



## Pathway for personality development: juvenile red knots vary more in diet and exploratory behaviour than adults

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Evidence is accumulating that foraging behaviour and diet link to personality traits, yet little is known about how these associations emerge during development. Behaviour is expected to become more consistent with age and with foraging experience. We compared exploratory behaviour and diet variances of juvenile and adult red knots, *Calidris canutus islandica*, shortly after migration to marine intertidal mudflats from terrestrial tundra breeding grounds. By identifying the timing of the switch from terrestrial to marine isotopic signatures, we were also able to ask whether juveniles that arrived earlier, and thus had longer experiences in a particular environment (nonbreeding grounds), were more consistent in exploration behaviour. We found that juveniles had a more diverse diet and were less repeatable in their exploratory behaviour than adults. This change in repeatability was largely driven by greater within-individual behavioural variance in the juveniles compared to the adults. The amount of time juveniles experienced in a marine environment did not affect the variation in their exploratory behaviour, suggesting that consistency in exploration was developed over a longer period than the 4 weeks of our study. Our findings suggest that after initial exploration of a novel habitat, juveniles likely try out foraging techniques which later develop into consistent behaviours that differ between individuals. This study illuminates how personality can develop with experience in a free-living animal.

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Personality traits that are consistent within, but vary between, individuals have been shown to be associated with dispersal (Cote et al., 2010) and foraging behaviour (Araújo et al., 2011; Sheppard et al., 2018; Toscano et al., 2016). How these associations arise is elusive and requires studies on the developmental origin of personality traits. It has been suggested that personality traits reflect genetic variation (Dingemans et al., 2002; Drent et al., 2003; Van Oers et al., 2004); however, heritability is often low (Araya-Ajoy & Dingemans, 2017; Doctermann et al., 2015; Stirling et al., 2002), indicating that the development of personality traits is more strongly influenced by the environment (Groothuis & Trillmich, 2011; Laskowski et al., 2022). Differences in experience (also reflecting environmental influences) can induce positive feedback

loops that gradually fix the behaviour of individuals on different developmental trajectories (Sih et al., 2015; Urszán et al., 2018; Wolf & Weissing, 2012). While studies on the role of experience and learning in developing personality traits has advanced in the last decade (since Stamps & Groothuis, 2010), significant gaps in our understanding of how different factors such as personal experience operate on the development of personality is still poorly understood (Cabrera et al., 2021).

Individuals may gradually diverge from one another in behavioural tendencies as they age and have different experiences (i.e. fanning-out pattern, Stamps & Biro, 2016); juveniles are therefore usually found to have lower among-individual variation than adults (e.g. Kim et al., 2012). While among-individual variation increases with age, within-individual variation decreases with age and individuals become more consistent in behaviour (e.g. Carlson & Tetzlaff, 2020; Masilkova et al., 2022). Individual differences in experience and the feedback between behaviour and its outcome

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are likely to affect this divergence and consistency of behaviour (Sih et al., 2015; Stamps & Frankenhuis, 2016; Tariel et al., 2020). For example, studies indicate that the prey environment experienced during early life can shape an individual's foraging behaviour (e.g. Heinsohn, 1991; Slagsvold & Wiebe, 2007). Positive feedbacks between learning to detect, catch and process food can lead to behavioural consistency and divergence (O'Brien et al., 1989). In adults, foraging behaviour and personality traits such as exploration (magnitude of space use in novel environment) and boldness (approaching a novel object) have been linked in several studies (e.g. Kurvers et al., 2010; Patrick et al., 2017; van Overveld & Matthyssen, 2010). While evidence is accumulating that foraging behaviour and diet link to personality, little is known about how these associations emerge during development.

