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Red Knots (*Calidris canutus piersmai* and *C. c. rogersi*) depend on a small threatened staging area in Bohai Bay, China

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Abstract. We monitored numbers of Red Knots (*Calidris canutus*) staging in Bohai Bay, China (39°02′N, 118°15′E) on northward migration. Knots were identified to subspecies, and we systematically searched for colour-banded birds from the non-breeding grounds. We modelled migratory turnover, and revised estimates of flyway population using recently published counts from the non-breeding grounds. Two Russian-breeding subspecies occurred at our study site: *C. c. rogersi* (migrating to Chukotka), and *C. c. piersmai* (migrating to the New Siberian Islands); they co-occur on non-breeding grounds in Australia and New Zealand, but differ markedly in timing of migration. We conservatively estimate that our study site, comprising only 20 km of coastline, was used by over 45% of the combined world population of adult *C. c. rogersi* and *C. c. piersmai* – a conclusion supported by the independent data on frequency of resighting of colour-banded birds from north-western Australia and New Zealand. Much of this vital staging area is now being destroyed through construction of the Caofedian Industrial Zone and more westerly developments, which comprise only some of the many tidal flat 'reclamation' projects in the region. Preservation of the remaining tidal flats of Bohai Bay is essential to the conservation of Red Knots in the East Asian–Australasian Flyway.

Introduction

The Red Knot (*Calidris canutus*) is an iconic migrant, nesting in polar deserts of the high Arctic and carrying out very long-distance migrations to non-breeding grounds, mostly in the southern hemisphere (Piersma *et al*. 2005; Piersma 2007). It is highly specialised, foraging mainly on shellfish, with adaptations to this diet including a remote sense that enables detection of pore-water pressure differentials to locate hard, buried prey (Piersma *et al*. 1995, 1998) and a massively muscular gizzard for crushing bivalves which are swallowed whole (Piersma *et al*. 1993; van Gils *et al*. 2003, 2005*a*). It has a strictly coastal distribution outside the breeding grounds, being characteristically restricted to large tidal flat systems (Piersma 2007).

The migration systems of Red Knots that migrate through Europe and Africa have been studied intensively and are well known (Piersma and Davidson 1992; Nebel *et al*. 2000; Leyrer *et al*. 2009). In contrast, the migration system of Red Knots in the East Asian–Australasian Flyway (EAAF) is poorly known. Two subspecies occur in this flyway: *C. c. rogersi*, which nests in Chukotka, in far-eastern Siberia, and the recently described *C. c. piersmai* (Tomkovich 2001), which nests on the New Siberian Islands (Tomkovich 2001; Zöckler and O'Sullivan 2005). The non-breeding destination of these subspecies is imperfectly known, as they cannot be distinguished in non-breeding plumage. It is widely supposed that *C. c. rogersi* migrates predominantly to eastern Australia and New Zealand, whereas *C. c. piersmai* migrates predominantly to north-western Australia (e.g. Lindström *et al*. 1999; Piersma *et al*. 2005; Piersma 2007). However, few data were available when these ideas were initially proposed. Observations of both subspecies in breeding plumage in north-western Australia and New Zealand (Tomkovich and Riegen 2000; D. I. Rogers, C. J. Hassell and A. N. Boyle, pers. obs.), observations of birds colour-banded in north-western Australian in Chukotka (Minton 2007) and some documented movements of Red Knots between north-western Australia and New Zealand (Minton *et al*. 2005; Riegen *et al*. 2005; New Zealand Wader Study Group, unpubl. data; P. R. Battley, pers. comm.) suggest there may be more

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geographical overlap between the subspecies on the non-breeding grounds than previously thought.

Given the size of the non-breeding population of Red Knots in the EAAF, estimated at 220 000 individuals by Bamford *et al.* (2008), surprisingly few Red Knots have been found at staging sites in this Flyway. This situation was rectified to some extent by Barter *et al.* (2001), who counted 14 277 staging birds in the Tianjin Municipality in the west of Bohai Bay, China. Yet even after compiling all available count data for the Yellow Sea and extrapolating to estimate numbers in unsurveyed areas, Barter (2002) could account for only 66 300 birds (~30% of the supposed non-breeding population) on northward migration.

A potential explanation for the low numbers of staging Red Knots counted on northward migration was suggested by the discovery that Red Knots from north-western Australia are late migrants (Battley *et al.* 2005), with many birds not leaving north-western Australia until May. The peak in numbers at their staging grounds could, therefore, be in mid- to late May, later in the year than the completion of many previous shorebird surveys in the Yellow Sea. Climate records from the breeding grounds, and comparison of arrival times at the breeding grounds of other subspecies of Red Knot would suggest that *C. c. rogersi* arrives on the breeding grounds close to the start of June, and *C. c. piersmai* close to mid-June. Accordingly, another implication of the late migratory departures of Red Knots from north-western Australia is that they have little time for staging and refuelling in Asia before moving on to the breeding grounds. Consequently they are likely to require staging grounds with high quality of prey to migrate successfully (Battley *et al.* 2005).

