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When slow explorers are fast: Personality-related differences in timing of migration in Red Knots (Calidris canutus)

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The timing of migration varies significantly among individuals, even within populations sharing breeding sites. Consistent individual behavioural differences, known as personality traits, have been linked to variation in movement behaviour. However, little attention has been given to investigating whether personality traits can explain such variation in the timing of migration. We studied post-breeding migration of Red Knots *Calidris canutus islandica* breeding in the High Arctic and wintering in European coastal areas. We captured Red Knots in the Dutch Wadden Sea, a main non-breeding and moulting site, and assessed their exploration behaviour, a personality trait, before releasing them with colour-rings. We first investigated whether arrival timing in marine areas was associated with exploration speed. Secondly, we asked whether slow explorers were more likely to fly non-stop to the Wadden Sea compared with fast explorers, as faster explorers were expected to move more and visit more staging sites. To determine arrival timing in marine non-breeding areas and non-stop flights to the Wadden Sea, we analysed isotope signatures in blood samples collected after capture, as these differ between the terrestrial breeding grounds (arthropod diet) and marine non-breeding and moulting sites (benthic invertebrate diet). Thirdly, we estimated arrival time in the Wadden Sea based on primary moult progress, allowing us to examine the relationship between arrival timing estimated from isotope values and the onset of moult. Our findings revealed that slower exploring Red Knots departed earlier from the breeding site and were more likely to fly non-stop to the Wadden Sea than were faster exploring individuals. Arrival timing to marine areas as estimated from isotope analyses predicted arrival timing in the Wadden Sea (via moult progress) but this relationship exhibited significant variation, possibly due to individual differences in the use of staging sites en route. By migrating early, slower explorers can better outpace the aerial predators also arriving at the Wadden Sea moulting site and thereby reduce mortality risk due to predation.

Keywords: animal personality, diet-switch, exploration, moult, shorebirds, stable isotope analysis, timing of migration.

Timing and patterns of migration vary not only among species but also within species, even among those that breed at the same locations (Gwinner 1990, Verhoeven *et al.* 2020, Brown *et al.* 2021). Long-term tracking data show this great variation, with individuals having their own timing and/or use of staging sites (e.g. Vardanis *et al.* 2011, Stanley *et al.* 2012, Senner *et al.* 2019). Variation in timing of migration can

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have important seasonal carryover effects, such as early arrival to the non-breeding sites that can be related to an advantageous position in roost sites and territories (Harrison *et al.* 2011, Leyrer *et al.* 2012). Earlier arrival to the non-breeding sites is also linked to earlier completion of primary moult, which helps individuals to gain their flight efficiency earlier and avoid migratory predators that arrive in autumn, too (Piersma *et al.* 1993a, van den Hout 2009). Even though individual differences can have large ecological effects (Walther *et al.* 2002, Jonzén *et al.* 2006), the behavioural mechanisms influencing timing of migration still remain to be studied.

Consistent among-individual differences in behaviour (also known as 'personality traits', Gosling 2001), such as exploration (magnitude of space use in a novel environment) or boldness (propensity to take risk), are often related and have been linked to movement behaviour and space-use in the wild, but mainly on small spatial scales. For example, faster (vs. slower) exploring individuals visit more areas and find more new foraging places (fish: Bullheads *Cottus perifretum* Kobler *et al.* 2009; bird: Blue Tits *Cyanistes caeruleus* Herborn *et al.* 2010). Bolder Great Tits *Parus major* tend to disperse farther than shyer Great Tits (Dingemanse *et al.* 2003). Some studies show correlations between personality traits and migratory behaviour. For example, bolder individuals are more likely to be migratory while shyer individuals are more likely to be resident (bird: warblers Mettke-Hofmann *et al.* 2005; fish: partially migrating Roach *Rutilus rutilus* Chapman *et al.* 2011). Exploratory Great Knots *Calidris tenuirostris*, compared with non-explorative individuals, visited more novel sites during post-breeding migration (Chan 2021). Because exploratory and bolder individuals tend to have larger space-use and visit more areas, we may expect them to differ in staging site use (e.g. the number of staging sites used or longer stays at sites) and thus differ in timing of migration (Vervoort *et al.* 2022). While personality traits have been found to explain differences in migratory movement patterns (e.g. Dingemanse *et al.* 2003, Kobler *et al.* 2009, Chapman *et al.* 2011), how personality traits might explain among-individual variation in timing of migration remains to be studied.

