It is likely that some of these sites have not as yet been discovered, and that conservation of small shorebird species requires a more complete accounting of unknown and understudied staging sites.

Additional keywords: body size, citizen science, migration strategy, phenology, staging, wader.

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Introduction

Many shorebird species in the East Asian–Australasian Flyway (EAAF) are declining (Amano *et al.* 2010; Wilson *et al.* 2011; Clemens *et al.* 2016), with two of the probable drivers being loss of wetland habitat through reclamation (Rogers *et al.* 2011; Piersma *et al.* 2015; Moores *et al.* 2016) and *Spartina* invasion (Gan *et al.* 2009). The Yellow Sea lies in the centre of the EAAF, and many shorebirds must stop there to replenish their energy reserves to complete their migration (Choi *et al.* 2009; Hua *et al.* 2013). However, two-thirds of the intertidal habitat in the Yellow Sea has been lost in the past 50 years and the remaining habitat is being degraded at an alarming rate (Murray *et al.* 2014, 2015). Determining the migration strategies of shorebirds and potential linkages between their intertidal habitats is necessary to understand the relative importance of different wetlands to different shorebird populations (Iwamura *et al.*

2013) and, thus, to ensure that critical sites in the EAAF are conserved.

The identification of important shorebird sites in the EAAF has led to regular monitoring efforts (Barter 2002; Gosbell and Clemens 2006; Bai *et al.* 2015), intensive banding studies and the analysis of banding recoveries and sightings of colour-marked birds throughout the Flyway (Minton *et al.* 2011*b*). These studies have provided a basic but incomplete understanding of the migration routes of many species and contain potential biases as only a small proportion of the EAAF is monitored. More recently, a detailed understanding of the migration patterns of several species, such as the Eastern Curlew (*Numenius mada-gascariensis*), Bar-tailed Godwit (*Limosa lapponica*), Ruddy Turnstone (*Arenaria interpres*) and Greater Sand Plover (*Charadrius leschenaultii*), has been revealed through tracking individuals with satellite transmitters or geolocators (Driscoll and Ueta 2002; Ueta *et al.* 2002; Minton *et al.* 2011*a*; Battley *et al.* 2012). Smaller scale research has also been conducted on Great Knot (*Calidris tenuirostris*), using radio-transmitters to study their movements between stop-over sites in China on northward migration (Ma *et al.* 2013*b*). These studies have revealed remarkable interspecific and intraspecific variation in migration patterns, with many species adopting a mix of long- and short-distance flights between stop-over sites and their non-breeding grounds, but many gaps remain in our understanding of how shorebirds use different wetlands, especially on southward migration.

For example, counts of shorebirds at many sites in East Asia during northward migration are considerably higher than num-bers recorded on southward migration, and the reason for this discrepancy remains poorly understood (Barter 2002; Anon. 2011). If it is caused by shorebirds using different migration routes during southward migration, then it is possible that im-portant staging sites remain undiscovered and perhaps insuffi-ciently protected. Alternatively, it is possible that the same routes are used on southward and northward migration, but that because the southward migration is more protracted, smaller numbers of birds are present at any one time at a staging site. Northward migration is tightly constrained in time because migrating adults of some species must initiate nesting just after the thaw in order to breed successfully during the short boreal summer (Meltofte *et al.* 2007). Southward migration appears to be more spread out in time, with successive waves of failed breeders, successful breeders and then juveniles migrating through stop-over sites (Tomkovich 1997; Choi *et al.* 2011). Satellite telemetry and geolocator studies on small numbers of birds have confirmed southward migration of Bar-tailed Godwit subspecies *baueri*, and some individual Ruddy Turnstone, is strikingly different to their northward migration, with trans-Pacific flights by south-bound birds (Minton *et al.* 2011*a*; Battley *et al.* 2012). Tracking studies have not yet discovered any differences in southward and northward migration routes for any other species in the EAAF, but coverage of species is limited and biased towards species that are large enough to carry a satellite transmitter, or have the high site-fidelity and high probability of recapture required to allow the retrieval of geolocators.

In this study we use a population approach to examine the southward migration strategies of shorebirds moving to Australia. We do this by estimating passage dates during southward migration from count data at 15 key stop-over and non-breeding sites in the EAAF. There have been previous compilations of raw and opportunistically collected data on passage times through the EAAF and arrival dates in Australia (Marchant and Higgins 1993; Higgins and Davies 1996) but these studies indicated mostly the first arrivals or last departures, making it difficult to identify peak arrival and passage periods.

With more refined estimates of passage dates we hoped to determine if there are periods during the southward migration when large numbers of some species cannot be accounted for. If gaps of this kind do occur it could suggest the existence of undiscovered stop-over areas, or clarify the role of poorly known sites. For example, in many species there are few or no tracking data, but resightings of colour-flagged birds indicate that some individuals migrating to southern Australia stop in northern Australia or at sites on the east coast (Minton *et al.* 2011*b*). Establishing whether such individuals are 'typical' is difficult unless additional data sources are available. Documentation of average arrival dates in southern Australia could help establish whether the bulk of the population arrives late (consistent with multiple short flights with stops down the eastern coast) or arrive at a similar time to the arrival of birds in northern Australia.

We were particularly interested in the correspondence of departure dates from the Yellow Sea with arrival times in Australasia, a distance of 5000–8000 km. Available shorebird counts from the intervening regions of eastern and south-eastern Asia are considerably lower than counts from the Yellow Sea or Australasia (Bamford *et al.* 2008) but this may reflect limited count coverage in a large region with few observers. Tracking studies have shown that some larger species (e.g. Eastern Curlew, Bar-tailed Godwit subspecies *menzbieri*) migrate from the Yellow Sea to Australia in a single direct flight of ~4–6 days duration, preceded by several weeks of refuelling in the Yellow Sea (Battley *et al.* 2012; Gosbell *et al.* 2012). Few tracking data are available for small-bodied species of shorebird in the EAAF but, as they have different metabolic capacities, they may have shorter potential flight-ranges (Piersma 1987; Pennycuick 1989; Klaassen 1996) and so may need to refuel somewhere between the Yellow Sea and Australia. We therefore compare the migration strategies of large and small-bodied shorebird species, considering how well arrival dates in Australia corre-spond with departure dates from the Yellow Sea, and whether the duration of staging in the Yellow Sea is consistent with substantial refuelling for long-distance flights.