Here we examine the migration of Red Knots through Bohai Bay, Yellow Sea, China (39°02′N, 118°15′E), in greater detail than has been managed previously. We counted numbers of Red Knots in our study area repeatedly throughout the northward migration of 2009. Pre-breeding moult was well advanced or complete by this time, so we were able to use plumage characters to assess the relative proportions of *C. c. rogersi* and *C. c. piersmai*. We compared these results against an independent dataset from the same site, comprising resightings of individually colour-banded Red Knots from non-breeding grounds in New Zealand and north-western Australia. We aimed to: (1) resolve the passage times of *C. c. rogersi* and *C. c. piersmai*; (2) determine how many individuals of each subspecies staged in our study area; and (3) assess the importance of the region to the Flyway population of Red Knot. The final objective is especially urgent, as Bohai Bay is bordered by one of the most densely populated regions in the world, and its tidal flats are rapidly being lost to coastal realignment projects. The largest of these so far, to develop the Caofedien Industrial Zone, is in progress on the margins of our study area, with more reclamations just west of this area in 2010.

Methods

Fieldwork was carried out in northern Bohai Bay, China (Fig. 1). The study site comprised ~20 km of coastline, dominated by tidal

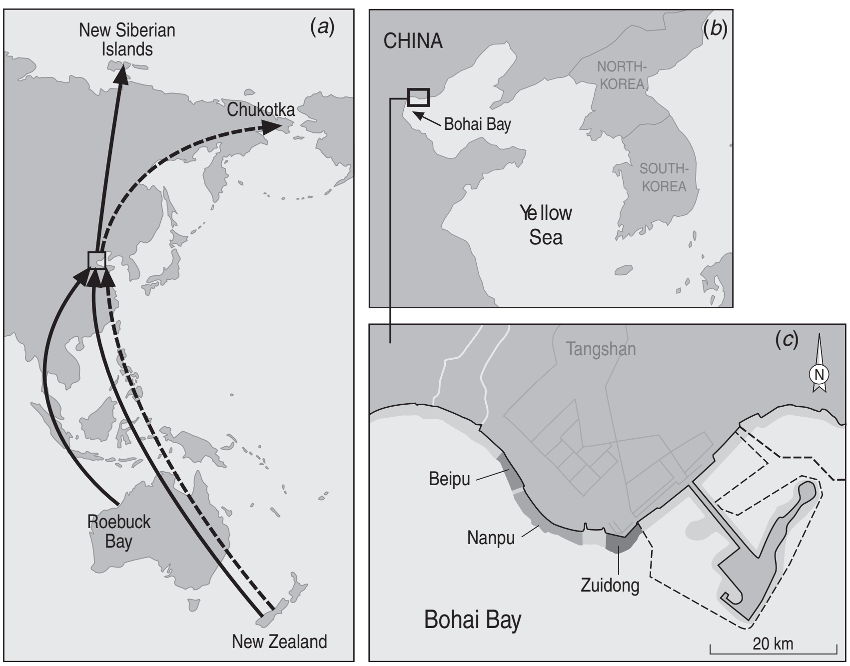

Fig. 1. Maps showing the locations mentioned in this paper. (*a*) The generalised northward migration route of Red Knots assuming great circle routes (subspecies *C. c. piersmai* with solid arrows, *C. c. rogersi* with dashed arrows). (*b*) Location of the study area in the Bohai Bay. (*c*) The study area in 2009. The artificial structure east of Zuidong, linking a former island to the mainland, is a construction phase of the ongoing Caofeidian Industrial Project; the planned final extent of this development is indicated by the dotted line. In addition to this project, reclamation of the tidal flats of Zuidong and Beipu is now planned or in progress.

flats that were 1–3 km wide on the lowest tides and submerged at high tide. The upper margins of the tidal flats were bordered by sea-walls (mainly incremental reclamations for the development of saltworks and aquaculture). Counts were carried out by H.-Y. Yang and B. Chen when the tide had ebbed 0.5–1 km from the sea-walls, when all Red Knots had moved to the flats from high-tide roosts, yet were still close enough to the sea-wall to be counted. The survey area was broken into three discrete blocks (Fig. 1), separated by channels that could not be crossed on foot. It was only possible to count the shorebirds in one block per high tide, except early and late in the season when fewer birds were present and quicker counts were possible. Adjacent blocks were therefore counted on consecutive days, and data were summed from adjacent blocks to give an overall count of Red Knots for the region in intervals of 3 days.