Red Knots *Calidris canutus* are migratory shorebirds that breed in the Arctic tundra and use intertidal mudflat areas in temperate and tropical zones during the rest of the year (Piersma 2007). Female Red Knots leave the breeding grounds right after the eggs are hatched and males provide care for the chicks until the young are independent (Myers 1981, Tomkovich & Soloviev 1996). We studied the *islandica* sub-species that spends most of the non-breeding season on the intertidal mudflats of the Wadden Sea and other European estuaries (Quaintenne *et al.* 2011). During northward migration, most of the *islandica* population use western Iceland or northern Norway as staging sites before they continue to migrate north to breed on the Arctic tundra of north-eastern Canada and northern Greenland (Piersma 2007). During southward migration, Red Knots show variation in their staging site use, as some of them have been shown to skip potential staging sites and migrate non-stop from the breeding to non-breeding site in the Wadden Sea intertidal mudflats of continental Europe (Dietz *et al.* 2010, Kok *et al.* 2020). Birds that use a staging site during southward migration arrive 12–15 days later in the Wadden Sea (Wilson & Morrison 1992, Dietz *et al.* 2010).

After leaving the breeding sites and arriving in the marine staging and/or moulting sites, Red Knots switch their diet from terrestrial arthropods to marine shellfish (Piersma *et al.* 1993b). The terrestrial diet on the breeding site has a different isotope signature than the marine diet in the staging or non-breeding sites, and thus it is possible to calculate migration timing (i.e. diet switch) through analysing the $\delta^{13}C$ isotope value in blood (Klaassen *et al.* 2010). When migration ends and within days after arrival on non-breeding sites such as the Wadden Sea, Red Knots start moulting their primary feathers. The earlier individuals start primary moult, the earlier they are finished (Boere 1976, Dietz *et al.* 2010, 2013). The gap in the wing during moult effects flight efficiency, and actively moulting birds have been shown to be more vulnerable to aerial depredation (Hedenström 2003). Thus, earlier primary moult also helps Red Knots to avoid predation from their main predator, Peregrine Falcon *Falco peregrinus*, which arrives to the Wadden Sea in autumn (Piersma *et al.* 1993a, van den Hout 2009, Dietz *et al.* 2013).

In this study, we assessed the exploratory personality of individual Red Knots using a mobile experimental set-up. Our objective was to determine whether the timing of their diet switch from terrestrial to marine habitats (hereafter 'arrival timing in marine areas') and the probability of

non-stop migration from breeding to non-breeding sites could be predicted based on their exploration speed in a standardized personality assay. First, we estimated the number of days spent in marine areas based on isotope values from blood samples and asked whether arrival timing in marine areas was correlated with exploration speed. Secondly, we identified birds that flew non-stop from the breeding to the non-breeding site in the Wadden Sea based on the degree to which the isotope signature in the blood signalled terrestrial prey. Because exploratory birds are expected to visit more staging sites (e.g. Chan 2021), we predicted that slower exploring Red Knots are more likely to fly non-stop to the Wadden Sea than faster exploring birds. Thirdly, as Red Knots start moulting primary feathers after migration in the non-breeding sites, e.g. when they arrive in the Wadden Sea, we estimated arrival time to the Wadden Sea with primary moult progress and investigated how arrival timing in marine areas (estimated using isotope analyses) relates to arrival timing in non-breeding sites in the Wadden Sea (estimated using moult progress). Because male Red Knots take care of their chicks after hatching, males (vs. females) are expected to depart later from the breeding sites (Whitfield & Brade 1991, Nebel *et al.* 2000). Therefore, we control for sex effects in all our timing analyses.