Materials and methods

Study areas

We collated count data from 15 shorebird sites in the EAAF where experienced observers have conducted frequent counts (at least monthly) throughout at least one southward migration (Fig. 1). The attributes of these sites are summarised in Table 1 (also see Table S1 in supplementary material available online). Notes on the broad strategic use of the sites by shorebirds are given below.

The most northerly site, Yalu Jiang coastal wetland in northern China, is only occupied by small numbers of a few shorebird species during the boreal winter, but it is one of the
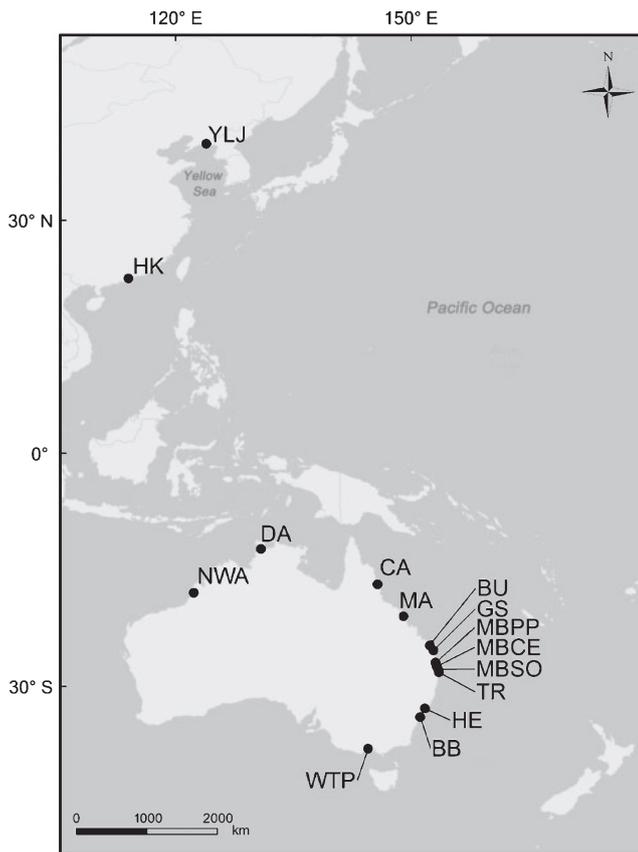
Fig. 1. The 15 areas analysed in this study. YLJ, Yalu Jiang coastal wetland; HK, Mai Po Inner Deep Bay; NWA, north-western Australia; DA, Darwin, Northern Territory; CA, Cairns, Queensland (Qld); MA, Mackay, Qld; BU, Bundaberg, Qld; GS, Great Sandy Strait, Qld; MBPP, northern Moreton Bay (Pumicestone Passage), Qld; MBCE, central Moreton Bay, Qld; MBSO, southern Moreton Bay, Qld; TR, Tweed River, Qld–NSW; HE, Hunter River estuary, NSW; BB Botany Bay, NSW; WTP, Western Treatment Plant, Victoria. (This map was created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.)

most important staging sites in the EAAF during the northward migration (Q.-Q. Bai, Y. Chen, C.-Y. Choi, unpubl. data), supporting >250 000 shorebirds between March and May (Riegen *et al*. 2014; Choi *et al*. 2015). Its role to shorebirds during southward migration is less well known. Satellite telemetry of Bar-tailed Godwits (Battley *et al*. 2012) and sightings of leg-flags and bands of most species considered in this paper (Tables S2, S3) indicate strong migratory links with both Australia and New Zealand (Minton *et al*. 2011*b*; Riegen *et al*. 2014).

Further south in East Asia, Mai Po Inner Deep Bay Ramsar site in Hong Kong is a non-breeding destination and moulting area for large numbers of shorebird species, with internationally important numbers present during the boreal winter. It is also used as a stop-over site by birds migrating to non-breeding areas further south (Anon. 2011) such as Curlew Sandpiper (*Calidris ferruginea*; with evidence from banding and resighting data (Minton *et al*. 2011*b*; Table S2)). Data from Mai

Po represented the only available data from south-eastern Asia and the consistent and regular counts conducted in Mai Po may provide evidence for shorebird species that make short-distance flights from the Yellow Sea during southward migration.

Most of the study sites were in Australia and details of the local count programs have been published elsewhere: the northern beaches of Roebuck Bay in north-western Australia (Rogers *et al*. 2006*a*, 2006*b*, 2011); Lee Point to Buffalo Creek, Darwin, Northern Territory (Lilleyman *et al*. 2016); Cairns, Mackay, Bundaberg, Great Sandy Strait, northern Moreton Bay (Pumicestone Passage), central Moreton Bay and southern Moreton Bay, Queensland, and the Tweed River on Queensland–New South Wales (NSW) border (Milton and Driscoll 2006); Hunter River Estuary (Spencer 2010) and Botany Bay, NSW; and the Western Treatment Plant, Victoria (Rogers *et al*. 2013). The key features of these shorebird sites are summarised in Table 1. Banding and flagging studies have shown that the sites in southern Australia are non-breeding grounds where shorebirds reside for several months whereas those in northern Australia are known to serve as both non-breeding areas and stop-over areas, depending on the species (Minton *et al*. 2011*b*; Table S1). However, it remains unclear how many birds stop on the northern Australian coast *en route* to non-breeding grounds in southern Australia or New Zealand.