Birds were identified as subspecies *rogersi* or *piersmai* on the basis of the colour and pattern of breeding plumage. Birds identified as *C. c. piersmai* had deep brick-red underparts and reddish napes. The mantle and scapulars were black, boldly marked by rufous fringes and panels within each feather; many scapulars had narrow white tips, but these were inconspicuous and did not dominate the appearance. Birds identified as *C. c. rogersi* had paler, peachier underparts, and whitish napes. They had more extensive silvery variegation on the upperparts caused by a combination of broader grey-white tips to individual feathers, the presence of many scapulars with grey-white panels within the feather, and only a pale rufous tinge to other markings within the scapulars. These characters can be used to distinguish subspecies *piersmai* and *rogersi* on the breeding grounds in June–July (Tomkovich 1992, 2001), indicating that they should not be confused because of plumage wear when staging on northward migration. In China we found distinguishing these plumage extremes was usually straightforward provided birds were not obscured by other birds in the flocks. Some individuals were difficult to identify early in the migration season before they had developed extensive diagnostic breeding plumage, and were not identifiable to subspecies. It was not practical to scan all flocks closely enough to carry out separate counts of *C. c. piersmai* and *C. c. rogersi*. Instead we carried out scans to assess the relative proportions of *C. c. piersmai* and *C. c. rogersi* in subsets of birds. These scans were carried out by two separate field teams: H.-Y. Yang and B. Chen, and C. J. Hassell and A. N. Boyle. Within particular days, scans were consistent between observers and between sites, and data from different observers are pooled here. Subspecies scans were not practicable every day. Accordingly, daily subspecific proportions of *C. c. piersmai* were gently smoothed (SYSTAT 11, Systat 2005: NONLIN Smooth and Plot Feature with polynomial smoothing, Gaussian kernel, nearest neighbour proportion = 0.25) and values for missing days interpolated. The smoothed values were used in subsequent analyses. Standard errors associated with these proportions assumed a binomial distribution. No data were collected on subspecies representation in the first two counts. The plot of known *C. c. piersmai* proportion increased almost linearly for the next four counts. A linear regression ($r = 0.988$) result for the four data points from Days 116 to 130 was extrapolated and gave first *C. c. piersmai* arrivals on Day 99, i.e. after the first count, and a proportion of 0.218 *C. c. piersmai* for Day 130 with a standard error of the estimate of 0.022. We calculated the number of *C. c. piersmai* and *C. c. rogersi* present on each shorebird survey day as the product of the total number of Red Knots and the proportion of each subspecies within Red Knot flocks at that time.

From 10 to 29 May 2009, C. J. Hassell and A. N. Boyle conducted intensive searches for individually colour-banded birds from banding projects in New Zealand, and Roebuck Bay in north-western Australia (Fig. 1). Birds with unique engraved leg-flags were also recorded, though it was often impossible to approach closely enough to read the engravings. Birds marked only with plain leg-flags (yellow if initially captured in north-western Australia, orange if initially captured in south-eastern Australia, white if initially captured in NZ) were also recorded systematically. Within each day it was possible to ensure that leg-flagged individuals were not double-counted, but as the birds with single leg-flags could not be individually distinguished, some individuals might have been sighted repeatedly on different days. Many colour-marked birds were undoubtedly overlooked, as they mingled in large dense flocks and it was never possible to examine every leg of every individual in a single day. Whenever possible, resighted birds were identified to subspecies on the basis of plumage characters. Comparing these identifications against the known non-breeding origin of the resighted birds provided insights into the location of the non-breeding grounds of the two subspecies. It also provided some insight into the repeatability of subspecific identifications made on plumage characters: of 45 individuals that were seen more than once, only one was assigned to different subspecies on different occasions.

We modelled our count data using the approach proposed by Thompson (1993) to estimate passage times and number of birds migrating through the staging area. Date of arrival and departure of each subspecies were assumed to be normally distributed. Iterative modelling enabled us to estimate the number of individuals that staged in the study site and the dates of arrival and departure (and associated standard errors) that best explained the changes in numbers of birds counted through the study period. Realistic starting values for the calibrations were obtained by an iterative branch-and-bound procedure. In this, at each iteration, the ranges bounding the 'best' values of each parameter were successively reduced. Final parameters and standard errors were estimated using the NONLIN procedure in SYSTAT 11 (Systat 2005) with a sum-of-squares loss function.

Attempts to model turnover by calculation of apparent daily survival probability of colour-banded individuals (Schaub *et al*. 2004; Verkuil *et al*. 2010) were unsuccessful, because too large a proportion of the colour-banded birds observed were sighted only once. Instead, we estimated the number of colour-banded birds that were present but undetected by examining the distribution of the number of times that individually marked birds were resighted. Another measure of the proportion of the flyway population occurring in the study site was a direct comparison of the number of birds present compared with estimates of the non-breeding population. Estimates of shorebird populations in non-breeding grounds of the EAAF (Barter 1992, 2002; Watkins 1993; Bamford *et al*. 2008) were based to some extent on maximum historical counts, many of which are out of date. We updated the estimates on the basis of published counts of major non-breeding sites in Australia and New Zealand over the last five years, when possible using average non-breeding counts (between November and February) from 2004–05 to 2008–09 as an index of current population size.

