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Fuelling and moult in Red Knots before northward departure: a visual evaluation of differences between ages, sexes and subspecies

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Abstract. The departure of migratory birds from their non-breeding grounds is thought to be driven by the phenology of their breeding destination. In north-west Australia, two plumage morphs of Red Knot (*Calidris canutus*) prepare for a 5500-km journey to Yellow Sea staging areas. These morphs are recognised as the subspecies *C. c. piersmai* and *C. c. rogersi*, which breed at different latitudes and have different seasonalities. From February to May 2011, we observed the migratory preparation of individually marked birds of known age, sex and type. This enabled a comparison of fuelling rates and pre-alternate moult among these classes. First-year birds did not prepare for migration. Second-year birds accumulated smaller fuel stores and reached lower plumage scores than adults. Adults of both types reached their highest abdominal profile scores by the end of April when they were last observed in Roebuck Bay. This lack of difference between types in the timing of fuelling and departure is surprising. Based on the differences in staging and breeding phenology, *C. c. rogersi* is expected to leave north-west Australia 2–4 weeks before *C. c. piersmai*. Assuming that types and subspecies are equivalent, our findings in combination with other research on Red Knots in the East Asian–Australasian Flyway suggest that it takes more than breeding origin alone to explain annual cycles in migratory birds. Concurrent migratory schedules imply that, during northward staging in the Yellow Sea, there is strong variation in fuelling rates between and within subspecies depending on non-breeding origin. The ongoing loss of staging habitat may therefore have differential effects on Red Knots in the East Asian–Australasian Flyway.

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Introduction

It is widely assumed that organisms attempt to maximise fitness, which is equivalent to current and future reproductive output. Reproduction is therefore commonly seen as the driving force of life-history strategies (Stearns 1992). For migratory birds exploiting seasonally favourable habitats throughout a flyway, reproductive timing should then drive the timing of the annual cycle (e.g. Alerstam *et al.* 2003; Drent *et al.* 2006). In species that breed over a range of sites with distinct seasonal patterns and occupy the same non-breeding area, it has indeed been possible to relate differences in preparation for and timing of departure from the non-breeding area to differences in breeding-site specific reproductive timing (Fry *et al.* 1972; Wood 1992; Conklin *et al.* 2010). Here we examine migratory preparation and departure in two subspecies of Red Knot (*Calidris canutus*) that have distinctive plumage characters and share non-breeding areas but breed in disjunct tundra regions with different patterns of seasonal reproductive accessibility.

Red Knots have a Holarctic breeding distribution, with six populations using distinct migration flyways that connect their Arctic breeding areas with non-breeding grounds. Red Knots have been studied worldwide and increasingly serve as a model for the research and interpretation of ecological contrasts and flyway evolution in long-distance migratory birds (Piersma *et al.* 2005; Piersma 2007, 2011). Of the six subspecies of Red Knot, two use the East Asian–Australasian Flyway (EAAF): *C. c. piersmai* and *C. c. rogersi* (hereafter *piersmai* and *rogersi*); the two subspecies can be visually distinguished in alternate (breeding) plumage (see Figs S1e, f in supplementary material online) (Tomkovich 2001; Hassell *et al.* 2011b). Our assignments of subspecies are based on visual observations from a distance, that is on discernible external morphology rather than genetic assignment or detailed measurements of birds in the hand. As we shall discuss later, our observations raise the possibility that the morphological variation recorded may not correspond directly with subspecies. For this reason we use the neutral word ‘type’ to

indicate *piersmai*- and *rogersi*-type individuals as described by Tomkovich (2001) and elaborated by Hassell *et al.* (2011b) in discussing our observations and results.

Although these subspecies share the EAAF and use the Yellow Sea as a key staging area during northward and southward migration, they breed in disjunct areas (Tomkovich 2001) that become available at markedly different times in the boreal spring. Subspecies *rogersi* breeds on the Chukotka Peninsula in far-eastern Russia, at latitude 62–70°N, whereas *piersmai* breeds on the New Siberian Islands at latitude 75–78°N (Tomkovich 2001; Piersma *et al.* 2005; Tomkovich *et al.* 2013; Fig. 1a). As snow-melt follows a latitudinal gradient, the breeding grounds

of *rogersi* are accessible 2–4 weeks before those of *piersmai* (NOAA 2011). Consequently, the breeding season of *C. c. rogersi* begins in late May, 2–3 weeks before that of *C. c. piersmai* (Battley *et al.* 2005; Piersma *et al.* 2005; Buehler and Piersma 2008).