Survey methods and data selection

Following Clemens *et al*. (2014), we analysed surveys in which all major count areas (usually roosts with clearly defined natural boundaries) within a shorebird area (a larger area within which shorebirds reside and move) were counted. Double-counting or failing to count birds were avoided by surveying count areas at consistent times relative to high tide and by minimising the time between counts in adjacent count areas. Surveys usually took 1–2 days (maximum 5 days). Surveys conducted over multiple days were given the mean date of the surveys in analyses. For the most part we analysed recent counts (after year 2000), in case passage dates have changed over time, although convincing evidence for such change has yet to be reported in shorebirds in Australia. At one site (Western Treatment Plant; Fig. 1), data from 1983–84 were included, as monthly count data were otherwise too sparse to estimate arrival dates.

At 12 sites we aggregated data from several separate migration seasons (Table 1) to calculate average passage dates over several years. This was often necessary because of a lack of data; at sites where only one count was done per month, the data collected in a single year were usually too sparse to fit our models. At the Hunter River Estuary and Botany Bay, NSW, where there were sufficient data to compare years, no annual variation in timing was detected. Nevertheless, simulations (Fig. S6) suggest that small annual variations in average timing could be caused by annual variation in breeding success (and hence the proportion of early failed breeders, and of late-migrating young birds present), an issue discussed later in this paper. At Yalu Jiang, Great Knots, Bar-tailed Godwits and Grey Plovers (*Pluvialis squatarola*) were aged in the field (using the general approach of Rogers *et al*. 2003), allowing us to estimate passage dates of adults and juveniles separately.

Table 1. Survey sites and regions, monitoring periods and frequency of surveys

For Conservation importance: IBA, Important Bird Area (BirdLife International 2016); Ramsar, Ramsar site (Ramsar 2016). For data source: QWSG, Queensland Wader Study Group; NSWWSG, NSW Wader Study Group; AWSG, Australasian Wader Studies Group. Under region: N., northern; E., eastern; S., southern; SE., south-eastern

Shorebird site	Region	Country	Coordinates	Main roles in shorebird annual cycle	Conservation importance	Survey year(s)	Interval between surveys	Number of valid surveys used in analysis for each non-breeding season and total number	Data source
Yalu Jiang coastal wetland	N. Yellow Sea	China	39°48′58″N, 123°56′53″E	Migration stop-over	IBA	2012	Fortnightly during migration period (June–October)	12, 12	Q.-Q. Bai
Mai Po Inner Deep Bay Ramsar site	South-East Asia	China	22°29′20″N, 114°1′44″E	Migration stop-over, Wintering	IBA, Ramsar	2007–12	Weekly during migration period (July–October)	18, 117	Agriculture, Fisheries and Conservation Department via the Hong Kong Bird Watching Society
North-western Australia, Western Australia	N. Australia	Australia	17°58′52″S, 122°20′13″E	Migration stop-over, Wintering	IBA, Ramsar	2007	Weekly during migration period (August–September)	11, 11	K. G. & D. I. Rogers
Darwin, Northern Territory	N. Australia	Australia	12°20′31″S, 130°53′6″E	Migration stop-over, Wintering	IBA	2009–12	Fortnightly to monthly	6, 25	A. Lilleyman, G. O'Brien & A. Keates
Queensland									
Cairns	N. Australia	Australia	16°54′36″S, 145°46′11″E	Migration stop-over, Wintering	NA	2008–12	Monthly	6, 30	QWSG
Mackay	N. Australia	Australia	20°59′53″S, 149°3′25″E	Migration stop-over, Wintering	IBA	2007–12	Mainly monthly	7, 40	QWSG
Bundaberg	Central E. Coast	Australia	24°46′19″S, 152°23′24″E	Migration stop-over, Wintering	NA	2008–12	Monthly	6, 29	QWSG
Great Sandy Strait	Central E. Coast	Australia	25°22′41″S, 152°51′54″E	Migration stop-over, Wintering	IBA, Ramsar	2012	Monthly	6, 6	QWSG
Northern Moreton Bay (Pumicestone Passage)	Central E. Coast	Australia	26°58′16″S, 153°7′34″E	Wintering	IBA, Ramsar	2007–12	Monthly	5, 32	QWSG
Central Moreton Bay	Central E. Coast	Australia	27°25′34″S, 153°15′36″E	Wintering	IBA, Ramsar	2009–12	Monthly	5, 18	QWSG
Southern Moreton Bay	Central E. Coast	Australia	27°48′36″S, 153°25′52″E	Wintering	IBA, Ramsar	2008–11	Mainly monthly	5, 19	QWSG
Tweed River, Queensland–NSW border	Central E. Coast	Australia	28°12′18″S, 153°32′17″E	Wintering	NA	2007–12	Monthly	6, 34	QWSG
Hunter River estuary, NSW	SE. Australia	Australia	32°52′55″S, 151°47′28″E	Wintering	IBA, Ramsar	2000–12	Monthly	6, 91	A Lindsey & Hunter Bird Observers Club
Botany Bay, NSW	SE. Australia	Australia	33°59′49″S, 151°10′19″E	Wintering	Some are Ramsar	2001–14	Monthly	6, 101	P. Straw & NSWWSG
Western Treatment Plant, Victoria	S. Australia	Australia	38°2′37″S, 144°32′2″E	Wintering	IBA, Ramsar	1983–84; 2010–11	Mainly monthly	6, 38	Arthur Rylah Institute for Environmental Research (Heidelberg, Victoria) and AWSG

We did not have sufficient data to make this separation at any other sites.

To analyse southward migration, we truncated datasets to July–December. This reduced the risk that models would be confounded by fluctuations in numbers caused by northwards migration or dispersive movements of immature birds. There were two exceptions: (1) June counts from Yalu Jiang were included as this is the northernmost site, with returning birds known to be present as early as June (Q.-Q. Bai, Y. Chen, C.-Y. Choi, unpubl. data); and (2) January counts were included in the southernmost sites in NSW and Victoria because inspection of scatterplots indicated that some birds resided in these sites during the austral winter and shorebird numbers often peaked in January.