Results

Red Knots were absent from the study area from January to March 2009; the first migrating birds were counted on 8 April. Numbers built up rapidly through April and peaked in early May, with single counts of 36 890 birds being made on 1 May, and 35 610 on 10 May; numbers remained high until the last week of May but thereafter declined rapidly, with only 26 birds present on 2 June (Fig. 2). The proportion of birds identified as *C. c. piersmai* on plumage characters increased steadily from 26 April to the end of May. The proportion of *C. c. rogersi* declined correspondingly, and by the end of the study period, only *C. c. piersmai* was present (Fig. 2).

Using plumage characters to assess the proportion of *C. c. piersmai* and *C. c. rogersi* present over time, we modelled the passage times of both subspecies. They migrated on different schedules (Table 1; Fig. 3), with *C. c. rogersi* arriving earlier (average date of arrival, 21 April) and departing earlier (average date of departure, 17 May). Arrival and departure dates of *C. c. rogersi* showed similar scatter, with little difference between the results of a model that assumed that standard deviations of these dates were the same, and another model which calculated standard deviations of arrival and departure dates independently. *C. c. piersmai* arrived later (average date of arrival, 29 April) and departed later (average date of departure, 28 May) with departures being concentrated in a much smaller period than the period of arrivals. As a result, late-arriving *C. c. piersmai* have less time to stage than early arriving individuals, unlike *C. c. rogersi* in which our data are consistent with all individuals having a stopover duration of ~29 days. Average stopover duration of *C. c. piersmai* was similar, but the models imply that 16.3% of *C. c. piersmai* stage for 21 days or less, and that 3.3% stage in Bohai Bay for 14 days or less.

The passage-schedule models indicated that the Bohai Bay study area was used by a total of 39 760 Red Knots on northward migration: 17 660 *C. c. rogersi* and 22 100 *C. c. piersmai*. This constitutes 18.1% of the Flyway population estimate of 220 000 of Bamford *et al.* (2008). However, this estimate is out of date, and reappraising the Flyway population estimate to include the most recent published data (Table 2), it appears that the Flyway population is only ~105 000 birds, 37.9% of which staged in our study site in the Bohai Bay. As non-breeding counts from

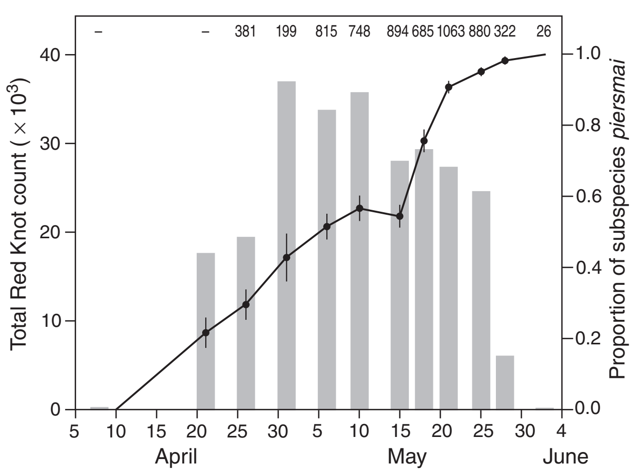

Fig. 2. Count totals (grey bars, plotted against the left *y*-axis) and proportion of *C. c. piersmai* within flocks (points plotted against the right *y*-axis) by date. Error bars for subspecies proportions indicate 95% confidence limits. Number of birds identified to subspecies are given above the bars. Proportion for 21 April obtained by interpolation (see Methods). No standard errors for 8 April when all birds were estimated to be *C. c. rogersi*, or for 2 June when all birds were *C. c. piersmai*.

Table 1. Number of birds (±standard deviation), and passage times of Red Knot subspecies *piersmai* and *rogersi* through Bohai Bay

Results presented for models that assumed equal standard deviations of arrival and departure dates, and for models that calculated them independently. Standard deviations of dates given in days

Model	Number of birds	Average date of arrival	Average date of departure
C. c. piersmai			
Equal s.d.	20 557 ± 1459	1 May ± 0.38	28 May ± 0.38
Independent s.d.	22 066 ± 2232	29 April ± 8.60	28 May ± 0.38
C. c. rogersi			
Equal s.d.	17 755 ± 2014	18 April ± 5.10	17 May ± 5.10
Independent s.d.	17 661 ± 1944	18 April ± 5.89	17 May ± 4.49

