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How do red knots *Calidris canutus* leave Northwest Australia in May and reach the breeding grounds in June? Predictions of stopover times, fuelling rates and prey quality in the Yellow Sea

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In general, Arctic-breeding waders leave non-breeding grounds in Australasia from March (New Zealand) to mid-April (Northwest Australia). Here we provide evidence from radio-tracking and visual observations that many red knots *Calidris canutus* do not leave Roebuck Bay, Northwest Australia, until early or mid-May. Late-departing red knots probably belong to the subspecies *piersmai*, which breeds on the New Siberian Islands, 10,400 km from Northwest Australia. Based on comparisons of temperatures on the breeding grounds of different knot subspecies, we predict that *piersmai* knots would not arrive on the breeding grounds until early June, leaving at most 3–4 weeks refuelling in Asia. Using a model of fuelling capacity in relation to prey quality and gizzard mass, we show that these knots must fuel very differently in Australia and Asia. In Australia, knots have seemingly suboptimal gizzard sizes and deposit fuel slowly. In the Yellow Sea, birds could only fuel up within the available time if they either enlarged their gizzards substantially or encountered prey qualities much higher than in Australia, for which we provide quantitative predictions.

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Timing of arrival on the breeding grounds may be critical to the breeding success of individual birds, and places a premium upon the appropriate timing of migration. Waders that breed in the Arctic but winter in the Southern Hemisphere can start preparing for northwards migration as early as January or February, and typically depart in March and April (Tulp et al. 1994, Battley 1997). Species undertaking long flights generally have at least one refuelling stopover en route to the breeding grounds, while species making shorter flights may have several.

The timing of departures from the non-breeding grounds on migration is often determined visually, and this can provide a good index of departures as long as birds are highly visible as they migrate. But often some species are poorly recorded in observations, giving few data with which to establish the timing of their migration. Intensive radio-tracking can provide much more detail on exactly when birds migrate. We radio-tagged red knots *Calidris canutus* (subspecies *piersmai*; Tomkovich 2001) in Roebuck Bay, Northwest Australia in February and March 2000 as they prepared for migration. Here we demonstrate from radio-tracking and visual data that some red knots leave Northwest Australia as late as early-mid May, leaving as little as 3–4 weeks to reach the breeding grounds over 10,000 km away.

While such a claim may seem far-fetched at first, we back this up with the first detailed counts of knots through the staging period from a stopover site in the Yellow Sea, China, a comparison of climate and arrival dates of knot populations globally, and a predictive model of staging time in relation to gizzard size and prey quality.

Methods

Northwest Australia

We studied red knots at Roebuck Bay (18°00′S, 122°22′E) from February to April 2000. In late February and early March 21 adults were tagged with 1.8 g Holohil 2-stage radio-transmitters. The presence of birds in the bay was determined via 14 automatic receiving stations (used up to 10–15 April; see Battley et al. 2004 for details) and hand-held telemetry (which continued until 1 May). Six birds were not recorded frequently enough to allow an accurate assessment of their daily occurrences, so only the 15 birds with high recording rates are discussed.

All radio-tagged birds were individually colour-banded, as were a further 27 knots (total 48). Searches were made of high-tide roosts and exposed mudflats to relocate colour-banded birds. When birds were seen, an estimate of the breeding plumage score was made.

Departures were observed by our expedition team, led by CJH and AB, from the northern coasts of Roebuck Bay in April 2000. From 1600–1800 h each day, teams sat on the northern shore of Roebuck Bay scanning the tidal flats and skies for departing birds. The flock size and species composition were determined for each flock seen leaving.

Observations in China

Weekly counts were made by H-YY at a site on the north side of Bohai Wan, China (39°02′N, 118°21′E), from January to June 2004. Wading birds were counted at high tide on a 6-km stretch of coast and adjacent salt pans. In the East Asian-Australasian Flyway, banders place country- or region-specific flags on the birds that they capture. Scans were made for leg-flagged shorebirds whenever possible.