METHODS

Catching, sampling, housing

Adult Red Knots were caught by mist-netting during three catching events in the western Dutch Wadden Sea (53°15′N, 5°15′E) during new moon periods on 14 August 2018 ($n = 38$), 10–13 September 2018 ($n = 94$) and 3–4 August 2019 ($n = 11$). Data collected from 111 of those adult Red Knots were also presented earlier in Ersoy *et al.* (2022). The birds were given a numbered metal ring for individual identification and moult was scored for all primary feathers in the right wing from 0 (old primary) to 5 (new primary; Ginn & Melville 1983). To obtain a primary moult score (ranging between 0 and 50), the 10 primary moult scores were summed per individual. From the brachial vein, a small blood sample (~ 80 µL) was taken for molecular sexing and stable isotope analysis. Blood samples were separated into plasma and blood cells by centrifugation (12 min, 5500 *g*), and plasma and red blood cells pipetted into separate glass vials and immediately stored in a freezer at the field site. Upon our return to the institute, samples were stored at −20°C until further analysis. These samples were used to determine the carbon and nitrogen stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) from plasma and red blood cells separately.

Immediately after the measurements the birds were moved to temporary outdoor aviaries of 2 × 0.75 × 0.4 m (L × W × H) made of linen with a net floor. These aviaries were placed on natural sand/grass ground and the birds were provided with *ad libitum* food (live and dried mealworms) and water (freshwater and seawater). The group size in aviaries varied between 8 and 12 birds.

Exploration assays at the field site

To score the exploration personality of Red Knots at the field site, we used a pyramid-shaped mobile unit of 2 × 2 × 2 m (referred to as 'mobile arena'; see Ersoy *et al.* 2022 for detailed explanation of the set-up). The floor of the unit consists of seawater of 20 cm depth in which four identical trays with wet sand (61 × 40 × 25 cm) were situated. Birds could explore these artificial patches in which no food was offered. To standardize the procedure and to motivate birds equally for personality assays, we placed them individually into a holding pen without access to food for 2 h. We started the experiments by gently placing the bird on the sand patch in the experimental unit. Individual trials lasted 20 min per bird. To calculate exploratory movement of individuals from videos recorded by the ceiling camera (GoPro Hero Black), we used video tracking software *idtracker* (Pérez-Escudero *et al.* 2014). The software produced position data (i.e. *x*- and *y*-coordinates) every 0.5 s during the 20 min a bird spent in the mobile arena. Errors in the tracking were filtered out by excluding speeds higher than 200 cm/s and applying a median smoother with a window of three locations. Exploration speed is calculated as a bird's mean speed ($\log_{10}$ cm/s) per trial.

Measurements for exploratory personality in Red Knots have been well established since Bijleveld *et al.* (2014) and the exploratory behaviour has been shown to be repeatable ($R_{\text{short-term (week)}} = 0.7$, $R_{\text{long-term (6 months)}} = 0.54$; Ersoy *et al.* 2022, and $R_{\text{long-term (2 years)}} = 0.55$; Kok *et al.* 2019). In view of animal welfare considerations and given the large repeatability, we measured exploratory behaviour

of Red Knots once only for this study. Birds were kept in captivity for a total of 2–3 days and released directly after exploratory assays. The birds were released with unique combinations of colour-rings, back into their natural habitat where they were caught. Because the birds were provided with *ad libitum* food during time in captivity and they were in good condition and bodyweight before releasing, the birds were not fed particularly before their release. All necessary permits to catch, handle, ring, test and keep Red Knots were granted to the NIOZ Royal Netherlands Institute for Sea Research by the Dutch law and regulation under protocol number NIOAVD8020020171505.

Isotope analysis

At NIOZ, blood samples were freeze-dried and isotope measurements obtained on a Thermo Scientific (Flash 2000) organic element analyser coupled to a Delta V isotope ratio mass spectrometer via a Conflo IV. A microbalance (Sartorius XM1000P) was used to weigh 0.4–0.8 mg of the freeze-dried samples into 5 × 9-mm tin capsules. Isotope values were calibrated to a certified acetanilide standard (Arndt Schimmelmann, Indiana University), controlled by certified urea and casein standards (Elemental Microanalysis), and corrected for blank tin capsules. Average precision for standards and replicate samples was ± 0.1‰ for $\delta^{13}C$ and 0.2‰ for $\delta^{15}N$.