Data analysis

Migration phenology was estimated using an extended version of the modelling approach proposed by Thompson (1993). This uses repeated count data at individual sites when migrants are present to estimate the number of birds transiting and their average arrival and departure times (with associated standard errors). The method assumes that dates of arrival and departure are normally distributed. In addition to this standard model, we consider situations where we have several years of data at the same location and assume the same timing parameters, but not migratory numbers, in each year. We also consider situations when the migration terminates and there are no departures. Details of the modelling approach are provided in Appendix S1.

We also carried out a series of simulations to investigate whether the assumptions made in applying these models were valid, and to explore the potential effects of differential migration by age and sex (Appendix S2). Briefly, the assumption of a normal distribution is generally likely to be true for shorebirds because they often stop for one to a few weeks, diminishing any pulses in migration timing (Figures S3 and S5). The central limit theorem would predict normally distributed arrival dates and departure dates for a single shorebird population, given that each date is the mean of a large number of independent random variables (the migration times of individual birds). A potential complication is situations where migratory shorebirds passing through a particular stop-over site or arriving in a particular non-breeding area, come from several populations or cohorts that differ in exact timing of migration. For example, on southwards migration failed breeders (which leave the breeding grounds early) are likely to arrive at stop-over sites earlier than birds that bred successfully, whereas juvenile shorebirds (on their first southwards migration) migrate later than adults (Yosef and Meissner 2006; Newton 2008). Similarly there are regional variations in the timing of breeding and hence (presumably) the onset of southward migration. For example, of the two Red Knot subspecies that migrate to Australia, subspecies *rogersi* begins breeding in Chukotka in the last week of May (Tomkovich *et al.* 2013), whereas subspecies *piersmai* probably starts breeding in the New Siberian Islands at least 3 weeks later, in mid-June (Battley *et al.* 2005). We ran simulations to explore the potential effects of multiple cohorts

on estimates of passage time from count data (Fig. S6). The simulations indicated that in the situations likely to apply to the migrating shorebirds in this study, arrival and departure dates approximate a normal distribution. When there are mixed distributions, the Thompson models estimate average arrival and departure times over all cohorts, weighted by the relative abundance of each cohort. The standard deviations estimated by Thompson models are indicative of the spread or variability of passage dates whereas asymptotic standard errors are indicative of the uncertainty around the estimated parameters.

The fit of the models to the count data (for each species at each site) was evaluated based on the R-square, asymptotic standard error and the test statistic of the parameter estimates. A significance level of 80% was used in the test statistic of the parameter estimates owing to the small sample sizes and uncertainty in the precision of count data. The accuracy of estimated passage dates was evaluated by comparison with known passage dates based on satellite tracking and geolocator studies on the same populations.

Regression analysis was also carried out to examine if mean arrival date increased further south, which indicates that birds may 'hop' (*sensu* Piersma 1987) from the Yellow Sea to southern Australia. Results from preliminary analysis indicated that such a strategy was related to body weight so we pooled data from species weighing ≤ 130 g as small species and those > 130 g as large species in regression analysis. The data on weight used were mean masses in the non-breeding season (using data specifically from January when these were available) from Marchant and Higgins (1993) and Higgins and Davies (1996). We also used correlation analyses to test whether the spread of arrival times (as indicated by a larger standard deviation of the mean) varied with latitude. An increase in standard deviations further south would indicate multiple stops along the way (Fig. S5). All results are presented as means $\pm$ standard deviation (s.d.) unless stated.

Results

Migration phenology

We analysed counts from 15 sites (Table 1). Full details of the models are presented in Table S1, including model type, estimated parameters, asymptotic standard errors and R^2. Of the 28 species investigated, 15 occurred at many of our study sites and allowed the estimation of passage dates (Fig. 2).

Mean arrival times for eight species at the northern Yellow Sea (Yalu Jiang) were between mid-July and early August. On average, shorebirds staged for 5 weeks (36.8 ± 14.9 days, $n = 8$ species, range 21–63 days, estimated from the differences between mean arrival and departure dates). In the three species that were aged in the field at Yalu Jiang (Bar-tailed Godwit, Great Knot, Grey Plover), the average arrival date of juveniles was 41–50 days later than that of adults. Given this considerable difference, it is possible that estimated passage dates of other species at Yalu Jiang were also influenced by the proportion of juveniles present (Fig. S7, Table S8).