Model predictions and body composition data

Intake rates of red knots are strongly dependent on the size of the gizzard, which crushes their shellfish prey (van Gils et al. 2003), and the size of the gizzard interacts with prey quality to determine the fuelling period. The gizzard size of red knots varies through the year depending on whether birds are trying to maximise the energy intake or simply meet their daily energy requirements. To assess whether the fuelling windows we propose are realistic, and under which conditions, we use a model of how fuelling rate (and therefore stopover length) varies with prey quality and gizzard mass (van Gils et al. 2005) to model the optimal fuelling durations for knots in Australia and China. Assumed values were prey quality of 2.22 kJ/g dry mass shell (DM_{shell}; van Gils et al. 2005) in Australia and 0.1–10 kJ/g DM_{shell} in China, lean mass of birds without gizzard or intestine of 80 g (PFB and TP unpubl. data), gizzard mass of 5–13 g (fresh mass), mass increase from 105 up to 175 g in Northwest Australia (based on Piersma et al. 2005, but allowing for a later departure than assumed in that analysis), arrival mass in China of 98 g (Barter et al. 1997), and mass increase in China to 160 g or 185 g (no data exist, so we used a range in case they store nutrients to carry to the breeding grounds; see Morrison et al. 2005). The model predicts the optimal gizzard mass that minimises the time spent fuelling at each site. Because prey quality is known in Australia, a single relationship between gizzard mass and fuelling period was derived. In China, separate predictions of staging length were made for different prey quality scenarios.

Results

Departures from Northwest Australia

Very high daily detection rates of knots (average 98%, range 92–100%) indicated that only one knot left before the automatic receivers were removed (last recorded on 26 March). One other was last recorded by an automatic receiver on 13 April. Hand-held telemetry recorded one bird frequently until 28 April, one infrequently until 29 April, and the remaining 11 knots were still present on the final radio-searches on 1 May.

Standardised migration watches in April 2000 recorded only small numbers of knots departing. Ten flocks of red knots totalling 262 birds were seen departing from 10–30 April. Subsequent to the formal observation period there were observations of two noteworthy flocks. On 14 May 2000, a flock of 110 was seen leaving the bay. On 15 May 2000, a further 70 were seen departing in a single flock.

Searches (opportunistic rather than intensive) were made of the northern coasts of Roebuck Bay in the austral winter to determine if any colour-marked or radio-tagged knots remained there during the breeding season. No radio-tagged birds were seen in June and July 2000, but 10 were located the following non-breeding season (and another the next year) indicating that they had departed and subsequently returned.

One knot that was still present at the start of May 2000 was relocated equally late in the subsequent northward migration period (4 May 2001). It was one of 400 birds in full breeding plumage out of a flock of 600, which suggests that substantial numbers of red knots may not migrate until May.

Passage through the northern Yellow Sea

Arrivals or passage of small numbers of knots were noted in Bohai Wan in the first half of April 2004 (Table 1), but numbers rose thereafter and peaked in mid-May. Fifteen sightings of knots flagged in Australia or New Zealand were made. Birds from Northwest Australia were seen only in May.

Climate and arrival dates on the breeding grounds

Dates of departure for and arrival on the breeding grounds are poorly known for *piersmai* and *rogersi* (the subspecies found in eastern Australia and New Zealand). Instead, we used climate data from the National Climatic Data Centre (http://lwf.ncdc.noaa.gov/oa/climate/climateresources.html) to make a general temperature comparison between the breeding ranges of all red knot subspecies. Stations used for each subspecies were: *piersmai*, Kotelny Island, New Siberian Islands (76°00′N 137°54′E); *roselaari*, Wrangel Island, (70°59′N 178°29′W); *rogersi*, Cape Uelen, Chukotka (66°10′N 169°50′W); *rufa*, Coral Harbour Airport, Southampton Island (64°20′N 83°36′W); *islandica*, Grise Fiord Airport, Ellesmere Island (76°41′N 82°90′W,) and Resolute Airport, Cornwallis Island (74°71′N 94°98′W), Canada, and Thule (76°53′N 68°75′W) and Daneborg (74°30′N 20°21′W), Greenland; *canutus*, Cape Celuskin, Taimyr (77°43′N, 104°18′E). Daily data were generally available from 1994 to 2003. While these stations may not strictly represent the knots' breeding grounds, they are the nearest available.

Linear regressions of daily maximum temperature against day (for May and June data, where 1 May equals day one; day explained 91–97% of the variation in temperature) were used to predict the expected temperature at each site on 30 May and 15 June. The ordering of subspecies (from coldest to warmest) based on the maximum temperature on 30 May was *canutus* – *piersmai* – *islandica* (Canada) – *roselaari* – *islandica* (Greenland) – *rogersi* – *rufa*. The ordering was similar on 15 June, though Canadian *islandica* were now marginally warmer than *roselaari*.