On their non-breeding grounds – in north-west Australia, south-east Australia and New Zealand – there is a complex overlap in the distributions of these two subspecies (Rogers *et al.* 2010). The non-breeding population in north-west Australia consists mostly of *piersmai* birds, which outnumber *rogersi* birds by a ratio of ~4:1. The opposite is true for the non-breeding population in south-east Australia and New Zealand,

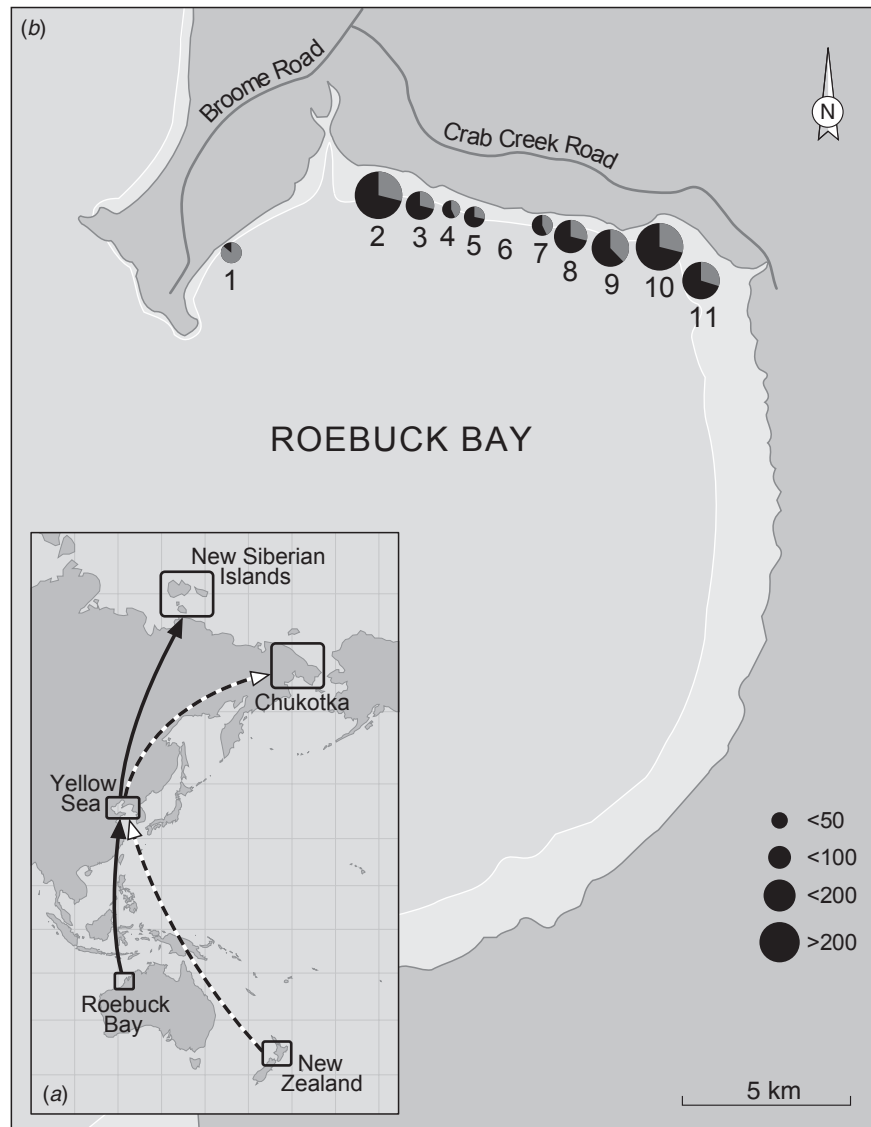


Fig. 1. (a) Migratory routes of Red Knots from non-breeding areas in New Zealand and north-west Australia to their breeding grounds. (b) Roebuck Bay area, north-west Australia. Pie-charts represent the proportion of each type (black is *piersmai* and grey is *rogersi*), and the size of the pie charts represents the number of sightings made. Observations undertaken on the northern beaches accessible from Crab Creek Road: 1, Simpsons Beach; 2, Quarry Beach; 3, Two Dog Hermit; 4, Nicks Beach; 5, Eagles Roost; 6, Campsite; 7, Tattler Rock; 8, Richards Point; 9, Wader Beach; 10, Wader Spit; 11, Crab Creek Beaches.

where *rogersi* outnumbers *piersmai* ~4:1 (Rogers *et al.* 2010; Hassell *et al.* 2011a). Corresponding with the difference in the timing of breeding between the subspecies, departure from the non-breeding grounds is also asynchronous: most *rogersi* from New Zealand leave in late March (Battley 1997; Piersma *et al.* 2005), whereas *piersmai* from north-west Australia leaves from the end of April to mid-May (Battley *et al.* 2005; Piersma *et al.* 2005). The two subspecies also differ in the timing of their use of the Yellow Sea: *rogersi* arrives in mid-April, a month earlier than *piersmai* (Rogers *et al.* 2010; Hassell *et al.* 2011a). Furthermore, *rogersi* departs to the breeding grounds well before *piersmai* (Rogers *et al.* 2010) and the two subspecies are thought to time their migratory preparations accordingly (Piersma *et al.* 2005; Buehler and Piersma 2008; Hua *et al.* 2013).