Estimating timing of switch from terrestrial to marine diet

Measuring the change in isotopic ratios in body tissue after a diet switch is a common technique to estimate the arrival date of migratory birds that move between terrestrial and marine environments (Hobson 2008). The terrestrial diet has a different isotope signature from the marine diet which can be analysed in individual blood samples. We adopted the single tissue model using the carbon isotope ratio ($\delta^{13}C$) to estimate arrival date (i.e. time since diet switch; Klaassen *et al.* 2010):

$$t = \frac{\log\left(\frac{\delta_{start} - \delta_{end}}{\delta_{indv} - \delta_{end}}\right)}{\lambda}$$

Start and end values were taken from Dietz *et al.* (2010). The start value indicates where the migration started, hence we took the Arctic tundra value ($\delta^{13}C = -24.7‰$). The end value indicates where the migration ended; because we caught the birds in the Wadden Sea, we used the Wadden Sea value ($\delta^{13}C = -14.0‰$). We took the turnover rate value for Red Knots ($\lambda = 0.046$) from Klaassen *et al.* (2010). We fitted individual carbon isotope ($\delta^{13}C$) values from red blood cells of our adult Red Knots (SOM Fig. S1). The result of this function is the days since the diet switch. To estimate the diet-switch date, we subtracted the date of capture (blood sampling) and transformed the date to continuous days since 1 January. It should be noted that the isotope value in other marine areas such as Iceland ($\delta^{13}C = -15.0‰$) is very similar to the Wadden Sea value ($\delta^{13}C = -14.0‰$). Therefore, our diet-switch estimation is a reflection of arrival timing from breeding grounds towards other marine areas which could be a staging site (such as Iceland or Norway) or the moulting and non-breeding site, such as the Dutch Wadden Sea.

Identification of birds that flew non-stop from the breeding to non-breeding sites

Dietz *et al.* (2010) showed that Red Knots differ in staging-site use and some birds fly non-stop from breeding to the Wadden Sea. Following Dietz *et al.* (2010), adults with a $\delta^{13}C$ ratio below −19.3‰ were identified as non-stop flyers skipping potential staging sites because they have a clear Tundra signal in their blood cells. Those birds with a $\delta^{13}C$ ratio above −19.3‰ (indicating a more marine diet) were difficult to label. These birds could have staged en route in marine sites, or they could have been in the Wadden Sea for at least 2 weeks prior to their capture (hereafter 'non-classified birds').

Estimation of moult start date

Adult Red Knots start moulting from their first primary feather to the last (10th) primary feather on both wings simultaneously. Because Red Knots start moulting their flight feathers when they arrive in the Wadden Sea, the estimated start day of first primary moult reflects arrival timing to the Wadden Sea. As we captured Red Knots soon after their arrival in the Wadden Sea and wanted to back-calculate their moult start date, we selected birds with an actively growing first primary ($n_{total} = 49$) to estimate the date at which

primary moult started (Dietz *et al.* 2013). Data from birds captured in 2018 and 2019 were combined to enlarge our sample size for the estimation of arrival timing with active moult in first primary ($n_{2018} = 38$; $n_{2019} = 11$). We back-calculated the date at which the first primary was shed using the primary score at capture and the moult duration for the first primary. Because males and females differ in moult, we used different values of primary moult duration for the sexes (females 16 ± 1.9 days, males 15 ± 2.5 days for first primary feather; values are taken from Dietz *et al.* 2013). We transformed the start date of primary moult to days since 1 January.

Statistical analysis

We excluded one adult male for which the diet-switch date was more than 60 days before capture, suggesting that either it did not leave the marine environments for migration to the breeding sites or there was a mistake in the isotope analysis ($n_{final} = 131$). We formulated linear mixed-effect models using the *lme4* package (Bates *et al.* 2015) and checked for collinearity, overdispersion and model assumptions (homogeneity and normality of residuals). First, we fitted a linear model with Gaussian error distribution to investigate the effects of sex (categorical; 'male' or 'female') and exploration speed (continuous; $\log_{10}$ mean speed cm/s) on the estimated arrival day in marine areas. To investigate the probability of non-stop flight from the breeding to the non-breeding range, we fitted flight (categorical; 'non-stop' or 'non-classified' (including stopovers or very early arrivals in the Wadden Sea)) on exploration speed (continuous; $\log_{10}$ mean speed cm/s) in a regression model. Finally, using the birds that have active moult in first primary ($n_{2018} = 38$; $n_{2019} = 11$), we formulated a linear regression model with Gaussian error distribution between arrival timing measured via isotope and via moult progress to investigate whether arrival timing in marine areas (via isotope analyses) relates to arrival timing in non-breeding site in the Wadden Sea (via moult progress). All data analyses were carried out in R statistical software v. 4.2.1 (R Core Team 2021).