Good departure or arrival data exist for *islandica* migrating to Greenland and Canada, *canutus* migrating from Europe to Taimyr Peninsula, Russia, and *rufa* migrating from Delaware Bay, U.S.A., to Canada. Knots migrating to Greenland and Canada leave staging sites in late May: 25–29 May for *islandica* in Norway (Strann 1992), 25–31 May for *islandica* in Iceland (Alerstam et al. 1990), and 28–30 May for *rufa* in Delaware Bay (Baker et al. 2004). In contrast, *canutus* knots heading from European stopover sites to Taimyr Peninsula, Russia, leave much later. Birds have been recorded departing Germany from 2–10 June (Dick et al. 1987), flying over southern Sweden from 4–21 June (Gudmundsson 1994) and passing through the Gulf of Finland from the end of May until mid-June (median date 9 June; Pettay 1995). On Taimyr Peninsula, first arrivals have been recorded from 7–21 June, with last arrivals (where known) from 10–24 June (Tomkovich and Soloviev 1996).

Knots migrating to the New Siberian Islands are likely to migrate on dates closer to those of *canutus* than *islandica* or *rufa*, particularly as first departures of *islandica* probably take advantage of the comparatively mild conditions in Greenland (3.5°C warmer than Canadian sites on 30 May). Departures towards the New Siberian Islands are therefore likely to occur in early June rather than late May, leaving approximately three weeks of potential fuelling time in Asia for birds that depart Australia as late as mid-May.

Table 1. Counts and leg-flag sightings in 2004 of red knots in Bohai Wan, China. Abbreviations represent Northwest Australia, Southeast Australia and New Zealand respectively.

Date	Count	Flags		
		NWA	SEA	NZ
3 April	4			
10 April	201			
17 April	17			1
24 April	1795			
4 May	3001	2	5	1
15 May	3814			
21 May	2016	1	2	1
29 May	656			
09 June	130		1	1

Predictions of fuelling duration in Australia and China

In general, a larger gizzard results in a shorter fuelling period, because larger gizzards can process more shell material than smaller gizzards. Fuelling time therefore decreases as gizzard mass increases up to a point where the optimal time-minimising mass is reached (see Fig. 1). At this point energy intake is high, but the additional costs of having to carry a heavy gizzard do not yet counteract the benefits gained. For a knot in Northwest Australia, the fastest fuelling would be achieved with a gizzard mass of 10.6 g (dot on the line in Fig. 1). Increasing body mass from 105 up to 175 g would take around 15 days. Knots in Northwest Australia do not fuel anywhere near this quickly, however. The estimated fuelling period of 57 days (Piersma et al. 2005) implies that birds fuel with a gizzard of 7.4 g (horizontal line in Fig. 1), rather than increasing the mass to the optimal time-minimising level. This is exactly what body composition analyses have found (mean gizzard mass for six fuelling knots from Northwest Australia was $7.4 \pm$SE 0.9 g, PFB and TP unpubl. data).

The equivalent predictions for fuelling in China require simulations for a range of potential prey qualities. We also modelled scenarios for birds varying in two factors: (1) gizzard masses are kept the same as in Australia regardless of prey quality (we refer to this as an 'inflexible' gizzard) or are adjusted depending on prey quality ('flexible' gizzards), and (2) birds depart at either 160 g or 185 g.

The predictions (Fig. 2) show that unless prey quality in China is much higher than in Northwest Australia (ca. 3.5–4.5 vs. 2.2 kJ/g DM_{shell}), a knot that does not strategically adjust its gizzard mass (Fig. 2A) has no chance of fuelling in the available time window (Fig. 2B). In contrast, a bird that can adjust its gizzard could, in theory, fuel sufficiently across a wide range of prey qualities (Fig. 2D). In reality, however, prey qualities lower than 2–3 kJ/g DM_{shell} would require dramatic enlargement of the gizzard (Fig. 2C), beyond what is realistic is such a short timeframe. If prey qualities exceeded ca. 4.5 kJ/g DM_{shell}, a knot could even reduce its gizzard mass and still fuel successfully.