Using visual observations, we examined whether and how *rogersi* individuals reach readiness for departure earlier than *piersmai* individuals. For example, *rogersi* could start to fuel or begin moult earlier or do these at faster rates than *piersmai*. By describing changes in abdominal profile and breeding plumage in individually marked Red Knots, we were able to compare migratory preparation between types as well as between age and sex classes. In north-west Australia, heat-stress may limit storage rates and carrying of large fuel loads (Battley *et al.* 2003) and Red Knots may also be limited in the speed at which they can fuel for migration for reasons of food limitation or salt stress (Battley *et al.* 2005; Piersma *et al.* 2005; Gutiérrez *et al.* 2015). We therefore predicted that *rogersi* would achieve earlier departure than *piersmai* by beginning to fuel and moult earlier. Furthermore, it has been suggested that Red Knots preparing for migration from north-west Australia do not overlap their pre-alternate moult with fuelling (Battley *et al.* 2005; Buehler and Piersma 2008). This led us to predict even greater differences in the timing of migratory preparation between *rogersi* and *piersmai*. Regarding potential age-related differences in fuelling and moult, we predicted that first-year Red Knots – which do not migrate to the breeding grounds during the boreal summer (Rogers 2006) – would not moult into breeding plumage or fuel for migration. It is thought that second-year birds, which did not migrate the previous year, either migrate at the end of their second austral summer or do not achieve maturity for another season. For this reason, we predicted that second-year birds would show intermediate behaviour, with some individuals that would fuel, moult and migrate and other individuals that would not.

Methods

Fieldwork

Starting in 2006, Red Knots in Roebuck Bay (18°00'S, 122°22'E; Fig. 1) were marked with colour-bands and a flag allowing long-range identification, and bled for molecular sexing (Baker *et al.* 1999). Based on plumage characteristics in the hand, individuals were determined to be either in their first year (i.e. in their second calendar year), their second year (third calendar year) or in at least their third year of life (fourth calendar year or older) (Rogers *et al.* 2005). We refer to these age-classes as first-year, second-year and adult birds respectively. At the time of this observational study in 2011, there were 815 individually marked Red Knots of known age and sex. From 1 February to 15 May 2011, with the exception of the period from

21 February to 13 March, we (M. A. Verhoeven, J. van Eerbeek and C. J. Hassell) conducted observations on the portion of Roebuck Bay accessible from Crab Creek Road (Fig. 1). We undertook observations of Red Knots daily from 3 h before high tide until 3 h after high tide. Upon encountering an individually marked Red Knot, we scored its plumage and abdominal profile and, if possible, assigned it to either *rogersi* or *piersmai*.

Scoring of plumages and abdominal profiles

In the months before northward departure, Red Knots perform a pre-alternate moult from non-breeding to breeding plumage. The extent of breeding plumage was scored on a scale ranging from 1 (no breeding plumage) to 6 (complete breeding plumage) (see Piersma and Jukema 1993; Battley 2006; Fig. S1). Abdominal profile was used to describe the extent of pre-migratory fattening (fuelling) and was scored according to a published scale (Wiersma and Piersma 1995), which ranges from 1 (lean, convex belly with slightly protruding cloaca) to 5 (fat, bulging belly).

Distinguishing the two types

In breeding plumage, the *piersmai*-type has a dark-reddish nape, brick-red underparts and chestnut fringes to the scapulars and feathers of the mantle. In contrast, *rogersi* has a silvery nape, peach-orange underparts and silvery fringes to the scapulars and feathers of the mantle. The two types also differ in the extent of their breeding plumage, with *piersmai* having a higher average plumage score (Hassell *et al.* 2011b; see Results). Fig. S1e shows a typical *rogersi*-type in full breeding plumage and Fig. S1f a typical *piersmai*-type in full breeding plumage. Determining type based on plumage characteristics is only possible when Red Knots are in fresh and near-full breeding plumage (Hassell *et al.* 2011b), so marked individuals were assigned to type either towards the end of their stay in north-west Australia or on the staging grounds in Bohai Bay during northward migration (see Rogers *et al.* 2010).

Analysis

We analysed our data to test for the effects of age, sex, type, and their interactions, on rates of change in extent of breeding plumage and abdominal profile. As data on extent of breeding plumage and abdominal profiles were categorical and ordered, we performed multinomial logistic regression using cumulative link mixed models in R package 'ordinal' (Christensen 2013). The number of sightings varied between days, which significantly affected our calculation of daily averages of extent of breeding plumage and abdominal profile on days with few sightings. We therefore grouped all sightings by week for each individual and then analysed the maximum breeding plumage and abdominal scores to account for the fact that scores increased over the course of each week. Because we did not collect data between 21 February and 13 March (Weeks 8–10), we analysed changes in plumage and abdominal profile using data collected from 14 March to 8 May (Weeks 11–18). To avoid pseudoreplication, individual was included as a random effect in all models. We used only observations of Red Knots of known age, sex and type, and excluded all individuals that were observed during only one week of the season. For comparison of breeding plumage and abdom-

inal profile scores among age-classes, our dataset consisted of 519 plumage scores and 463 abdominal profile scores of 113 adults, 59 second-year birds and 14 first-year birds that remained in north-west Australia for their first boreal summer. We then excluded the first-year birds from further analyses because they differed considerably from older birds (see Results), and used a dataset that consisted of 397 plumage scores and 355 abdominal profile scores of adults and second-year birds.

We used linear regressions to determine whether the date on which an individual Red Knot was last observed in Roebuck Bay was related to its age, sex or type. To establish whether fuelling and pre-alternate moult overlapped during migratory preparation, we calculated the Pearson product-moment correlation coefficient to describe the relationship between abdominal profile score and plumage score. We included only adult and second-year birds that had started migratory preparation by excluding sightings of an individual before it had achieved a plumage score >1 or an abdominal score >2 . All analyses were carried out in the R version 3.1.0 (R Development Core Team 2013).