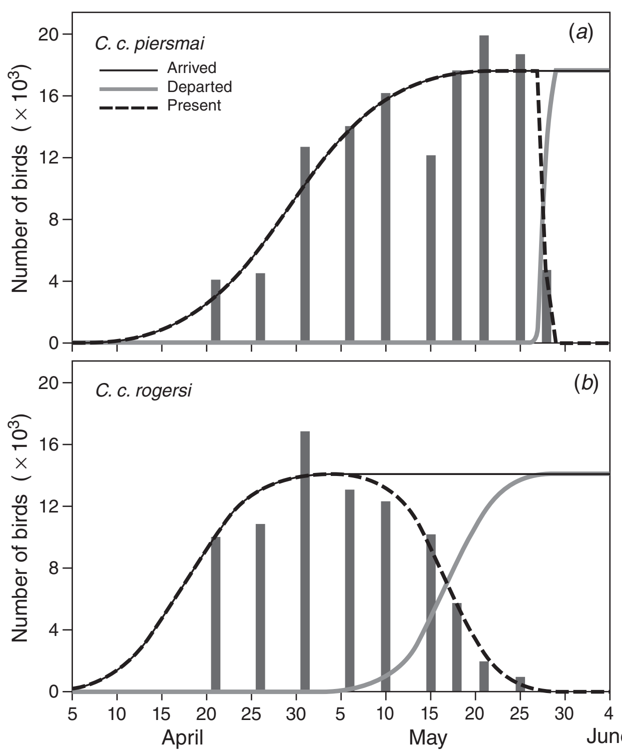

Fig. 3. Staging of subspecies *C. c. piersmai* (*a*) and *C. c. rogersi* (*b*) in the Bohai Bay study area. The black line indicates the number of birds calculated to have arrived; the grey line the number of birds that had departed, and the stippled line indicates the calculated number of birds present in the study area. Direct counts of staging birds in the study area are indicated by grey bars.

Table 2. Numbers of Red Knots at main non-breeding sites in Australia and New Zealand

Official estimate by Bamford *et al.* (2008); updated estimate based on the most recently available austral summer counts (November–February, during the non-breeding season). Site are arranged following Bamford *et al.* (2008) from most birds to fewest birds for both Australia and New Zealand

Site	Bamford *et al.* (2008)	Revised estimate	Source for revised estimate
Australia			
Eighty Mile Beach, WA	80 700	23 123	Rogers *et al.* (2009)[A]
South-eastern Gulf of Carpentaria, Qld	23 657	23 657	P. V. Driscoll, unpubl. report[B]
Roebuck Bay, WA	11 200	2131	Rogers *et al.* (2009)[C]
Corner and Shallow Inlets, Vic.	7110	894	Minton *et al.* (unpubl. data)[D]
Roper River Area, NT	3100	3100	Chatto (2003)[E]
Lake Macleod, WA	2566	2566	No recent published data
Port Pirie coast, SA	4800	4800	Wilson (2000)
Ceduna bays, SA	2788	2788	Wilson (2000)
New Zealand			
Farewell Spit, South Island	24 227	8220	Southey (2009)[F]
Manakau Harbour, North Island	22 433	12 522	Southey (2009)[F]
Kaipara Harbour, North Island	16 910	10 186	Southey (2009)[F]
Parenarenga Harbour, North Island	13 500	3200	Southey (2009)[F]
Firth of Thames, North Island	7819	5259	Southey (2009)[F]
Whangerei Harbour, North Island	4198	1988	Southey (2009)[F]
Houhara Harbour, North Island	2855	1200	Southey (2009)[F]
Rangaunu Harbour, North Island	2500	4067	Southey (2009)[F]
Waitemata Harbour, North Island		1036	Southey (2009)[F]
Estimated Australian total	135 000	63 059	This study
Estimated New Zealand total	68 000	41 927	Southey (2009)
Estimate total population	220 000	104 986	This study

[A]Previous total was based on aerial survey with restricted ground-truthing. Average of three complete ground counts of Eighty Mile Beach in 1999, 2001 and 2008 was 25 898 (23 123–29 679).

[B]From March 1999; no complete non-breeding surveys have been done since (see P. V. Driscoll 2001 report to Queensland Environmental Protection Agency (Brisbane), 'Gulf of Carpentaria wader surveys 1998–99').

[C]Average of peak summer counts 2005–2008 (two counts done annually). No complete count of Roebuck Bay has exceeded 2825 birds since the 1980s.

[D]Average counts 2004–2009. Corner Inlet is counted once each summer; the last summer count exceeding 3000 birds was in 1993 (C. D. T. Minton, P. Dann, A. Ewing, S. Taylor, R. Jessop and P. Anton, unpubl. data).

[E]Chatto (2003) estimated the population of Red Knot in the Northern Territory was >24 000 birds but further analysis is required given the difficulties in assessing numbers of this species from aerial surveys.