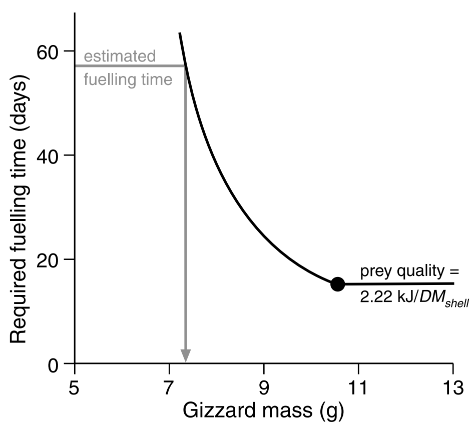

Fig. 1. The relationship between gizzard mass and fuelling time for knots preparing to migrate north from Northwest Australia. Prey quality is assumed to be 2.22 kJ/g DM_{shell}. The curve gives the time it takes a bird to fuel up from 105–175 g, depending on the gizzard mass. The horizontal line shows the estimated fuelling time based on body masses (Piersma et al. 2005), and the vertical arrow gives the corresponding gizzard mass. The dot gives the optimal time-minimising mass.

Discussion

When do red knots migrate to and from the Yellow Sea?

Several lines of evidence indicate that a large proportion of the red knots in Roebuck Bay, does not depart on northward migration until early to mid-May. Eleven of 15 radio-tagged birds were still present on 1 May 2000 (none of which was located visually later that austral winter). Flocks were seen departing on 14 and 15 May 2000, and subsequent observations found large numbers in breeding plumage present in early May 2001. Such late departures were not suspected before our radio-telemetry study. Red knots were presumed to depart from late March through April (Barter 1992), and birds present in Northwest Australia in late April have been thought to be individuals passing through from non-

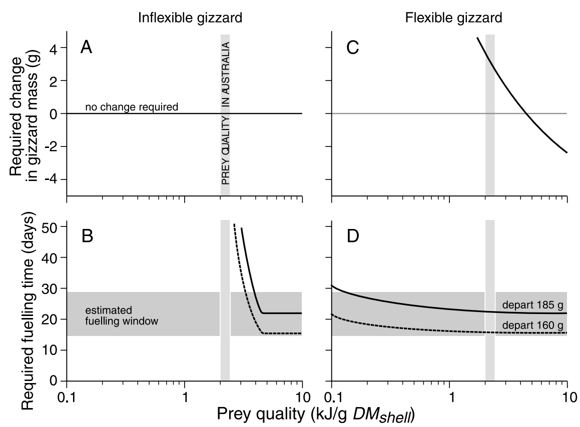

Fig. 2. Fuelling schedules for knots preparing to migrate north from the Yellow Sea. Left-hand plots (A and B) are for birds that do not adjust their gizzard mass after arrival (inflexible gizzards), and right-hand plots (C and D) are for birds that do (flexible gizzards). Prey quality (which is unknown) increases along the x-axes. The upper plots show the predicted change in gizzard mass required to fuel optimally (as (A) models an invariant gizzard, no change occurs). The lower plots show the time required to fuel up to either 160 g or 185 g before departure, depending on the prey quality and (in D) the gizzard mass. The estimated 'fuelling window' based on presumed arrival and departure dates is shaded as is, for reference, the prey quality in Northwest Australia.

breeding quarters further south (Higgins and Davies 1996, Minton et al. 1997).

It is more likely that some adult red knots routinely depart as late as early May. This is much later than knots from eastern Australia and New Zealand. Red knots leave New Zealand from the second week of March to the end of March or start of April (Battley 1997, Tomkovich and Riegen 2000), and Southeast Australia from the third week of February until the last week of April (Starks and Lane 1987).

Departure dates from the non-breeding grounds need to be interpreted in relation to the timing of migration to the breeding grounds, and there may be a sizeable difference in when *piersmai* (migrating from Northwest Australia) and *rogersi* (migrating from eastern Australia and New Zealand) leave the Yellow Sea. Based on climate comparisons, we suggest that *rogersi* will be one of the earliest subspecies to reach the breeding grounds, *piersmai* one of the latest. There could feasibly be a 1–2 week difference in when birds of different subspecies leave the staging grounds. For *piersmai*, many birds may not migrate until early June. This is confirmed by old records in Russian literature, in which the dates of first arrival of knots on the New Siberian Islands were 4 June 1903, 6 June 1886, 8 June 1902, 9 June 1956 and 11 June 1937 (P. Tomkovich pers. comm.).

To date, few red knots have been located in the Yellow Sea, in contrast to the well-documented aggregations of 50–60,000 great knot *Calidris tenuirostris* in the Yellow Sea (Barter 2002). The largest counts of red knot in China are in the Northwest Yellow Sea (Tianjin Municipality), where 14,277 were counted from 9–14 May 2000 and 9,358 from 24 April to 9 May 2002 (Barter et al. 2003). Barter (2002) estimated the Chinese population during northward migration as 62,000, which is less than one third of the migratory portion of an East Asian Flyway population of 220,000 (of *piersmai* and *rogersi* together). While this shortfall in numbers may indicate that the sites where large populations occur are yet to be located, it is also possible that substantial numbers of red knots do not reach the northern Yellow Sea until mid-May, and have thus been missed in Yellow Sea surveys that took place earlier in the migration season.