Average arrival dates in northern Australia were slightly later than average departure dates from the northern Yellow Sea for adult Bar-tailed Godwit subspecies *menzbieri* (by 7–18 days),
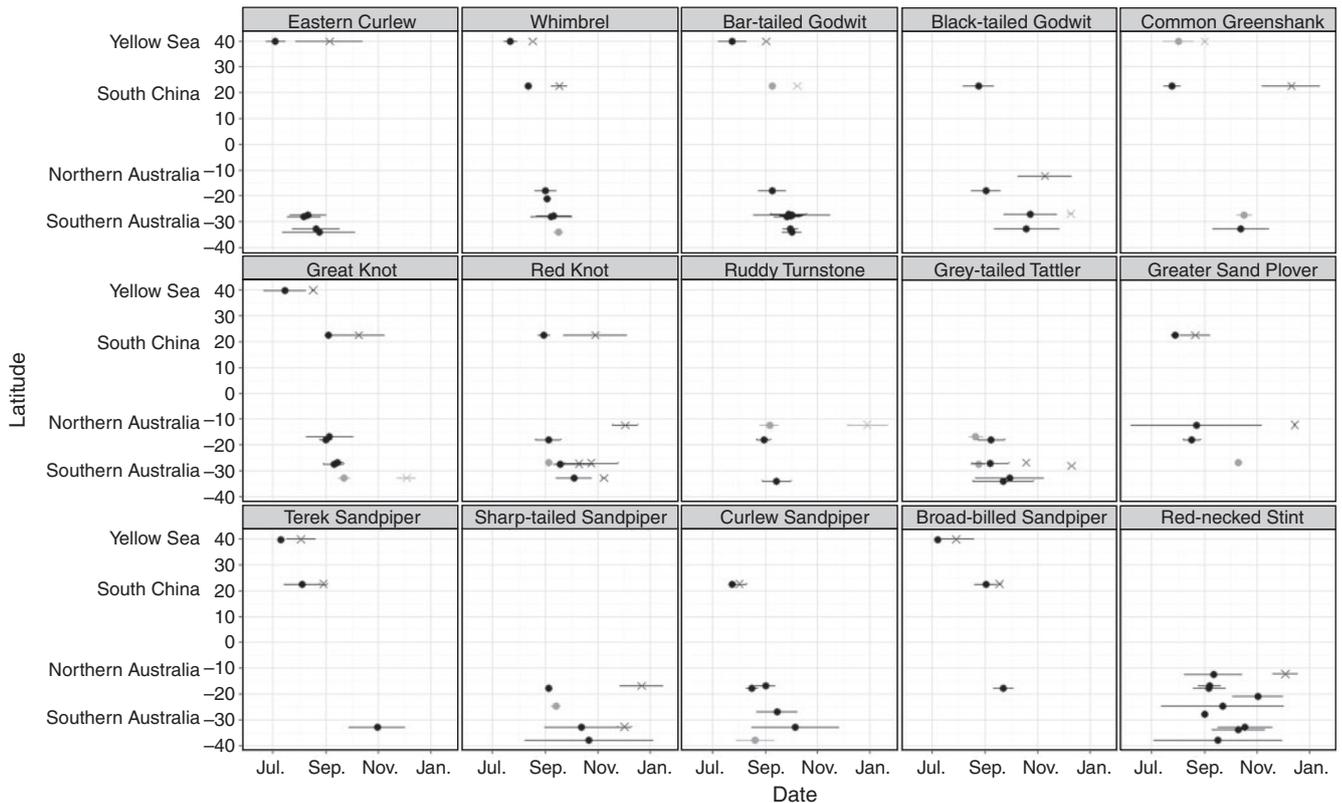
Fig. 2. Estimated passage dates of adults during southward migration for 15 shorebird species at 15 sites between China and Australia. With the exception of north-western Australia (NWA), locations are arranged from north to south (site abbreviations as Fig. 1). Values for each site are the modelled mean and standard deviation of date of passage. Species are arranged in order of decreasing mass from the top left to bottom right (based on Marchant and Higgins 1993, Higgins and Davies 1996). Circles denote mean arrival date and crosses denote mean departure date. Symbols in black denote the parameters estimated from the model were significantly different from zero at 0.05 level whereas those in grey were at 0.2 level. Bar-tailed Godwits at the sites YLJ, HK and NWA were subspecies *menzbieri* whereas those along the eastern coast of Australia were mainly subspecies *baueri* (Wilson *et al.* 2007; Battley *et al.* 2012). Detailed results of the parameter estimates can be found in Table S1 of the supplementary material, available online.

adult Great Knot (by 15–19 days), and Whimbrel (*Numenius phaeopus*, by 15 days) (Fig. 2). Intervals were substantially longer for Broad-billed Sandpiper (*Limicola falcinellus*; 55 days to north-western Australia) and Terek Sandpiper (*Xenus cinereus*; 89 days to Hunter River Estuary), suggesting an indirect journey between continents and one or more stops in sites not covered in this study. Several other smaller species for which there were no departure data from the Yellow Sea arrived in northern Australia at a similar time to Broad-billed Sandpipers (Fig. 2). Average arrival times of Eastern Curlews in Australia were earlier than departure time from the northern Yellow Sea, an unexpected outcome considered further in the discussion below.

Average departure dates from Hong Kong were within 1 week of average arrival times in northern Australia for several species – Whimbrel, Broad-billed Sandpiper and Greater Sand Plover – potentially indicating direct flights, especially in Greater Sand Plovers. The interval between departure from Hong Kong and Australian arrival was slightly longer for Curlew Sandpiper (14–15 days) than for those species listed above. In several other species departing from Hong Kong, it is likely that estimated passage dates (especially departure dates) were skewed by late-migrating juveniles. For example, estimated

arrival dates in Australia were earlier than departure dates from Hong Kong for Great Knot (by 17–34 days), Red Knot (*C. canutus*) (25–55 days), Bar-tailed Godwit (10–20 days) and Eastern Curlew (11–30 days). Field observations indicate that populations of the two knots and Bar-tailed Godwits in Hong Kong are dominated by juveniles during southward migration (Carey *et al.* 2001; no age-ratio data were available for Eastern Curlew in Hong Kong). In contrast, our models indicated that average passage dates for Curlew Sandpipers and Terek Sandpipers through Hong Kong were early in the migration season (late July to mid-August), and estimates of age of population in this period in Hong Kong were dominated by adults (Carey *et al.* 2001).

Arrival dates of Red Knot, Curlew Sandpiper, Sharp-tailed Sandpiper (*Calidris acuminata*) and Red-necked Stint (*C. ruficollis*) across Australia were later at more southerly sites, suggesting that these species might make stops within Australia while migrating south (Fig. 2). This was supported by a negative relationship between mean arrival date and latitude in small shorebirds (pooling species weighing ≤130 g; $P = 0.002$, adjusted $R^2 = 0.19$, 95% C.I. = –0.18 to –0.67). In contrast, Eastern Curlew, Bar-tailed Godwit (subspecies *baueri*), Whimbrel and Great Knot arrived in different regions

of Australia on similar dates, suggesting that they mostly fly directly to their non-breeding grounds instead of making a series of short flights within the continent (Fig. 2). There was no significant relationship between mean arrival date and latitude within Australia in large shorebirds (pooling species weighing >130 g; $P = 0.13$, adjusted $R^2 = 0.05$, 95% C.I. = −0.6 to 0.09).