Repeatability in individual level traits is the most used measure in animal personality studies (Bell et al., 2009). Repeatability ( $R$ ) is often measured as a ratio of among-individual variation divided by the sum of among- and within-individual variation. Personality studies comparing adults and juveniles in behaviour use these  $R$  ratios in either a longitudinal approach (i.e. measuring the same individual over different life stages), a cross-sectional approach (i.e. comparing individuals belonging to different life stages) or a combination of both. While comparing  $R$  ratios between different life stages can be useful for understanding the relative magnitude of variation, different variance components give different information on behaviour (Wilson, 2018). For example, within-individual variation reflects the individual consistency in behaviour and is likely to decrease during development as individuals gain different experiences (Delaney et al., 2020). Therefore, investigating factors affecting within- and among-individual variation as well as repeatability during development is helpful for understanding the mechanisms by which consistent differences arise (Dingemanse et al., 2022; Dochtermann & Royauté, 2019; O'Dea et al., 2022).

Under laboratory conditions, adult red knots, *Calidris canutus islandica*, show high repeatability in their exploratory behaviour of a novel environment (Bijleveld et al., 2014; Ersoy et al., 2022; Kok et al., 2019), and exploratory behaviour of an individual is correlated with its foraging tactics and diet in the wild (Ersoy et al., 2022). Slower exploring adult red knots were found to use mainly tactile foraging and eat hard-shelled prey (e.g. cockles, *Cerastoderma edule*), while faster exploring adult knots use both tactile and visual foraging and eat both hard-shelled and softer prey (e.g. brown shrimp, *Crangon crangon*; Ersoy et al., 2022). These links between exploration, foraging tactics and diet makes the red knot a useful study species to investigate how foraging behaviour, diet and personality interact during development.

The *islandica* subspecies of red knots breeds on the high Arctic tundra of northern Greenland and northeast Canada and migrates to intertidal mudflats of western Europe for the nonbreeding season (Piersma, 2007). Adult females leave the breeding grounds when the eggs have hatched, adult males leave when the young are independent and the juveniles leave when ca. 35 days old (Nettleship, 1974). Red knot chicks in their first month of life on the Arctic tundra feed only on terrestrial arthropods and larvae that require visual foraging (Schekkerman et al., 2003). After migration to the overwintering grounds, juvenile red knots encounter hard-shelled benthic prey for the first time. Unlike their prey in the Arctic, this prey type requires tactile foraging to detect (Piersma et al., 1993). It is therefore likely that the differences in foraging tactics and diet found in adult red knots are determined after their

arrival in the wintering grounds. Through positive feedback between foraging tactics and diet, first experiences of catching different prey as a juvenile could later develop into consistency in foraging tactics and exploratory behaviour (Bijleveld, 2015; Sih et al., 2015). However, one study on captive red knots showed that repeatability of exploration did not differ between juveniles and adults; nor did it increase significantly with age over time (Kok et al., 2019). In this case, juvenile red knots were captured ca. a month after their arrival on the wintering grounds and kept in aviaries in a controlled environment; repeatability was determined in four repeated assays conducted throughout a year. Lack of differences in exploration between juveniles and adults, or lack of increase in the repeatability of exploration in juveniles with age over time, could be due to captivity (a conclusion by Kok et al., 2019). For example, juveniles in captivity may have missed the opportunity to practise their foraging strategies in the wild, thus receiving no feedback in their behaviour. Therefore, measuring exploration of wild red knots at the field site right after capture together with estimating diet in the wild may help us to understand the developmental origin of exploration in red knots.

We caught wild red knots in their marine wintering grounds right after migration from the tundra breeding grounds. Immediately after capture, we took blood samples to determine the stable carbon and nitrogen isotope composition of blood cells and plasma to estimate diet in the wild, and changes therein to estimate the time that juveniles switch from a tundra to a marine diet. We then conducted repeated assays of exploration of juvenile and adult red knots in an experimental set-up at the field site. We expected juveniles to try different marine prey types and thus show larger variation in diet than adults. We also expected that juveniles would be less repeatable in exploration with larger within-individual and smaller among-individual variation than adult red knots. Finally, we predicted that juveniles that were repeatedly assayed for exploration soon after arrival on the wintering grounds would show a greater within-individual changes in exploratory behaviour than birds captured later because they had less time on the wintering grounds to refine their behavioural strategy.