Fuelling strategies in Australia and China

The prediction of fuelling length and gizzard mass has two important outcomes for understanding the migratory strategy of this population of red knots. The first is that knots in Australia seemingly take a suboptimal fuelling strategy and do not build a gizzard that would maximise the energy intake on the moderate-quality prey they encounter. Instead, they have relatively small gizzards that allow only a slow fuelling rate. It is notable that both red knots and great knots (Battley et al. 2004) do not seem to synchronise moult and fuelling. Some of the red knots in this study were in almost full breeding plumage by early March (PFB and DIR unpubl. data), yet remained in Australia for at least another 6–7 weeks, implying that fuel deposition occurs after moult in these birds. This is understandable if knots can only fuel slowly and cannot afford conflicts with moult requirements. The question then arises of why knots in Australia do not build larger organs; one explanation could be that heat load problems (Battley et al. 2003) make the lower heat production of a small digestive system preferable to that of the time-minimising optimal mass.

Once in the Yellow Sea, however, fuelling at such a slow rate is not an option, with some birds having only 20–30 days available. There are two ways in which birds could fuel successfully in this time-frame. One is by enlarging the size of the digestive system upon arrival. There will be, of course, a delay in this, especially if organs have been catabolized during migration (Battley et al. 2000). Another is by selecting sites on migration that have much higher prey quality than experienced in Australia. Fig. 2B indicates that if knots had similar-sized gizzards in China as in Australia (the ‘inflexible gizzard’ situation), prey quality would have to be 60–100% higher for birds to be able to fuel up in time. The predicted energetic return of 3–4 kJ/g DM_{shell} is the same as is encountered by migrating *canutus* in The Netherlands and *rufa* in eastern Argentina (van Gils et al. 2005), so is not an unreasonable expectation.

Prey quality tends to increase in the Northern Hemisphere spring (Piersma et al. 1994, 2005), and it is possible that the knots’ ‘late’ arrival in the Yellow Sea occurs because only then is prey quality high enough to enable fast refuelling. If so, such a situation seems to be peculiar to red knots. Great knots leave Roebuck Bay earlier than red knots (25 March to 13 April for equivalent radio-tagged birds to the ones discussed here; Battley et al. 2004) and are widespread around the Yellow Sea (Barter 2002). Given red knots’ global dietary habits (molluscs, particularly bivalves, almost everywhere) we would predict that red knots concentrate in areas with high densities of small shellfish. Because the knots’ processing requirements for bivalves are essentially the same regardless of species involved, measuring the flesh ash-free dry mass and shell dry mass of prey in these areas would answer the question of whether red knots migrate late to capitalise on a rapidly improving food source.

The speed of migration of red knots from Northwest Australia at first seems extremely high, if only the time from departure from Australia is considered. The true speed of migration, though, takes the initial fuelling into account. With 57 days of fuelling in Australia, 25 in China, and 6.7 days of flying, the overall speed of migration is 117 km day^{-1}. This is low compared with *canutus* migrating from southern Africa (175 km day^{-1}: Hedenström and Alerstam 1998), but is higher than calculated for *rogersi* from New Zealand (about 122 days to cover 11,400 km = 93 km day^{-1}). These estimates would be too low if we have not accurately determined when fuelling starts, but it is clear that on average knots from Northwest Australia do not make a quick migration to the breeding grounds. They would have to fuel 30 days faster than assumed to match the speed of migration claimed for *canutus*. Northwest Australian knots do, however, greatly speed up their migration, from 106 km day^{-1} in the leg from Australia to China to 128–166 km day^{-1} in the second leg from China to Russia (range covers refuelling periods of 21–28 days).

For red knots to complete a journey of approximately 10,400 km within a month implies a remarkable fuelling episode in the northern Yellow Sea, during which fuelling rates must be far higher than achieved in Australia. The likely mechanism for this is by feeding on prey of much higher quality than in tropical Australia. Locating the staging areas for red knots is a matter of urgency, given the pressure on intertidal areas in Asia and the susceptibility of such populations to reductions in food supply (Baker et al. 2004).

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