In most species, the spread of arrival times, as indicated by their standard deviations, was greater towards southern Australia (see error bars in Fig. 2). Pearson correlation coefficients between standard deviation and latitude were negative for 13 of 14 species, significantly so for Grey-tailed Tattler and Sharp-tailed Sandpiper ($P < 0.05$). A plot of correlation coefficients against body size hinted at a tendency for the spread of arrival times to be more strongly correlated with latitude in small species than in large species, but this relationship was not significant (Fig. 3).

Most modelled passage dates were similar to dates estimated from remotely tracked birds (Table 2). The 95% confidence interval of estimated passage dates overlapped with the corresponding ones from tracking studies in 10 of 14 cases (71%), excluding cases where only one individual bird was tracked. The estimated average arrival dates in Bar-tailed Godwit and Greater Sand Plover were within 0–8 days of the average arrival dates of tracked birds in similar locations. The correspondence of estimated arrival dates of Red Knot, Grey-tailed Tattler and Eastern Curlew was less close (14–19 days) to average arrival times of tracked birds, perhaps because sample sizes of tracked birds were small (3–6 individuals). The greatest discrepancy between estimated and tracked arrival dates occurred in Ruddy Turnstone (30 days); it was an imperfect comparison because arrival times were estimated on the coast of NSW and

Queensland but the tracked records were from birds marked in Victoria.

Estimated departure dates were similar to tracking records for two comparisons (Bar-tailed Godwits from Yalu Jiang and Red Knots from south-eastern Australia, a difference of 3–5 days), but very different in two others (Eastern Curlew from Yalu Jiang and Red Knot from northern Australia, differences of 31 and 57 days respectively).

Discussion

The passage dates estimated in this study correspond well with records from tracking studies, giving us confidence in the results of this first, population-scale, cross-species comparison of movement patterns of shorebirds in the EAAF. Our results indicate that southward migration strategies differ between species and that body size might play an important role in the migration strategy used by shorebirds. In larger species, adults are likely to fly from staging sites in the northern Yellow Sea to final non-breeding destinations in Australia without stopping or with very brief stops. In contrast, smaller species are likely to make multiple stops in between. It is likely that juvenile shorebirds of all sizes also make multiple stops, given their later passage dates through the Yellow Sea and arrival in Australia (also see Rogers *et al.* 2003). The conservation of these smaller species and juveniles require efforts to uncover any potentially important but as yet unidentified sites in East and South-East Asia.

Do shorebirds migrate directly from the Yellow Sea to Australia on southward migration?

A non-stop flight from the northern Yellow Sea to Australia would be expected to take ~4–6 days (Battley *et al.* 2012;
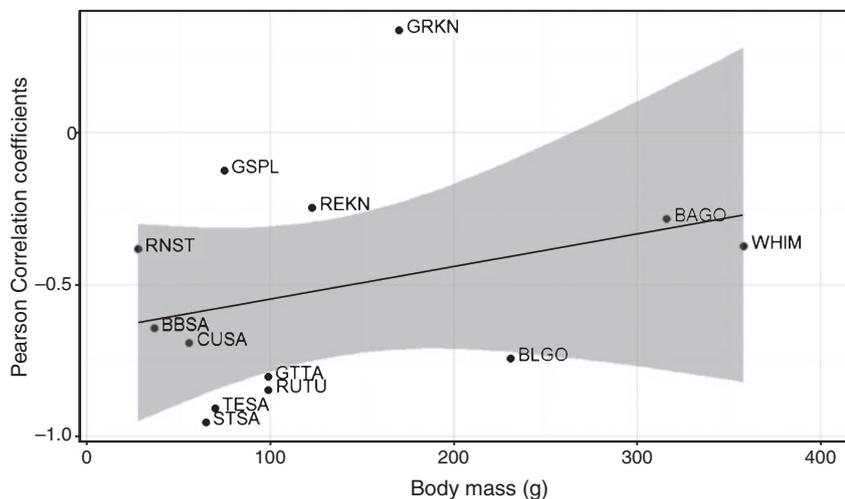

Fig. 3. Correlation coefficients between latitude and the standard deviation of estimated mean arrival date for 15 shorebird species at 15 sites during southward migration, plotted against body mass. Latitude in the southern hemisphere was treated as negative (i.e. latitude decreased further south). The smoothed line was generated using loess function and the grey shaded area denotes 95% confidence intervals. BAGO denotes Bar-tailed Godwit, BBSA Broad-billed Sandpiper, BLGO Black-tailed Godwit, CUSA Curlew Sandpiper, GRKN Great Knot, GSPL Greater Sandplover, GTTA Grey-tailed Tattler, REKN Red Knot, RNST Red-necked Stint, RUTU Ruddy Turnstone, STSA Sharp-tailed Sandpiper, TESA Terek Sandpiper and WHIM Whimbrel.

Table 2. Comparison between estimated dates of southward migration from this study and those reported in tracking studies (presented as mean ± standard error (s.e.))

Locations in Australia grouped into Northern Australia (NWA, DA and CA; abbreviations of sites as Fig. 1), Central Eastern Coast (MA, BU, GS, MBPP, MBCE, MBSO and TR) and South-eastern Australia (HE, BB and WTP). Tracking results were based on published satellite tracking and geolocator studies (Driscoll and Ueta 2002; Conklin and Battley 2011; Minton *et al.* 2011*a*, 2013; Battley *et al.* 2012; Gosbell *et al.* 2012) and one unpublished geolocator study (P. F. Battley, unpubl. data)