[F]From New Zealand counts 1995–2003; populations of Red Knot were estimated to have declined by 14% overall in New Zealand since a similar summary was prepared by Sagar *et al.* (1999) for the period 1983–1994, and declines are thought to have occurred since (I. Southey, A. Riegen and R. Schuckard. pers. comm.).

Australia and New Zealand include first-year birds that are not old enough to migrate north (Rogers *et al*. 2006), the proportion of migrating adult Red Knots using Bohai Bay is higher still. The average proportion of first-year Red Knots in north-western Australia from the austral summers of 1998–99 to 2008–09 was 17.0% (Minton *et al*. 2009). Assuming a similar proportion of first-year birds occurs elsewhere in the non-breeding range, the migrating population can be calculated as 87 150 adult Red Knots in the Flyway, 45.6% of which staged in our small study area.

The banding origin of birds resighted in the Bohai Bay area and identified to subspecies at the time of observation (Table 3) revealed substantial overlap in non-breeding grounds between *C. c. piersmai* and *C. c. rogersi*. Searches for colour-banded birds were made between 10 and 29 May, a period in which our models indicate that numbers of *C. c. piersmai* peaked (>90% of the staging population present on all days between 11 and 24 May). However, *C. c. rogersi* had already begun to depart: 20% of *C. c. rogersi* had already migrated from the study area by the beginning of the resighting period on 10 May and <1% remained by the end of the month. The average daily proportion of *C. c. rogersi* present during the colour-band resighting period was 30.3%. If we use this factor to account for departed birds we can calculate the relative proportions of *C. c. rogersi* and *C. c. piersmai* from several non-breeding populations for which we resighted many colour-banded or leg-flagged birds (Table 2): subspecies *C. c. piersmai* constituted 83.1% of the migrants from north-western Australia, 35.2% of the migrants from Victoria and 24.6% of the migrants from New Zealand. There was no relationship between date and the proportion of north-western Australian birds present among colour-marked birds ($r = 0.287$, $n = 18$). In contrast there was a clear relationship between date and the proportion of *C. c. piersmai* identified on plumage (Fig. 2 and above). Together, these results suggest that the timing of northward migration of each subspecies through

Table 3. Numbers of colour-banded and leg-flagged Red Knots from different banding sites observed in the Bohai Bay study sites, 10–29 May 2009

Identification of subspecies based on plumage characters when observed in Bohai Bay. Corrected *C. c. rogersi* is the number of *C. c. rogersi* observed divided by 0.303 (the average daily proportion of *C. c. rogersi* present during the resighting period); this value was used in the calculation of the percentage of *C. c. piersmai* in the study area (final column)

Origin	Unidentified subspecies	*C. c. piersmai*	*C. c. rogersi*	Corrected *C. c. rogersi*	Percentage of *C. c. piersmai*
Chukotka, eastern Siberia	0	0	1	3	0
Kamchatka, eastern Siberia	0	0	2	7	0
Chongming Dongtan, China	15	21	11	36	36.6
Sumatra, Indonesia	1	2	0		100
North-western Australia	51	276	17	56	83.1
South-eastern Queensland, Australia	0	0	1	3	0
South Australia, Australia	1	0	0	0	
Victoria, Australia	25	68	38	125	35.2
New Zealand	29	55	51	168	24.6
Total	122	422	121	400	51.4

Bohai Bay is driven more by migratory destination than by migratory origin.

Discussion

The study site in Bohai Bay – a 20-km stretch of coastline – proved to be extraordinarily important to Red Knots, supporting over 45% of the Flyway population of Red Knots during northward migration. Outside Bohai Bay, no other staging sites of comparable importance to Red Knot have been found in the Yellow Sea (Barter 2002). However, historical data suggest that our study site is probably not the only area within Bohai Bay with staging Red Knots. Barter *et al*. (2003) found over 14 000 Red Knots staging near Tianjin in 2002, some 40 km to the west; over 2400 Red Knots were found in eastern Zuidong just east of our study site; and patchy count data suggest that Red Knots also occur in the coastal areas between Tianjin and our study site (H.-Y. Yang, unpubl. data). These counts may already be out of date, so overall numbers of Red Knots staging in Bohai Bay remain unclear, but it is clear that this fairly small area is the key staging area on northward migration for well over half of the Red Knots in the East Asian–Australasian Flyway. Exactly why they should be so localised during this time of year has yet to be resolved. The Bohai Bay mudflats discovered in this study may provide exceptionally high quality prey, a condition required by Red Knots in general (van Gils *et al*. 2005*b*) and especially the late-migrating migrants from north-western Australia (Battley *et al*. 2005).