RESULTS

The isotope analyses showed that Red Knots switched from a tundra to a marine diet between 11 July and 24 August 2018, with an average of 1 August. As expected, females switched to marine diets on average 8 days earlier than males, indicating that the females left the breeding grounds and arrived at marine areas earlier than males (Table 1, Fig. 1a). Arrival timing to marine areas was predicted by exploration speed, with slower exploring Red Knots arriving on average 10 days earlier than faster exploring birds (Table 1, Fig. 1b). To investigate the robustness of our results, we additionally ran the model without one individual that had an extremely low (< -0.1) and one with a high (> 1.2) exploration speed ($\log_{10}$ cm/s). Results did not change, and we present the results without these individuals (SOM Table S1). Doing similar analyses with arrival timing estimated from the progress of primary moult, we also found that females arrived earlier than males and exploratory scores predicted arrival timing (SOM Table S2).

We identified 31 Red Knots with terrestrial isotope signatures in their blood at capture in the Wadden Sea, indicating that they arrived shortly before their capture on a non-stop flight from breeding to non-breeding sites. The remaining 100 individuals were problematic to classify and include a mix of birds that may have switched diet at staging sites in Iceland or Norway, or in the Wadden Sea after an early arrival. We found that birds that flew non-stop on average had lower exploration scores than birds that we could not classify (the difference between groups (95% confidence interval (CI)) = 0.11 (0.02–0.19), $R^2 = 0.035$, $n = 131$; Fig. 2).

The estimated arrival timing in marine areas (estimated with isotope analyses) was correlated with estimated arrival timing in the Wadden Sea (estimated with primary moult analyses; Intercept (95% CI) = 121.32 (91.58–151.07), Slope (95% CI) = 0.46 (0.31–0.60), $R^2 = 0.47$, $n = 49$; Fig. 3).

Table 1. Effects of exploration speed ($\log_{10}$ mean speed cm/s) and sex on the estimated arrival day (day number since 1 January) in marine areas (estimated with isotope analyses). Bold font indicates confidence intervals do not overlap with zero.

Predictors	β coefficients	95% CI
Intercept	204.59	**199.57–209.61**
Exploration speed	9.89	**2.32–17.46**
Sex (Male)	7.65	**4.13–11.17**
R^2	0.16	
n	131	