## METHODS

### Capture Events

We used data collected between 2018 and 2021. In all years, we used night-time mist netting for ca. 1 week during new moon periods in the western Dutch Wadden Sea (53°15'N, 5°15'E). Red knots were given a numbered metal ring for individual identification and their age was classified based on plumage characteristics (juvenile: <6 months; second-calendar year: 6–18 months; adult: >18 months; Prater et al., 1977). We focused on juveniles and adults and did not work with birds that were identified as second calendar year birds because of the lower sample size ( $N = 13$ ). Data collected from 57 adult red knots in 2018 were presented earlier in Ersoy et al. (2022) and used here for comparison of exploration speed between juveniles and adults (see below). As we captured few juveniles in most years, we accumulated data from 1–3 September 2019 ( $N = 4$ ), 3 October 2019 ( $N = 16$ ), 16–18 October 2020 ( $N = 9$ ) and 6–12 September 2021 ( $N = 44$ ) and used these for analyses comparing exploration speed between juveniles and adults (see below). In September 2021, we also captured 45 adult red knots. Juveniles ( $N = 44$ ) and adults ( $N = 45$ ) from that catching event were used in analyses comparing diet variance between juveniles

and adults (see below). Juveniles from September 2021 were also used in analyses investigating how days since the diet switch from tundra to marine may influence the juvenile consistency in exploratory behaviour (see below).

### Stable Isotope Measurements

Blood samples (ca. 80  $\mu$ l) for stable isotope analyses were taken from individuals during the catching event in September 2021. The samples were separated into plasma and red blood cells by centrifugation (12 min, 7000 rpm), pipetted into separate glass vials and immediately stored in a freezer at the field site. In the laboratory, samples were freeze-dried before analysis 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  $\times$  9 mm tin capsules. Isotope values were calibrated to a certified acetanilide standard (Arndt Schimmelmann, Indiana University, Bloomington, IN, U.S.A.), controlled by certified urea and casein standards (Elemental Microanalysis, Okehampton, U.K.) and corrected for blank tin capsules. We did not always have enough plasma samples to finalize isotope analysis ( $N_{\text{excluded}} = 8$ ; juveniles  $N_{\text{final}} = 37$ , adults  $N_{\text{final}} = 44$ ).

### Diet

For the diet comparison between juveniles and adults in the Wadden Sea, we used stable isotope values of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from blood samples that were collected in September 2021 from juvenile and adult red knots. Red blood cell isotope values reflect diet from the past ca. 45 days while plasma samples reflect diet from the past ca. 14 days (Klaassen et al., 2010). For the diet estimation in the wintering grounds, we used only values for plasma because most of the red blood cell samples of our red knots contained signatures from the Arctic breeding grounds, while none of the plasma samples had signature from breeding grounds.

To compare the variance in diet between adult and juvenile red knots, we used the R package SIBER and calculated the standard ellipse area as a measure of diet width for each age group (Jackson et al., 2011). Standard ellipse area is a bivariate measure of the distribution of individuals in trophic space; each ellipse represents the core dietary niche of each group (Jackson et al., 2011). To account for variation in sample sizes, we calculated a Bayesian estimate using Markov chain Monte Carlo simulation with 4 000 000 iterations with 1 000 000 burn in and with two chains for each group with default priors. Overlap between ellipse areas and extent of overlap proportion were also calculated to indicate the extent of resource sharing.

### Short-term Captivity

After taking biometric measurements and blood sampling, we moved the birds to temporary outdoor aviaries of 2  $\times$  0.75 and 0.4 m high made of linen with a net floor covered in dried hemp (Hemparade). These aviaries were placed at the field site on natural sand/grass ground. The birds were provided with ad libitum food (live and dried mealworms) and water (freshwater and sea water in two separate containers). Group size in the aviaries was 8–12 birds. Exploratory behaviour was measured twice with on average 4 days in between (range 2–6 days). After completing the behavioural assays, all birds were released back to their natural habitat, the Wadden Sea, with unique colour coded rings for identification later.