Results

First-year birds accumulated some abdominal fuel stores and breeding plumage during the period in which older birds were preparing for migration (Figs 2a, 3a). However, they did so to a lesser extent than did second-year and adult birds (Abdominal Profile: d.f.=1, $[LR]_1=52.18$, $P<0.001$; Plumage: d.f.=1, $[LR]_1=89.4$, $P<0.001$). Because of the considerable differences between age groups in fuelling and pre-alternate moult, first-year birds were excluded from further analyses.

Adult Red Knots ($n=93$) attained higher abdominal profile scores than did second-year birds ($n=41$) (d.f.=1, $[LR]_1=9.81$, $P<0.01$; Fig. 2a). No differences, however, were observed in abdominal profile scores between males ($n=62$) and females ($n=72$) (d.f.=1, $[LR]_1=0.04$, $P>0.05$; Fig. 2b) nor between *rogersi* ($n=35$) and *piersmai* ($n=99$) in terms of the rate at which abdominal profile scores increased (d.f.=1, $[LR]_1=0.37$, $P>0.05$; Fig. 2c).

Adult Red Knots ($n=95$) reached higher breeding plumage scores than did second-year Red Knots moulting into full breeding plumage for the first time ($n=41$) (d.f.=1, $[LR]_1=36.68$, $P<0.001$; Fig. 3a). We also observed that males ($n=64$) and females ($n=72$) differed in the extent of their final breeding plumage scores (d.f.=1, $[LR]_1=21.46$, $P<0.001$; Fig. 3b), and found that *piersmai* ($n=101$) achieved higher breeding plumage scores than *rogersi* ($n=35$) (d.f.=1, $[LR]_1=4.58$, $P<0.05$; Fig. 3c). Overall, 15% of second-year birds and 32% of adult birds reached a breeding plumage score of 6; 15% of females and 40% of males reached a breeding plumage score of 6; and 9% of *rogersi* individuals and 31% of *piersmai* individuals reached a breeding plumage score of 6.

At the individual level, there was a positive correlation between abdominal profile score and breeding plumage score ($r=0.73$, $n=515$, $P<0.001$). Regardless of sex or type, most Red Knots attained abdominal profiles of 4 or 5 by the end of April (Fig. 2), when migratory departure occurred (Fig. 4). Departure from Roebuck Bay (i.e. date of last observation) was not correlated with age ($F_{1,135}=0.85$, $P>0.05$) or sex

($F_{1,135}=0.11$, $P>0.05$). Departure was, however, related to type ($F_{1,135}=5.53$, $P<0.05$): *rogersi* left an average 0.67 weeks (95% confidence interval: 0.11–1.23) later than *piersmai* (Fig. 4c).

Discussion

Age-specific differences in migratory preparation

Second-year Red Knots, preparing for migration for the first time, developed breeding plumage and accumulated fat stores at lower rates than adult Red Knots. However, no second-year Red Knots were observed to accumulate fat stores or change plumage to the minimal extent observed in first-year birds. Further, no second-year birds were observed on the non-breeding grounds during the boreal summer; all four Red Knots resighted in Roebuck Bay during June 2011 were first-year birds. Lastly, several second-year Red Knots from north-west Australia were observed during the staging period in Bohai Bay, China (C. J. Hassell, A. Boyle and M. Slaymaker, unpubl. data). We therefore propose that in 2011 most second-year Red Knots migrated northward after remaining on the non-breeding grounds for one boreal summer.

One possible explanation for the variation in migratory preparation between age-classes is that adult Red Knots, compared with younger birds, are simply better at fuelling and moulting (see van den Hout *et al.* 2014). As is true for other performance measures (see Mueller *et al.* 2013; Sergio *et al.* 2014), such differences between age-classes may come about in various ways: (1) selective mortality, with less proficient individuals weeded out and the remaining adult group consisting of the more proficient individuals only; or (2) individual improvement, with birds attaining greater proficiency with age; or a combination of these. A third possibility is that second-year Red Knots do leave on northward migration with adults but do not complete a full migration to the Arctic breeding grounds. In this latter scenario, despite leaving the non-breeding grounds, second-year birds do not enter the breeding population for another breeding season.

We observed that first-year birds increased their abdominal profiles (Fig. 2a). This finding is unexpected, since first-year birds stay in Roebuck Bay throughout the boreal summer breeding season, although similar increases in juvenile mass have been observed elsewhere in the EAAF (Barter *et al.* 1988; Battley 1999). Such fuelling in first-year birds could be a preparation for their first wing-moult, which occurs during the austral winter (Rogers 2006); this would be considered a form of 'capital-moult' rather than 'income-moult' (*sensu* Drent and Daan 1980). Nutritional stores might also enable first-year birds to disperse to non-breeding locations at any time throughout the austral winter (Rogers *et al.* 1997). A non-adaptive, proximate explanation is that even in young birds the hormonal cycle regulating migratory preparation can be triggered by endogenous, environmental or social cues (Berthold 1996; Gwinner 2003).