Species	Region	Event	Estimated date of passage from Thompson model (mean ± s.e.)	Wald 95% Confidence Interval of estimated passage dates	Date of passage from tracking study (mean ± s.e.)	95% Confidence interval of passage date based on tracking study
Bar-tailed Godwit subspecies *menzbieri*	Northern Yellow Sea	Arrival	24 Jul ± 4.1 days	16 Jul–4 Aug	20 Jul ± 1.7 days (*n* = 8, Northern Yellow Sea)	15–24 Jul
	Northern Yellow Sea	Departure	2 Sep ± 0.4 days	1–3 Sep	30 Aug ± 1.8 days (*n* = 8, Northern Yellow Sea)	25 Aug–3 Sep
	Northern Australia	Arrival	9 Sep ± 3.6 days	9 Aug–11 Oct	10 Sep ± 4.8 days (*n* = 7, North-western Australia)	29 Aug–21 Sep
Bar-tailed Godwit subspecies *baueri*	South-eastern Australia	Arrival	1 Oct ± 4.3 days	22 Sep–9 Oct	23 Sep ± 2.9 days (*n* = 24, New Zealand)	16–29 Sep
Eastern Curlew	Northern Yellow Sea	Arrival	4 Jul ± 2.6 days	29 Jun–12 Jul	16 Jun ± 2.1 days (*n* = 5, Northern Yellow Sea)	10–21 Jun
	Northern Yellow Sea	Departure	5 Sep ± 23.1 days	14 Jul–30 Oct	6 Aug ± 8.1 days (*n* = 5, Northern Yellow Sea)	14 Jul–8 Aug
	Central Eastern Coast	Arrival	9 Aug ± 7.4 days	26 Jul–27 Aug	24 Sep (*n* = 1, Central Eastern Coast)	24 Sep
	South-eastern Australia	Arrival	24 Aug ± 5.8 days	12 Aug–4 Sep	5 Aug ± 1 days (*n* = 3, South-eastern Australia)	31 Jul–9 Aug
Greater Sand Plover	Northern Australia	Arrival	17 Aug ± 2 days (NWA)	29 Jul–6 Sep	15 Aug ± 6.1 days (*n* = 4 North-western Australia)	26 Jul–3 Sep
Grey-tailed Tattler	Central Eastern Coast	Arrival	1 Sep ± 7.9 days	22 Aug–23 Sep	20 Sep ± 8 days (*n* = 3, Moreton Bay)	16 Aug–24 Oct
Red Knot	Northern Australia	Arrival	4 Sep ± 3.7 days	5 Aug–3 Oct	4 Sep ± 4 days (*n* = 6, North-eastern Australia)	24 Aug–14 Sep
	Northern Australia	Departure	3 Dec ± 4.6 days	23 Nov–13 Dec	7 Oct ± 4.8 days (*n* = 6, North-eastern Australia)	25 Sep–19 Oct
	Central Eastern Coast	Arrival	18 Sep ± 1.5 days (Hunter River Estuary)	15–21 Sep	5 Oct ± 7.2 days (*n* = 3, North-eastern Australia)	4 Sep–5 Nov
	Central Eastern Coast	Departure	10 Oct ± 7.5 days	23 Sep–26 Oct	24 Oct ± 2.1 days (*n* = 3, North-eastern Australia)	15 Oct–2 Nov
	South-eastern Australia	Arrival	4 Oct ± 2 days (Hunter River Estuary)	30 Sep–8 Oct	12 Oct (*n* = 1, South-eastern Australia)	12 Oct
	South-eastern Australia	Departure	8 Nov ± 0.9 days (Hunter River Estuary)	7–10 Nov	3 Nov (*n* = 1, South-eastern Australia)	3 Nov
Ruddy Turnstone	South-eastern Australia	Arrival	14 Sep ± 5.2 days (Botany Bay)	4–24 Sep	14 Oct ± 18.8 days (*n* = 20, South-eastern Australia)	5–22 Oct

Minton *et al.* 2013). This brief time is consistent with the difference between departure times from the northern Yellow Sea and arrival times in at least northern Australia, for several of the larger species examined in this study – Bar-tailed Godwit, Whimbrel and Great Knot – indicating that these species may fly directly from north-eastern Asia to Australia during southward migration.

It was not possible to estimate passage times for all smaller species from Yalu Jiang in the northern Yellow Sea, because, for some species, few or none occurred at Yalu Jiang on southward migration or, for other species, because estimates were potentially complicated by the presence of late-arriving juveniles. However, it was noteworthy that for two small species, the Broad-billed Sandpiper and Terek Sandpiper, arrivals in north-western Australia and eastern Australia were almost 2 months and 3 months, respectively, later than departures from the northern Yellow Sea, strongly suggesting that there must be other stop-over areas between the northern Yellow Sea and Australia. We suspect many such areas must occur on the Chinese coast, between the northern Yellow Sea and Hong Kong. Chongming Dongtan in the southern Yellow Sea is a known refuelling site for smaller shorebird species during southward migration, with significant increases in body condition over time recorded there for most of the calidrid sandpipers (Choi *et al.* 2009). It seems likely that Lianyungang and Rudong, in the central and southern Yellow Sea respectively, are also refuelling sites, given the high counts made there, including more than half of the world population of the critically endangered Spoon-billed Sandpiper (*Calidris pygmaea*) (Tong *et al.* 2014). Additional fieldwork, detailed analysis of the latest count data, band-recoveries and leg-flag resightings, along with examination of age composition in East and South-East Asia, would help to verify and identify the existence of more important sites for shorebirds during southward migration.

Do shorebirds stop in northern Australia before moving on to southern Australia?

Arrival times of medium to large shorebirds were similar across Australia, suggesting that birds made direct flights to all locations. In contrast, later arrival dates of some smaller species in south-eastern Australia (e.g. Red Knot, Curlew Sandpiper, Sharp-tailed Sandpiper and Red-necked Stint), and increasing arrival spans (indicated by greater variability of mean arrival dates) with latitude, indicate that smaller species may make more stops on the way through Australia. This is supported by sightings of flagged shorebirds from Victoria along the eastern coast of Australia (Minton *et al.* 2011*b*) and by a geolocator study of Red Knots in which four of six birds stopped at more than one location in Australia *en route* to New Zealand (P. F. Battley, unpubl. data).