In fact our estimate of the proportion of the Flyway population of Red Knots staging in our study area is conservative, and the true value must be higher. Our count models, essentially the non-linear regressions, necessarily pass through the data points. However, given that some birds leave before all have arrived, the numbers present will always be lower than actual number that use the staging area. In addition, our revised estimate of the Flyway population is likely to be an underestimate. It was considerably lower than previous published estimates (Table 2). In part this was because former estimates of numbers occurring on Eighty Mile Beach, north-western Australia (based on extrapolation from aerial surveys), were inflated, but also because of population decline, with numbers of Red Knots in adequately surveyed areas of eastern Australia and New Zealand now considerably lower than they were in the 1980s. Although our revised estimate is a closer approximation of the current population of Red Knots in the EAAF, we emphasise that it needs to be refined further, as some important non-breeding sites (notably the Gulf of Carpentaria) have not been surveyed for many years.

An independent check of the proportion of the Flyway population of Red Knot staging in Bohai Bay can be made on the basis of frequency of resightings of birds colour-banded in the non-breeding grounds. Of the 93 individually colour-banded birds resighted and identified to subspecies in Bohai Bay, 83 were *C. c. piersmai* (71 from Roebuck Bay, 12 from New Zealand). It was clear from the distribution of the number of resightings that many more must have been present but undetected. Assuming that the frequency of resightings had an exponential distribution (Fig. 4), we estimated that a further 104 colour-banded *C. c. piersmai* were present but overlooked, bringing the total

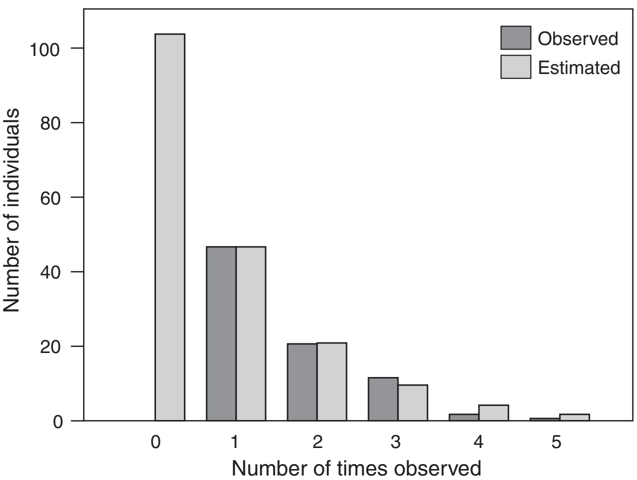

Fig. 4. Frequency (F) with which individually colour-banded *C. c. piersmai* were observed (n). Dark bars are observed frequencies; pale bars are estimated frequencies from the model: $F = Ae^{-\lambda \cdot n}$ where A = 104 (asymptotic standard error, ASE = 9.7), and $\lambda = 0.793$ (ASE = 0.068). The ordinate for $n = 0$ is the estimated number of colour-banded birds that were present but not observed.

number of individually colour-banded *C. c. piersmai* in the staging area to 187 (~160 from north-western Australia, ~27 from New Zealand). At the time of the study, 361 Red Knots had been individually colour-banded in north-western Australia (C. J. Hassell, T. Piersma and D. I. Rogers, unpubl. data). We can calculate that ~241 of these were alive during the resighting period in our study area (assuming average adult annual survival of 0.84; Brochard *et al*. 2002) and that ~200 of these living birds were *C. c. piersmai* (assuming 83.1% of the north-western Australian population was *C. c. piersmai*; see above). Following the same approach, we calculate that of the 370 Red Knots individually colour-banded in New Zealand, ~175 were still alive, and ~43 of these living birds were *C. c. piersmai* (assuming 24.6% of the New Zealand population was *C. c. piersmai*; see above). Using these figures we can roughly estimate that 80.0% of *C. c. piersmai* colour-banded in north-western Australia, and 62.8% of *C. c. piersmai* colour-banded in New Zealand, staged in the study area.

Only ten individually colour-banded *C. c. rogersi* were found during the study period, However, it is likely that we only found 45% of the birds present (assuming the same detection rate as for *C. c. piersmai*, see above). Moreover, our staging models indicate that the average daily proportion present of *C. c. rogersi* during the colour-band resighting period was 30.3%, many birds having already migrated north before we began to search for colour-bands. Correcting for these effects, we estimate 73 individually colour-banded *C. c. rogersi* staged in our study site (22 from north-western Australia, 51 from New Zealand). Using the approach described above for *C. c. piersmai*, we estimate that at the time of the study there were 203 individually colour-banded *C. c. rogersi* in the Flyway, 41 from north-western Australia (53.6% of which staged in our study area) and 132 from New Zealand (38.6% of which staged in our study area). These estimates are clearly crude, but they suggest that there is a tendency for Bohai Bay to be used more by staging Red Knots from north-western Australia than from New Zealand. In addition, the colour-band resighting data are consistent with the independent count data in indicating that Bohai Bay is used by a very large proportion of the Flyway population of Red Knots.