Moult

The differences in final breeding plumage scores between sexes and types did not reflect differences in the duration of moult, and instead reflected males and *piersmai*-types attaining larger quan-

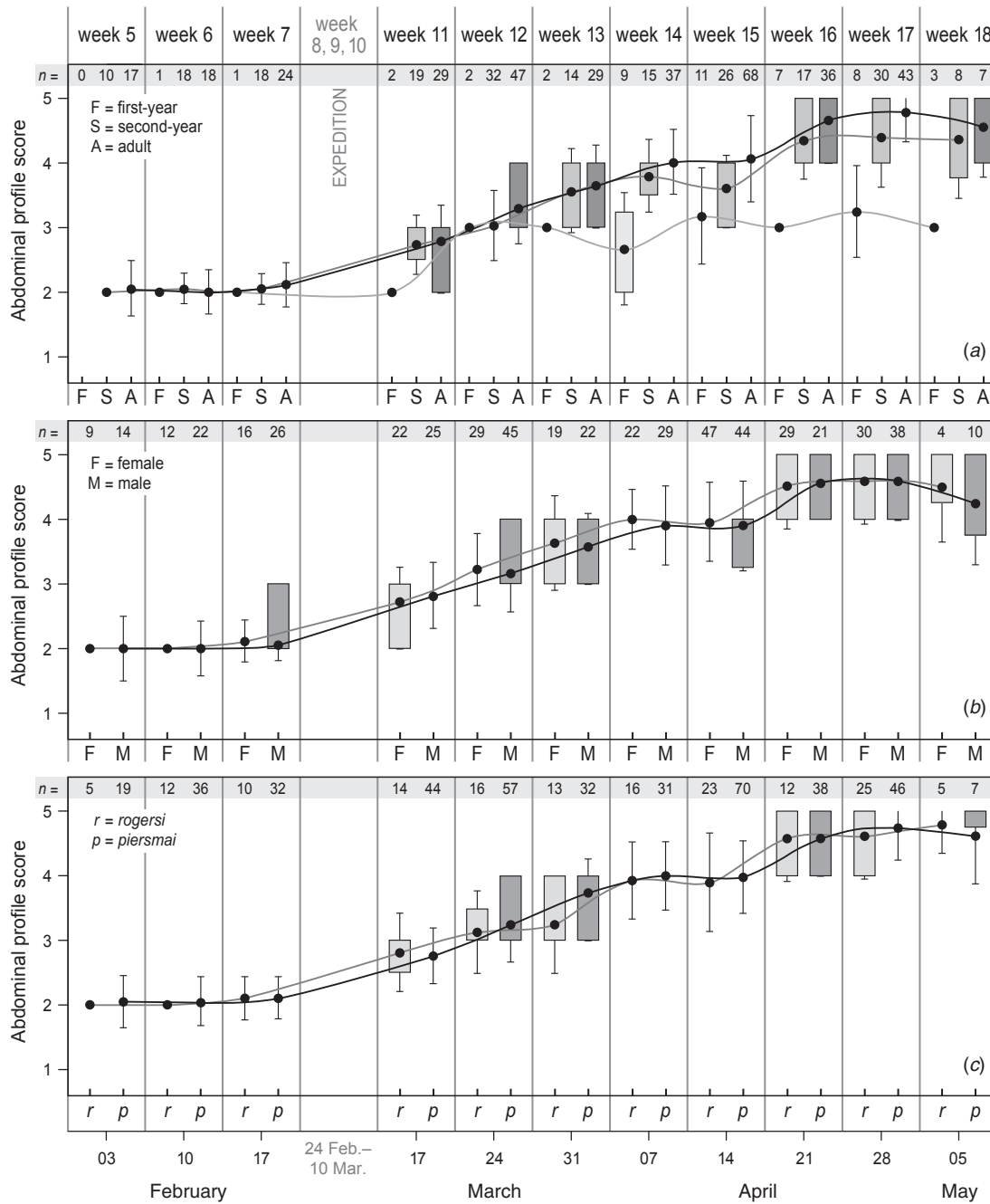


Fig. 2. Changes in abdominal profile score of Red Knots in Roebuck Bay, north-west Australia, in relation to (a) age, (b) sex and (c) type. Boxes show the interquartile range, whiskers the standard deviation, and dots are means (joined by lines).

ties of reddish plumage (Fig. 3). Undertaking a complete moult from basic to alternate plumage carries a non-trivial cost (estimated as the equivalent of 6 days of fuelling in Black-tailed Godwits (*Limosa limosa limosa*); Lourenço and Piersma 2015). We found that plumage scores were positively correlated with abdominal profile scores, so Red Knots appear capable of gaining resources at rates sufficient to invest simultaneously in both fuelling and moulting. Thus, at the fairly low fuelling rates observed in Roebuck Bay (Battley *et al.* 2005; Piersma

et al. 2005), a concurrent moult from basic into alternate plumage is possible.