Although the main patterns in our results are consistent with other work, these results are drawn from a limited number of sites in an immense flyway and therefore may not reflect patterns for all the sites in the Flyway, or any differences in migration strategies between subpopulations of the same species. Nonetheless, the migration strategies inferred from comparing passage dates between the northern Yellow Sea and

Australia, and those within Australia, led us to similar conclusions to other studies. It seems that large shorebird species in this Flyway depend on a small number of staging sites whereas small species make a series of stops on their way south and therefore need a series of wetlands to complete their migrations. Similarly, in the East Atlantic Flyway, the large Bar-tailed Godwit and Whimbrel can make direct, long-distance flights from the Banc d'Arguin to north-western Europe whereas small Dunlin (*Calidris alpina*) have stops in between (Zwarts *et al.* 1990).

The role of the Yellow Sea on southward migration

The onset of breeding in Arctic shorebirds that use the EAAF is likely to range between mid-May (e.g. Bar-tailed Godwits in southern Alaska; Battley *et al.* 2012) and mid-June (e.g. Red Knot on the New Siberian Islands; Rogers *et al.* 2010), and successful breeding attempts are likely to occur in a period of ~5–8 weeks, depending on species (Colwell 2010). Arrivals at Yalu Jiang from mid-July to mid-August were therefore early in the southward migration period, and there were unlikely to have been prolonged stops between the breeding grounds and the Yellow Sea. This finding is consistent with observations of fast turnover rates from sites on the coast of the Sea of Okhotsk on southward migration (Gerasimov 2004; Gerasimov and Huettmann 2006) and results of satellite telemetry showing direct flights of Bar-tailed Godwits from the Arctic to the Yellow Sea (Battley *et al.* 2012). In contrast, stop-overs at Yalu Jiang were prolonged (36.8 ± 14.9 days) suggesting that transiting individuals had time to accumulate sufficient fuel for long migratory flights of thousands of kilometres (Piersma *et al.* 2005), results that complement tracking studies indicating prolonged stops at the Yellow Sea (Battley *et al.* 2012; Minton *et al.* 2013). Available evidence indicates that the Yellow Sea is a critical staging region for most shorebird species on southward migration, that is, an area where substantial refuelling is carried out (Warnock 2010).

Our results indicate that the lower numbers of shorebirds counted during southward migration compared with northward migration (Barter 2002) could be a result of a combination of factors. Firstly, as southward migration is protracted, not all individuals will be present at any time and peak counts may underestimate the numbers of birds in an area. This is particularly true if adults that arrive early and juveniles arriving late are not analysed separately (Fig. S7). Secondly, tracking studies have shown that routes of northward and southward migration differ in at least some individuals of Bar-tailed Godwits, Ruddy Turnstones, Sharp-tailed Sandpipers and, potentially, Great Knots (Tomkovich 1997; Handel and Gill 2010; Minton *et al.* 2011*a*; Battley *et al.* 2012). As a result, some populations skip the Yellow Sea during southward migration. Finally, there was lower geographical and temporal coverage during southward migration in China during earlier surveys (Barter 2002; Hua *et al.* 2015). In some species the passage of many shorebird species through the Yellow Sea seems to take place in July and early August, earlier in the season than the timing of many previous shorebird surveys. Moreover, the numbers of some species, such as Dunlin and Eurasian Curlew (*Numenius arquata*), did not peak until mid-October or November in East

Asia, suggesting a preponderance of late-arriving individuals that was overlooked during earlier surveys (Table S1; Barter 2002; Q.-Q. Bai, Y. Chen, C.-Y. Choi, unpubl. data). Such limited geographical and temporal coverage is now partly being addressed by an increasing number of birdwatchers and survey effort (e.g. at Lianyungang and Rudong; Ma *et al*. 2013*a*; Bai *et al*. 2015). It is important to update and collate the most recent count data, especially from sites used on southward migration, not only to improve our understanding of the migration patterns of shorebirds but also for decision makers to determine priorities for conservation efforts.

Evaluation of the model estimates

For several species, it was possible to assess the accuracy of our modelling estimates through comparison with independent studies in which satellite transmitters or geolocators provided empirical observations of the timing of passage. In most cases the correspondence of count-based estimates and tracking studies was remarkably close; often, the average arrival dates determined by the two approaches were within 1–4 days of each other. We were surprised to find apparent departures of Red Knots from Darwin in December; these did not correspond with the migrations of tracked birds from New Zealand, and might have reflected local movements. We suspect that the early return of failed breeders in tracking studies (arrival of Eastern Curlews at Yalu Jiang and south-eastern Australia; Driscoll and Ueta 2002; Gosbell *et al*. 2012) could explain the discrepancy between our results and tracking results for Eastern Curlew. Our late estimates of passage dates for Eastern Curlews in Yalu Jiang were unlikely to be affected by the late arrival of juveniles because juveniles comprised <1% of the stop-over population at this site (based on proportions of juveniles to adults in field observations of >1000 individuals, from four different surveys; Q.-Q. Bai, unpubl. data). The relatively large spread in the modelled departure date at Yalu Jiang, the relatively late departure date at Yalu Jiang in relation to arrival date in Australia, and the report of birds in active moult (Q.-Q. Bai, unpubl. data), hinted that some Eastern Curlews at Yalu Jiang may either be immature birds or belong to a population that spends the boreal winter outside Australia.

An important assumption of the Thompson models is that arrival dates and departure dates are normally distributed. This seems to be reasonable in most scenarios (single population, single population after several stops, single population with multiple cohorts that differ in migration schedule) based on our simulations (Appendix S1). Violations of this assumption either lead to models failing to converge or unrealistic estimates, which can be identified as such if the results are checked carefully (Table S10). In short, Thompson models show great promise, especially as they can be applied to any species that can be counted regularly. We note that it is important to differentiate age-classes wherever possible. In addition to improving modelled estimates for adults (Fig. S7, Table S8), documenting the migratory timing of juveniles will improve our understanding of their migration strategies and potentially help to identify and conserve sites that they require – a priority as their survival is critical for the long-term viability of species.

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