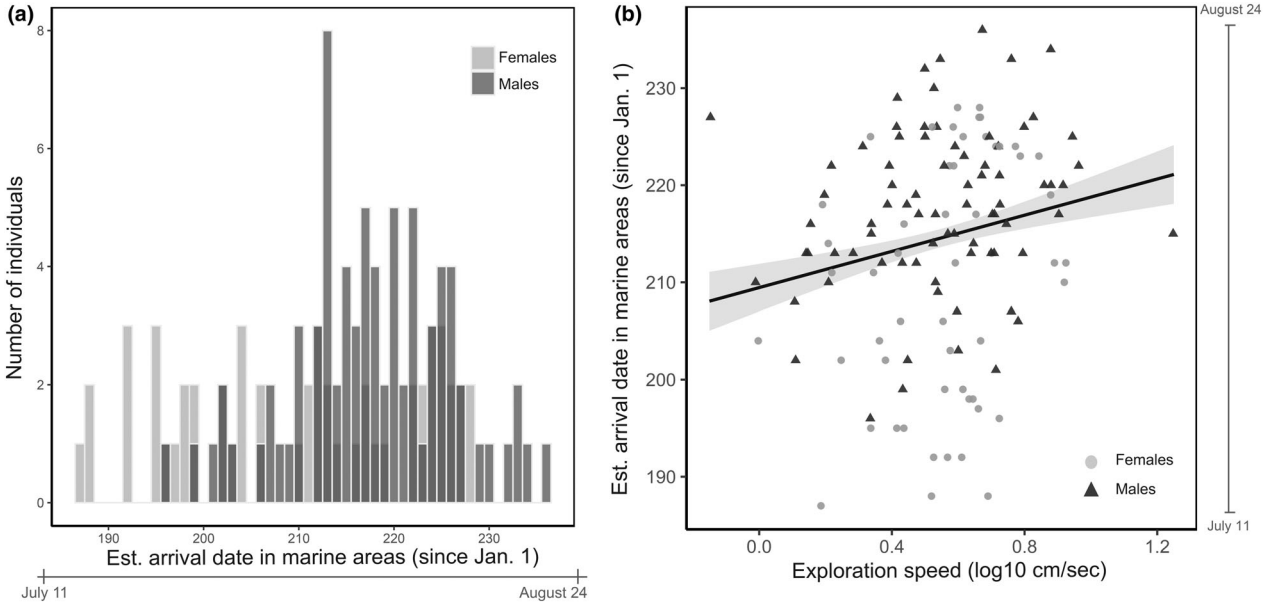

Figure 1. (a) Numbers of female (grey) and male (black) Red Knots on their estimated arrival dates in marine areas (1 January is day 1) and (b) exploration speed (log_{10} mean speed cm/s) measured in the experimental arena (*x*-axis) predicts individual arrival date to the marine areas that is estimated through diet-switch analysis based on $\delta^{13}C$ of red blood cells (*y*-axis). Slower explorers arrive earlier than faster explorers. For visualization purposes, the categorical variable 'Sex' is excluded from the model. Regression line and 95% confidence intervals are predicted by a generalized linear model (GLM) with Gaussian error distribution.

The results from analyses of other primaries revealed similar results (SOM Fig. S2). Because we used birds from two different years to increase our sample size of the birds that have active moult in first primary ($n_{2018} = 38$; $n_{2019} = 11$), we double-checked the results and controlled for capture year to the analyses; this did not affect the findings or conclusions (SOM Table S3).

DISCUSSION

We investigated whether exploratory personality could explain part of the variation in post-breeding migration timing of Red Knots. Based on the diet-switch analysis of isotope signatures, we showed that slower explorers left breeding sites and arrived at marine areas earlier than faster explorers. We also found that slower exploring Red Knots were more likely to fly non-stop from breeding to non-breeding sites than faster exploring Red Knots. Arrival timing in marine areas estimated with isotope analyses predicted the arrival timing in non-breeding sites estimated with moult progress in the Wadden Sea but did so with a large variation. Our findings show that the personality trait exploration measured at the fine scale of metres explained variation in the timing of global migrations.

Later arrival in the marine non-breeding sites can be caused by a later departure from the tundra breeding site. Consistent with previous studies (e.g. Dietz *et al.* 2010), we found from isotope and primary moult analyses that female Red Knots arrived in marine areas earlier than males, reflecting their abandonment of the hatchlings and earlier departure from the breeding grounds (Whitfield & Brade 1991). The amount and duration of staging sites (e.g. Iceland, Norway) used during migration and time spent at those stops can also affect arrival timing in non-breeding sites (such as in Black-tailed Godwits *Limosa limosa limosa*, Hooijmeijer *et al.* 2014). Some Red Knots have been reported to use staging sites such as Iceland when migrating, whereas others migrate non-stop (Dietz *et al.* 2010). We showed that slower (vs. faster) exploring Red Knots – independent of sex – arrived in marine areas earlier and were more likely to fly non-stop from the breeding to the non-breeding site in the Wadden Sea. Following the personality literature showing that faster individuals explore more areas (e.g. Dingemanse *et al.* 2003, Herborn *et al.* 2010), it is expected