### Ethical Note

Birds were kept for 1–3 days for this study and, after completing the assays, were released back to their natural habitat (i.e. where they were captured). Blood samples were taken from the brachial wing vein by certified experienced personnel. To reduce the stress during handling, birds were kept in a dark and quiet environment. All necessary permits to catch, handle, ring, test and keep red knots were granted to the Netherlands Institute for Sea Research (NIOZ) by the Dutch law and regulation under protocol number NIOAVD8020020171505.

### Exploratory Behaviour

The exploratory behaviour of adults ( $N = 57$  from 2018) and juveniles ( $N = 67$  from 2019, 2020, 2021) was measured after 24 h in captivity. The assays took place in a field-based arena (see Ersoy et al., 2022 for a detailed description of the method). Briefly, a pyramid shaped mobile unit of 2  $\times$  2  $\times$  2 m was filled with sea water (20 cm depth) and contained four identical trays (61  $\times$  40 cm and 25 cm high) of wet sand on which birds could explore. No food was offered during the experiment. A GoPro (Hero Black) camera was mounted at the ceiling to record the movement trajectories at 2 frames/s. To standardize the procedure and motivate birds equally for the personality tests, we placed them individually into a holding pen without access to food. After 2 h, we started the experiment by gently placing the bird on the sand patch in the experimental unit. Individual trials lasted 20 min per bird.

To calculate exploratory scores for individuals from videos, we used video tracking software idtracker (Pérez-Escudero et al., 2014). The software produced position data (x- and y-coordinates) for every frame (each 0.5 s) during 20 min that a bird spent in the mobile arena. Between two subsequent frames, we used the distance between estimated positions to calculate speed. Errors in the positioning algorithm were filtered out by excluding speeds higher than 200 cm/s. An individual's exploration speed was calculated as the mean speed (cm/s) during each trial.

To compare repeatability, within- and among-individual variance in exploration speed between juveniles and adults, we built a Bayesian multilevel model with the brms package (Bürkner, 2017). Exploration speed, the response variable, was  $\log_{10}$  transformed to correct for overdispersion prior to the analysis. Age group (juvenile or adult) was added as a fixed effect to test for an influence on the intercept and again in the dispersion part of the model (i.e. sigma) to test for an effect on the residual variance (i.e. to investigate within-individual variance). Individual ID nested in age group was added as a random effect to estimate separate variance components by age for the among-individual variance. We also added Year as fixed effect to account for the possible effects of different years in our data. We ran the model using three Markov chains for 50 000 iterations with 10 000 burn-in iterations, and a thinning interval of 40. Uninformative default priors were used on all parameters. Models converged as indicated by Rhat values of 1.0, effective sample size measures (Bulk > 2641, Tail > 2432), and assessment through visual inspection of the trace plots. Among-individual variance ( $V_i$ ) was extracted from the posterior samples of the standard deviation for random effects. Within-individual variance ( $V_w$ ) was extracted from the posterior samples of the dispersion part of the model (i.e. sigma). Repeatability was calculated as the among-individual variance divided by the sum of among- and within-individual variances. Repeatability and variance components of adults were subtracted from the corresponding values of

juveniles to investigate the magnitude of differences between the age groups ( $\Delta$ ).

#### Estimating Days Since Juvenile Diet Switch

Measuring the change in isotopic ratios in body tissue after a diet switch is a common technique to estimate arrival date (Hobson, 2008). We adopted the single tissue model using the carbon isotope ( $\delta^{13}\text{C}$ ) to estimate time since diet switch (following Klaassen et al., 2010):

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

Start and end values were taken from Dietz et al. (2010): for the start value, where the migration started, we took the Arctic tundra value ( $\delta^{13}\text{C} = -24.7$ ), and for the end value, where the migration ended, we took the Wadden Sea value ( $\delta^{13}\text{C} = -14.0$ ). We took the turnover rate value for red knots ( $\lambda = 0.046$ ) from Klaassen et al. (2010). We fitted individual carbon isotope ( $\delta^{13}\text{C}$ ) values from red blood cells of our juvenile red knots. The result of this function was the estimated number of days since their diet switched from tundra to marine (i.e. days since arrival in the Wadden Sea).