Differences between types

We found no differences between *rogersi* and *piersmai* in the timing of migratory preparation, and contrary to expectation, *rogersi* did not leave earlier than *piersmai*. Rather, both types left Roebuck Bay during the 3-week period from mid- to late

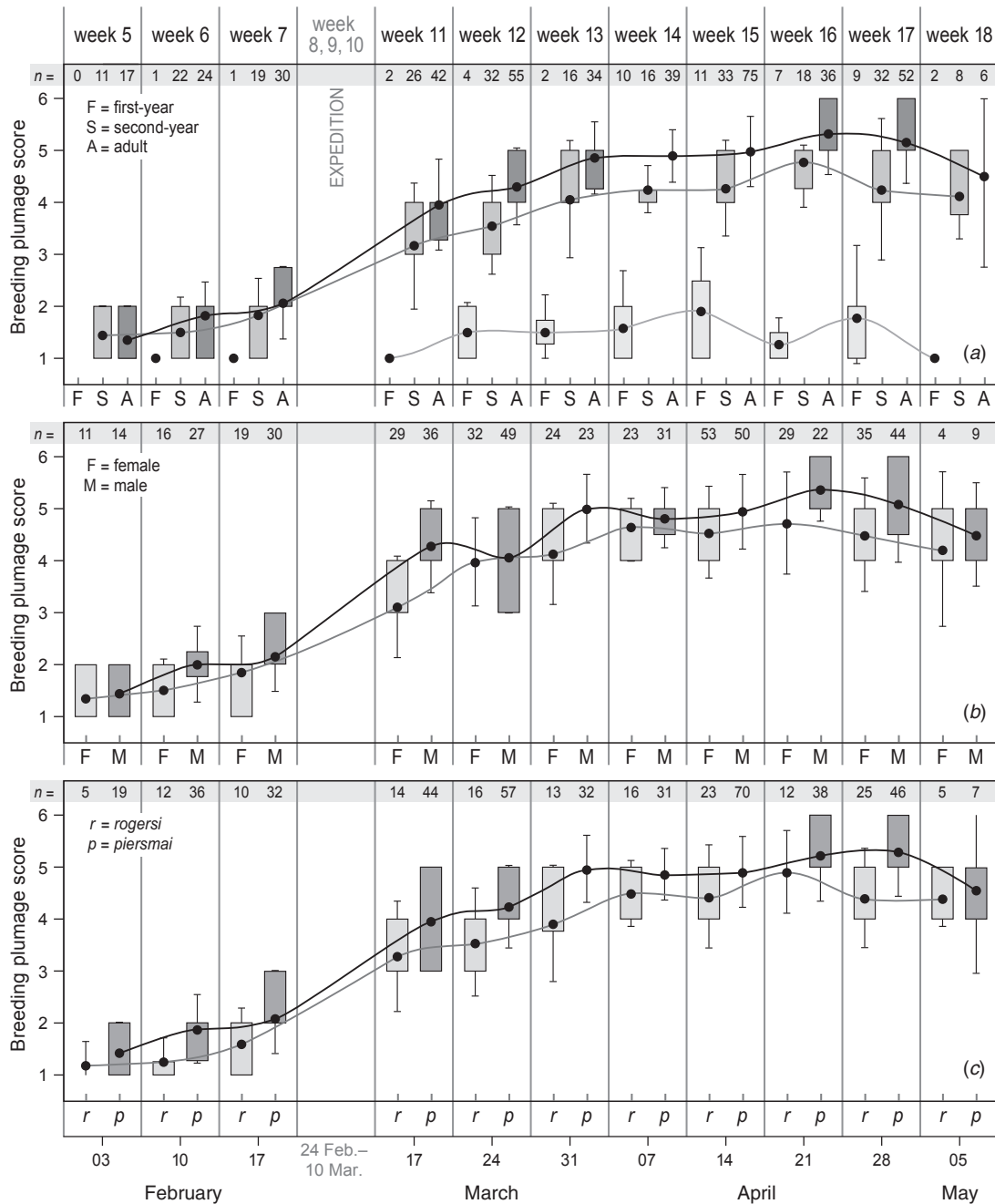


Fig. 3. Change in breeding plumage score of Red Knots in Roebuck Bay, north-west Australia, in relation to (a) age, (b) sex and (c) type. Boxes show the interquartile range, whiskers the standard deviation, and dots are means (joined by lines).

April; on average, *rogersi* may even have left slightly later than *piersmai*. This concurrent departure is surprising, given that the Chukotka Peninsula becomes reproductively accessible 2–4 weeks before the New Siberian Islands (NOAA 2011). We advance two possible scenarios to explain these observations. In the first, the types reliably reflect subspecies (Fig. 5a) and of the individuals from north-west Australia, *piersmai* spends a longer time fuelling in the Yellow Sea than *rogersi*. This might occur, for example, owing to a more energetically taxing migration or less predictable resources on the breeding grounds. It is also possible,

however, that types do not reliably reflect subspecies. In this second scenario, regardless of type, individuals from one non-breeding area migrate to the same breeding area during the same period (Fig. 5b). This would mean that the breeding grounds in Chukotka and the New Siberian Islands would each host a single population that would be a mixture of the two types in a 4 : 1 ratio, an idea that contrasts with the current understanding that the types breed separately.