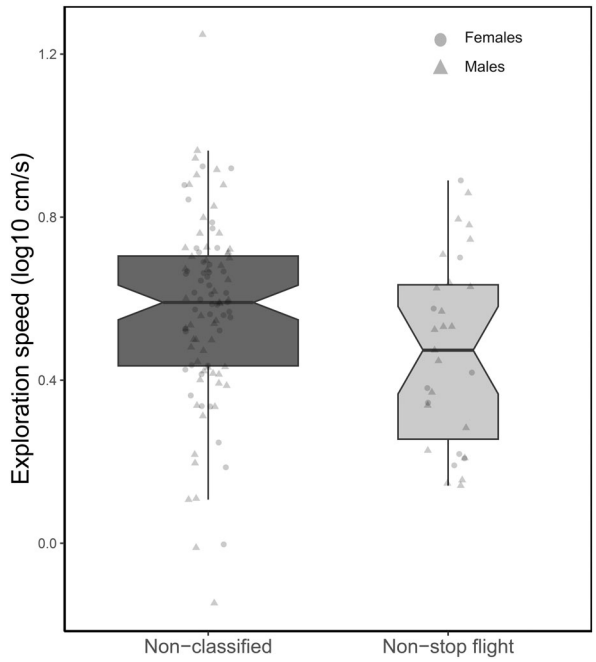

Figure 2. Red Knots that flew non-stop had, on average, lower exploration scores than birds that we could not classify. Adults in the Wadden Sea with $\delta^{13}C$ ratios below −19.3‰ were classified as skipping staging sites and flying non-stop from breeding to non-breeding marine areas (following Dietz *et al.* 2010). Those birds with $\delta^{13}C$ ratio above −19.3‰ were impossible to classify unambiguously, as they could have stopped in a staging site or they could have been in the Wadden Sea for a longer period of time.

that faster exploring birds use more stopover sites and thus fewer non-stop flights. In future studies, tracking Red Knots of different personalities on their entire migration should clarify whether fast exploring birds indeed make more and/or longer stopovers.

We found that arrival time in marine areas (estimated with isotope analyses) predicted the arrival time in the Wadden Sea (estimated with moult progress). We expected the two estimates to be similar for individuals that fly non-stop from the breeding to the non-breeding site in the Wadden Sea, and to be different for individuals that used staging sites en route. We found that while the two arrival timing estimations correlated highly with each other, the slope was significantly smaller than one with early birds showing large deviations from the $y = x$ line (Fig. 3). This could have two potential non-mutually exclusive explanations: (1) Individuals differ in whether they stage and for how long they are en route to the Wadden Sea. For instance, while birds that fly non-stop arrive in the Wadden Sea, the others stopped in Iceland to arrive (and hence start primary moult) in the Wadden Sea later. Birds that went to alternative marine areas before arriving in the Wadden Sea are expected to show a large discrepancy between arrival day estimated from isotopes and moult. Indeed, our data show a declining trend (Slope (95% CI) = −2.94 (−7.52 to 1.64), $P > 0.05$) in the differences between the two methods over the day of arrival, but this correlation was not statistically significant (SOM Fig. S3). (2) Individuals may differ in the time between arrival in the non-breeding sites and the start of moult. A study with Bar-tailed Godwits *Limosa lapponica baueri* showed that individuals have flexibility in when to begin moult. Moult could be delayed due to the energetic challenges of migration, or advanced slightly by individuals arriving 'late' (Conklin & Battley 2012). To what extent Red Knots differ in their moult speed and how this relates to exploratory personality remains to be studied.

Our results raise the question as to what the differences in arrival date might mean for Red Knots. Red Knots feed on soft terrestrial arthropods and larvae on breeding sites (Schekkerman *et al.* 2003) that are associated with a smaller gizzard (stomach muscle; Dekinga *et al.* 2001). Upon arrival to the non-breeding sites, they start eating hard-shelled prey that have higher digestive processing costs and are associated with a larger gizzard. Slower exploring Red Knots have been shown to have larger gizzards than faster explorers (Bijleveld *et al.* 2014) and mainly eat hard-shelled prey (Ersoy *et al.* 2022). Gizzard mass is flexible and may change over several days (Dekinga *et al.* 2001). It may be beneficial for slower explorers to arrive to the Wadden Sea earlier so they can shift to marine bivalves, with the appropriate gizzard mass, earlier.