#### Variation in Juvenile Exploration Scores Between Tests

We built a Bayesian linear regression model using brms to test whether the absolute difference between the exploration test repeats ( $\log_{10}$  cm/s) in juveniles (response variable) can be predicted by the number of days since arrival in the Wadden Sea. In other words, whether time in the wintering grounds would allow refinement of their behavioural strategy. We ran the model using three Markov chains for 50 000 iterations with 10 000 burn-in iterations and a thinning interval of 40. Uninformative default priors were used on all parameters. The model converged as indicated by Rhat values of 1.0 and assessment through visual inspection of the trace plots. All statistical analyses were performed with R version 4.1.2 (R Core Team, 2021).

## RESULTS

### Does Diet Differ Between Juveniles and Adults?

The posterior estimates of the standard ellipses represent the core dietary niche of each group. Standard ellipse areas of juveniles and adults overlapped ( $4.71\% \text{‰}^2$ , ellipse area  $\text{Juveniles} = 9.37\% \text{‰}^2$ , ellipse area  $\text{Adults} = 5.36\% \text{‰}^2$ ). The proportion of juveniles' diet overlap with adults was 0.50 and the proportion of adults' diet overlap with juveniles was 0.88 (Fig. 1a). Juveniles (median (95% credible interval, CI):  $1.5\% \text{‰}^2$  (1.07; 2.06),  $N_{\text{juveniles}} = 37$ ) showed a larger diet variance than adults (median (95% CI):  $0.88\% \text{‰}^2$  (0.76; 1.04),  $N_{\text{adults}} = 44$ ; Fig. 1b).

### Repeatability and Variance Components of Exploration

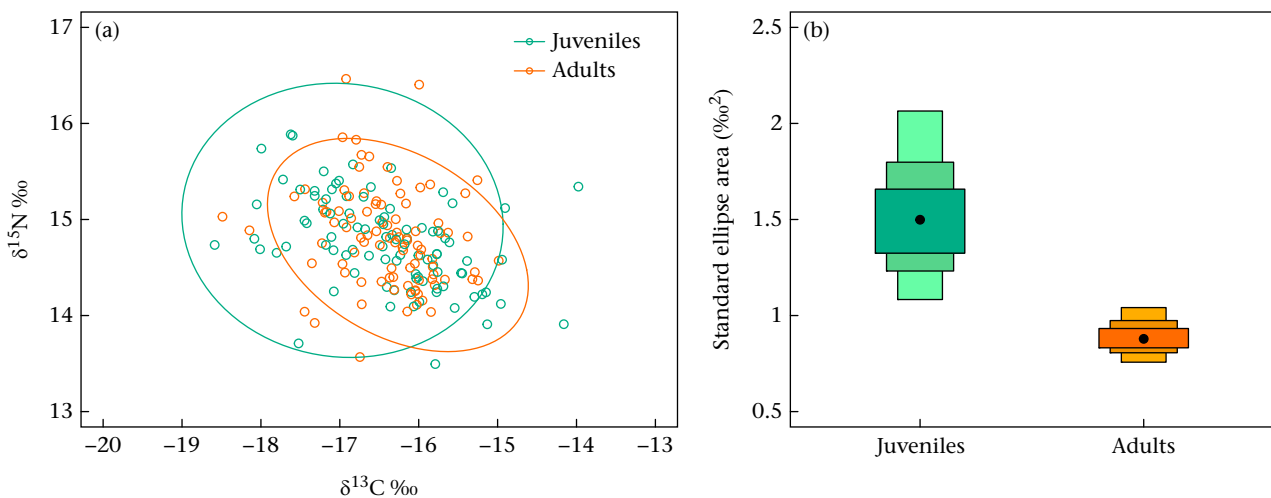
Juvenile ( $N = 67$ ) and adult ( $N = 57$ ) groups of red knots did not differ on their exploration speed (Table 1, Fig. 2). However, exploration speed of juveniles was less repeatable and had higher within-individual variance than for adults (Table 2, Fig. 3a and b) while there was no difference between adults and juveniles in among-individual variance in exploration (Table 2, Fig. 3c). Adding Year did not affect the estimated variance components (Table 1), nor did analysing the data per year (Appendix Tables A1–A4).