Separate estimates of the population size of *C. c. rogersi* and *C. c. piersmai* have never been made before because of the difficulty of distinguishing the subspecies on the non-breeding grounds (Delany and Scott 2006; Bamford *et al*. 2008). Applying our subspecies ratios to the non-breeding populations of north-western Australian, south-eastern Australia and New Zealand, and assuming that proportion of *C. c. piersmai* in the poorly known population in the Gulf of Carpentaria is intermediate between that seen in the populations of north-western Australia, we can tentatively make the first estimates of populations of the subspecies. The world population of *C. c. piersmai* is likely to be between 48 736 and 60 068 birds, and that of *C. c. rogersi* between 50 669 and 62 000 birds.

There were clear differences in the migration schedules of the two subspecies. *C. c. piersmai* was a late migrant, as was previously predicted on the basis of observations of departures from north-western Australia (Battley *et al*. 2005). The average arrival date for *C. c. piersmai* (29 April) corresponded closely enough in time to departure dates observed in north-western Australia (Battley *et al*. 2005) to suggest this subspecies makes a direct flight to Bohai Bay. In contrast, the average arrival date for *C. c. rogersi* was later (18 April) than observed departures from New Zealand by the end of March or start of April (P. F. Battley, pers. comm.), suggesting this subspecies uses an unknown staging area or areas elsewhere before arrival in Bohai Bay.

On average *C. c. piersmai* arrived 11 days later than *C. c. rogersi*, staged for a similar period and, most strikingly, had later departure dates that were far more compressed in time. One possible interpretation is that the timing of breeding varies more in *C. c. rogersi* than in *C. c. piersmai* because it has a more extensive breeding range (from at least 63°N to 69°N; Tomkovich 1992; Zöckler and O'Sullivan 2005). Alternatively, the difference may be explained by the differing terrains the subspecies fly over *en route* to their breeding grounds. For *C. c. piersmai*, the great circle route to the New Siberian Islands involves a long overland flight before reaching the shores of the Eastern Siberian Sea, which are frozen in late May and early June; they should therefore schedule their departures tightly in order to arrive on the breeding grounds when the thaw begins. Even when doing this they may encounter late snowfalls that force them to survive on their own body stores on reaching the breeding grounds, as has been demonstrated for subspecies *islandica* of the Red Knot in high arctic Canada (Morrison *et al*. 2005). In contrast, the great circle route from Bohai Bay to Chukotka takes *C. c. rogersi* parallel to the north-western shores of the Sea of Okhotsk (Fig. 1), where numerous estuaries, tidal flats and coastal lagoons may provide stopover opportunities for Red Knots should they encounter adverse wind conditions or heavy snow cover. Although there are few data, satellite imagery suggests there are ice-free areas along these shores in late May (e.g. http://www.natice.noaa.gov, accessed 22 September 2010) and there are observations of Red Knots from these shores consistent with such an interpretation (Gerasimov and Huettmann 2006). If *C. c. rogersi* does undertake further staging on northward migration, and does have more flexibility in arrival at the breeding grounds at a time when weather conditions are suitable, this could also explain another apparent paradox in our data: *C. c. rogersi* has a similar stopover period in Bohai Bay to *C. c. piersmai* (average 29 days), despite being slightly more distant from the breeding grounds (it is ~4700 km to from Bohai Bay to Chukotka, cf. ~4200 km to the New Siberian Islands).

The apparent dependence of Red Knots in this Flyway on Bohai Bay makes the conservation of *C. c. rogersi* and *C. c. piersmai* a matter of grave concern. In other flyways, subspecies *rufa* and *islandica* of Red Knots have suffered serious declines in population through degradation of staging areas (Baker *et al*. 2004; van Gils *et al*. 2006; Kraan *et al*. 2009). Bohai Bay lies in one of the most densely populated regions in the world, and it is undergoing rapid economic development, which includes conversion of tidal flats to land along much of the coastline. One of the biggest of these developments is at Caofeidian in northern Bohai Bay, a huge port and industrial development that had already destroyed approximately 110 km^2 of tidal flats and shallow water area by the end of 2008 (SOAPRC 2009), including the former Red Knot site at Zuidong East; this project is now expanding into our study area. The Tianjin sites to the west are being lost to an even larger development project, the Tianjin New Area, which has already resulted in the loss of

80 km^2 of tidal flats to the end of 2008 (SOAPRC 2009). Other development projects of similar scale are in progress elsewhere in Bohai Bay and at present there seems to be no legal impediment to further projects being planned. Protection of the remaining tidal flats of Bohai Bay is likely to be essential to the continued survival of Red Knots in the East Asian–Australasian Flyway.

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