Following their departure from north-west Australia between mid- and late April, the two types are expected to arrive in the

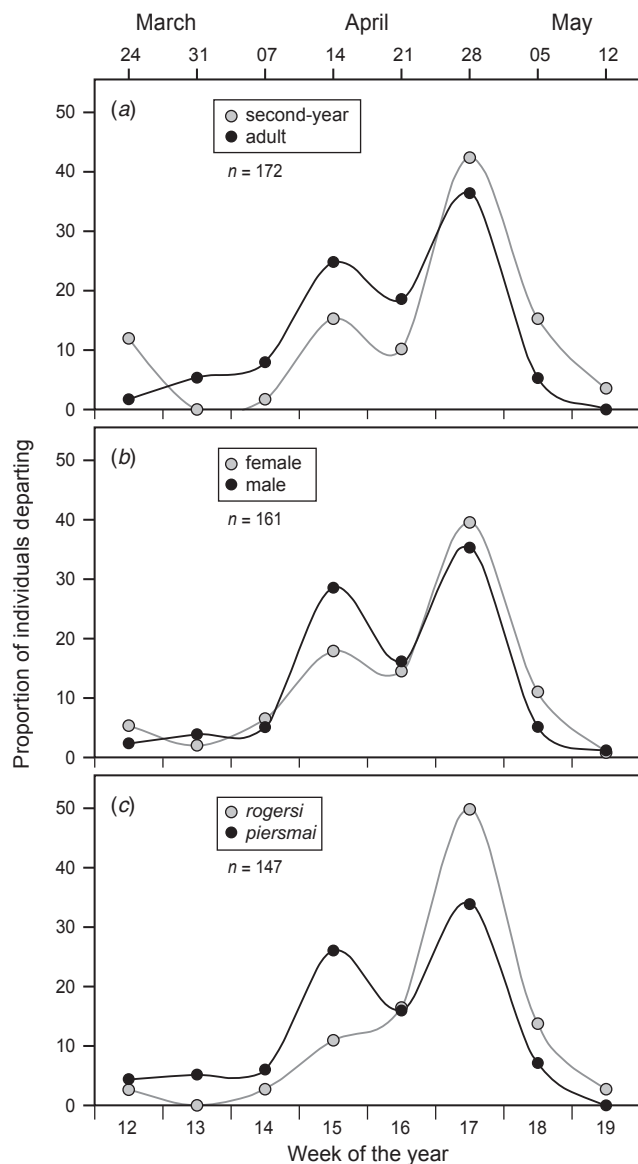


Fig. 4. Timing of departure of Red Knots from Roebuck Bay, north-west Australia (date of last observation of all individuals observed in the Bay during the study period), in relation to (a) age, (b) sex and (c) type. Graphs show the proportion of individuals departing.

Yellow Sea between late April and early May. This is supported by Rogers *et al.* (2010). Also, the proportion of *piersmai* in the Yellow Sea increases during this period, which further suggests the arrival of Red Knots from north-west Australia (Rogers *et al.* 2010; Hassell *et al.* 2011a). Whereas our results lead us to expect that Red Knots from north-west Australia start arriving in the Yellow Sea in late April and continue to increase in number through early May, Rogers *et al.* (2010) did not find an increase in the proportion of Red Knots originating from north-west Australia based on colour-band resightings. This may be because Rogers *et al.* (2010) did not look for colour-bands until 10 May; according to our departure data, most Red Knots from north-west Australia should have already completed the 3–4 day flight

and arrived in the Yellow Sea by that date. In recent years the Global Flyway Network consortium (<http://globalflywaynetwork.com.au/>, accessed 27 December 2015) has undertaken observations of colour-banded birds throughout the entire staging period, from the beginning of April until the end of May (e.g. Piersma *et al.* 2016); further analyses of these observations could potentially test our prediction (T. Piersma and T. Lok, in prep.). Such analyses would enable the reconsideration of the following conclusions made by Rogers *et al.* (2010): (1) that the timing through Bohai Bay is driven more by breeding destination than by migratory origin; (2) that Bohai Bay tends to be used more by Red Knots from north-west Australia than from New Zealand; and (3) that both types have a similar stopover duration in Bohai Bay.

In New Zealand, most individuals of both types are observed to leave in late March (Battley 1997; P. F. Battley, pers. comm.). Combined with our observation of concurrent departure from north-west Australia, and assuming that types reliably indicate subspecies, this suggests that the timing of departure from the non-breeding grounds is driven by non-breeding origin rather than migratory destination. This notion is consistent with recent observations by Tomkovich *et al.* (2013), in which the annual cycle of Red Knots from a single breeding location in Chukotka was documented on the basis of geolocation tracks. All Red Knots from this breeding location have been identified morphologically as subspecies *rogersi*, which supports the widely assumed correspondence between type and subspecies (Tomkovich 2001; Tomkovich *et al.* 2013). The three tracked individuals showed considerable differences in non-breeding location: two wintered in New Zealand (36°S) and one in north Australia (16°S). There were equally notable differences in the timing of departure for northward migration (the two birds wintering in New Zealand left on 27 and 29 March, whereas the bird wintering in north Australia left on 24 April).