### Time Since Diet Switch in Juveniles

The absolute difference between the exploration scores differed between test repeats in juveniles and ranged from 0.01 to 0.66 (median = 0.18). The estimated number of days since their diet switched from tundra to marine (i.e. days since arrival in the Wadden Sea) ranged from 14 to 33 days (median = 21.5) and did not explain the difference between the exploration test repeats ( $N = 26$ , Fig. 4).

## DISCUSSION

Personal experiences and the feedback between behaviour and its outcome influence the consistency of behaviour; however, little



**Figure 1.** Stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of plasma from 37 juvenile and 44 adult red knots. (a) Standard ellipses drawn to represent standard ellipse area of each age group. (b) Density plot showing the credible intervals of the Bayesian standard ellipse areas. Black dots represent their median, and the shaded boxes represent the 50%, 75% and 95% credible intervals from dark to light colours.



**Table 1**  
Results from analyses comparing juvenile and adults in exploratory behaviour

Predictors	Exploration speed (log cm/s)
	Estimates (95% CI)
Intercept	0.54 (0.49–0.59)
Age (Juvenile)	669.13 (–738.45–1537.98)
Year (2019)	–669.14 (–1538.01–738.50)
Year (2021)	–669.17 (–1538.00–738.41)
Sigma: Age (Adult)	–2.11 (–2.27––1.90)
Sigma: Age (Juvenile)	–1.64 (–1.82––1.44)
Marginal $R^2$ /Conditional $R^2$	0.01/0.53
N	119 (adult = 57, juvenile = 67)

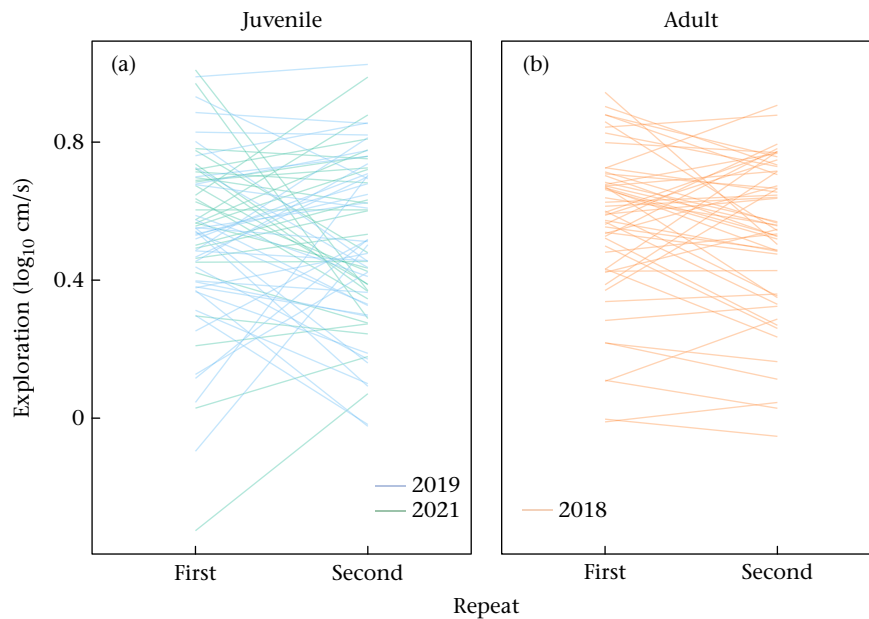
CI: credible interval.

is known about how individuals develop their personalities in the wild. We repeatedly observed the behaviour of juvenile and adult red knots and found that juveniles were less consistent in their explorative behaviour than adults. Similarly, juveniles had a less specialized dietary niche than adults. Together, these results indicate that juvenile red knots have not yet developed a clear personality, which suggests that the development of their exploratory personalities depends on early foraging experiences. We discuss how the feedback between learning to detect, catch and process food at an early age can favour behavioural consistency later in life.