Many shorebirds moult their feathers upon arrival to their non-breeding areas (Gwinner 1990). Because primary moult affects flight efficiency, actively moulting birds may be particularly vulnerable to aerial depredation (Hedenström 2003). Timing of migration in sandpipers has shown to be associated with the presence of their predators. For example, Western Sandpipers *Calidris mauri* migrate early and quickly to precede their predator, migratory Peregrine Falcons, all the way to their non-breeding sites, where they rapidly moult their flight feathers (Lank *et al.* 2003). In the

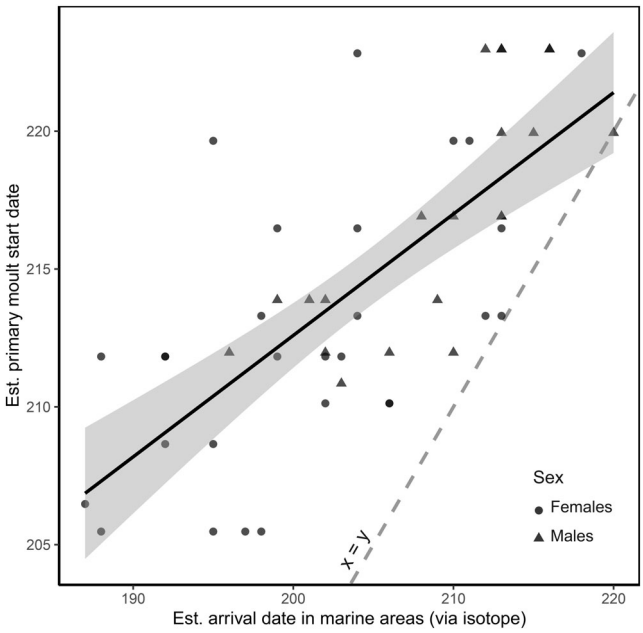

Figure 3. Relationship between estimated arrival date in marine areas (days since 1 January) and the estimated arrival timing in the Wadden Sea (from primary moult analyses) of individual male (triangle) or female (circle) Red Knots. Arrival day at the Wadden Sea was estimated from carbon isotope $\delta^{13}C$ ratios and the start of moult was calculated from first primary moult scores at capture. Regression line and 95% confidence intervals are predicted by a GLM with Gaussian error distribution.

Dutch Wadden Sea, the number of Peregrine Falcons shows a steep increase from 15 September onwards (van den Hout 2009). As Red Knots need *ca.* 70 days to moult their primary feathers completely (Dietz *et al.* 2013), earlier arrival in the Wadden Sea allows less overlap between moulting and the presence of Peregrine Falcons. By arriving early, slower (vs. faster) explorers lower the risk of predation when they are particularly vulnerable due to feather moult. Exploration in Red Knots was also related to body mass with slower explorers being heavier (Bijleveld *et al.* 2014). Because heavier birds are less agile in escaping predation (van den Hout *et al.* 2010), finishing primary moult before Peregrine Falcons arrive might be more important for slower than for faster exploring birds. Indeed, slower explorers have been shown to be more risk-averse than faster explorers (reviewed in Réale *et al.* 2010). However, no differences in survival were found between slower and faster exploring Red Knots (Bijleveld *et al.* 2014). Perhaps, faster individuals compensate for increased predation danger by moulting at a faster rate than slower explorers. To what extent faster exploring individuals benefit from using more staging sites and are less affected by later arrival in the non-breeding range needs further research.

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AUTHOR CONTRIBUTIONS

Selin Ersoy: Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; project administration; data curation; resources. **Ton G. G. Groothuis:** Supervision; conceptualization; writing – review and editing. **Theunis Piersma:** Conceptualization; supervision;

writing – review and editing. **Allert I. Bijleveld:** Conceptualization; investigation; methodology; validation; funding acquisition; writing – review and editing; project administration; supervision; resources.

ETHICAL NOTE

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CONFLICT OF INTEREST

None of the authors have any conflict of interest.

Data Availability Statement

Datasets are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.10444517 (Ersoy *et al.* 2023).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Effects of exploration speed and sex on the arrival day in marine areas without outliers estimated from stable isotope analysis.

Table S2. Effects of exploration speed and sex on the arrival day in marine areas estimated from the progress of primary moult.

Table S3. Correlation between estimated arrival date in marine areas based on isotope analysis and

estimated arrival timing based on primary moult analysis.

Figure S1. Relationship between stable carbon and nitrogen isotope ratios in red blood cells of Red Knots.

Figure S2. Start date from all primaries in relation to estimated arrival date in marine areas based on carbon isotope.

Figure S3. Relationship between exploration speed and migration strategy in Red Knots.