Again assuming that types reliably indicate and reflect subspecies, the concurrent departure of *rogersi* and *piersmai* from Roebuck Bay also suggests that there must be differences in fuelling rates between subspecies from north-west Australia during their stopover in the Yellow Sea. Because *rogersi* leaves the Yellow Sea 1–2 weeks before *piersmai* (Rogers *et al.* 2010), *rogersi* has a shorter stopover duration and therefore higher fuelling rates are expected. Furthermore, an individual of either type departing from north-west Australia has less time to complete its migration than does an individual of the same type that leaves New Zealand 4–5 weeks earlier (Battley 1997). This suggests within-subspecies variation in fuelling rates. However, Riegen (1999) proposed that some Red Knots leaving New Zealand stop one or more times during their journey. The existence of these stops has recently been confirmed (P. F. Battley, pers. comm.) with geolocators retrieved from eight Red Knots that left New Zealand between 21 March and 5 April (which is consistent with earlier observations; Battley 1997). All eight birds, seven *rogersi* and one *piersmai*, made a prolonged stop in either north Australia or Papua New Guinea. Therefore, some Red Knots from New Zealand arrive in Bohai Bay at the same time as Red Knots from north-west Australia. Conversely, the two *rogersi* individuals tracked by Tomkovich *et al.* (2013) flew from New Zealand directly to Bohai Bay. This means that Red Knots from the non-breeding areas in New Zealand migrate

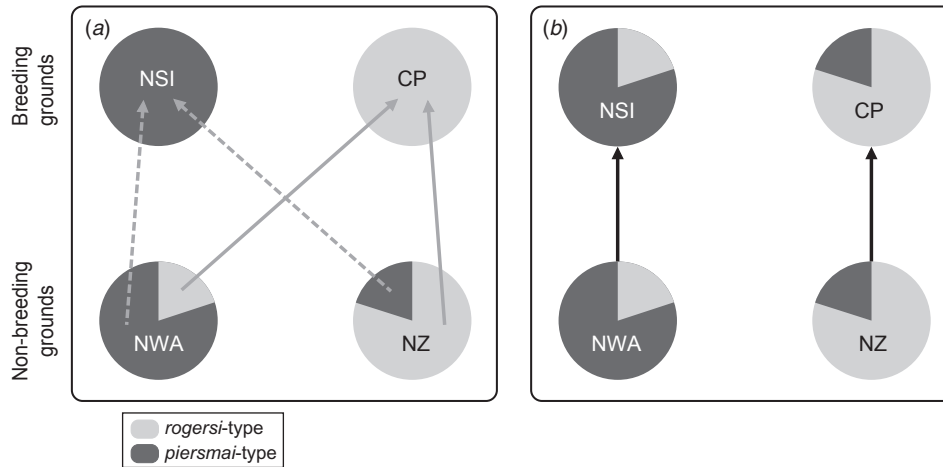


Fig. 5. Schematic representation of two possible scenarios to explain simultaneous departure of the two types of Red Knots from Roebuck Bay (see *Discussion*). (a) The scenario in which types are equivalent to subspecies. (b) The scenario in which types do not reliably identify and reflect subspecies. NSI = New Siberian Islands, CP = Chukotka Peninsula, NWA = north-west Australia, NZ = New Zealand.

in a variety of ways, and within-subspecies variation in fuelling rates is present in some but not all cases. For example, some birds – those arriving in Bohai Bay in late April from non-breeding grounds or stopover sites, and breeding in southern Chukotka (62°N, arrival *c.* 20 May) – have only 20 days to refuel in the Yellow Sea (Tomkovich *et al.* 2013). This strategy differs greatly from Red Knots that fly directly from New Zealand and then have 50–60 days to spend refuelling before their breeding grounds become accessible (Battley *et al.* 2005; Tomkovich *et al.* 2013). Such phenotypic variation in the timing of departure from non-breeding grounds runs counter to the way we view the geographical drivers of the timing of migration (Alerstam *et al.* 2003; Drent *et al.* 2006).

Conclusion

The fact that concurrent departure of types occurs in both north-west Australia and New Zealand (this study; P. F. Battley, pers. comm.), in addition to the knowledge that some Red Knots from New Zealand arrive in Bohai Bay in early April (Tomkovich *et al.* 2013), shows that the timing of northward migration of Red Knots through the Yellow Sea differs from our current understanding. At present the types are viewed as two units that operate independently, such that stopover sites in the Yellow Sea host two separate groups of Red Knots: first *rogersi* individuals, followed by *piersmai* individuals, with each subspecies present for *c.* 29 days (Rogers *et al.* 2010). Our findings, and those from New Zealand, suggest that it is more likely that the Yellow Sea first hosts a mixture of *rogersi* and *piersmai* originating from New Zealand, followed by birds of both subspecies or types originating mostly from north-west Australia, with substantial variation in the length of time individuals of each subspecies are present. Assuming that types and subspecies are equivalent, this implies differences in fuelling rates of Red Knots in the Yellow Sea, both between subspecies (*rogersi* vs *piersmai* from north-west Australia) and within subspecies (individuals of either subspecies from north-west Australia vs individuals of either type from New Zealand). We therefore predict that the ongoing

and considerable changes to habitat in the Yellow Sea (Ma *et al.* 2014) will have differential impacts on the fecundity and annual survival of Red Knots in the EAAF. The loss of staging habitat may have serious fitness consequences (Baker *et al.* 2004; Piersma *et al.* 2016), and we suggest that this will first become evident in both types that winter in north-west Australia rather than those wintering in south-eastern Australia or New Zealand (see discussion of Bar-tailed Godwits (*Limosa lapponica*) in Conklin *et al.* 2016).

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