Changes in repeatability with age could be caused by changes in within- only, among- only or within- and among-individual variances combined. Repeatability ( $R = 0.70$ ) in adult exploration scores in our study was higher than for juveniles ( $R = 0.43$ ). We did not find any differences in the among-individual variation in exploration between age groups. The increase in repeatability

between juveniles and adults was indeed explained by a decrease in within-individual variation during development. Indeed, other studies also found a decrease in within-individual variation leading to increased repeatability with age (e.g. in sea anemones, *Actinia equina*, Osborn & Briffa, 2017; mosquitofish, *Gambusia holbrooki*, Polverino et al., 2016). The value for repeatability in juveniles ( $R = 0.43$ ) in this study was similar to that in another study that measured exploratory personality of red knots captured as juveniles then raised and tested in captive conditions over 2 years ( $R = 0.48$ , Kok et al., 2019). In that study, juveniles' repeatability in exploration increased with age from the first (juvenile age  $R = 0.48$ ) to the second year (adult age  $R = 0.60$ ). Although this increase was not statistically significant (Kok et al., 2019), it was close to the effect size of the birds in our study. Together with the relatively high repeatability of juveniles and the lack of differences in the among-individual variation between adult and juveniles found in our current study, we conclude that part of juveniles' personality had already developed before we captured them. This suggests that processes like genetics, epigenetics or first experiences on the tundra breeding grounds play an important role in shaping exploratory behaviour of red knots. Nevertheless, our findings on the decrease in within-individual variation between age groups shows that experiences that juvenile gain in their first month on the wintering grounds are important and this influences the consistency of exploratory behaviour later in life.

We found that within the first month after arriving on the wintering grounds, juveniles were more likely to eat a variety of prey types than adults. Juvenile red knots, unlike adults, have been observed eating atypical food items (e.g. algae) in atypical locations (e.g. harbours) in the Wadden Sea (observed in 2 separate years,

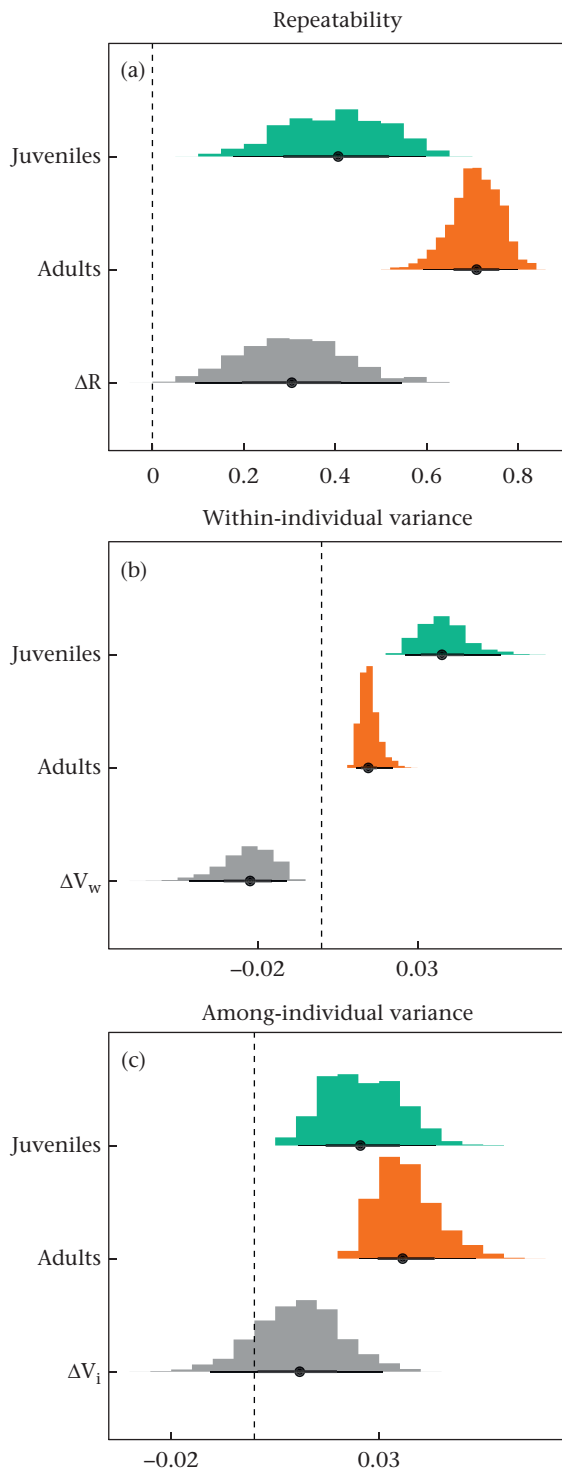


**Figure 2.** Raw data of repeated measurements of exploration speed ( $\log_{10}$  cm/s) on (a) 67 juveniles and (b) 57 adults in 2019 and 2021. Each line depicts an individual red knot.

**Table 2**  
Comparison of repeatability and variance components in exploration speed by age group

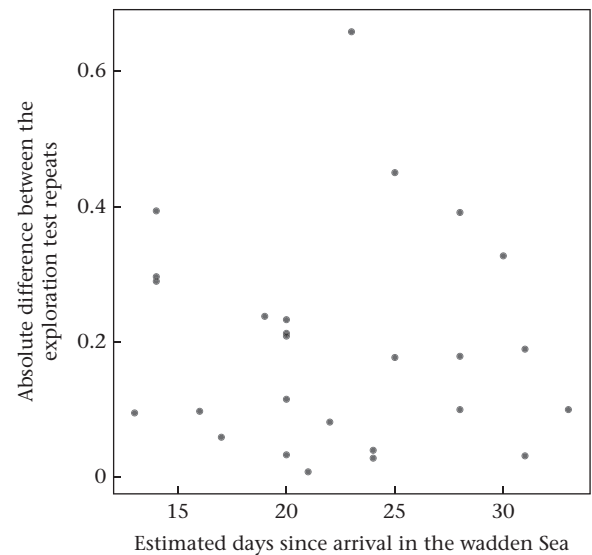
Variance and ratio	Age groups		Difference $\Delta$
	Juveniles median (95% CI)	Adults median (95% CI)	Adult – Juvenile median (95% CI)
Repeatability ( $R$ )	0.41 (0.18; 0.60)	0.71 (0.59; 0.80)	<b>0.30 (0.09; 0.55)</b>
Within-individual variance ( $V_w$ )	0.04 (0.03; 0.06)	0.01 (0.01; 0.02)	<b>–0.02 (–0.04; –0.01)</b>
Among-individual variance ( $V_i$ )	0.03 (0.01; 0.04)	0.04 (0.03; 0.05)	0.01 (–0.01; 0.04)

Magnitude of the difference in variability between age groups is shown with  $\Delta$ . Posterior medians and 95% credible intervals (CI) estimated from a Bayesian mixed model. Bold font indicates credible intervals do not overlap with zero.



**Figure 3.** Comparison of variance components and ratios of exploration speed between age groups. Posterior distribution of (a) repeatability of age groups ( $R$ ) and the difference in repeatability ( $\Delta R = R_{\text{adults}} - R_{\text{juveniles}}$ ), (b) within-individual variance of age groups and the difference in within-individual variance ( $\Delta V_w = V_{w,\text{adults}} - V_{w,\text{juveniles}}$ ) and (c) among-individual variance of age groups and the difference in among-individual variance ( $\Delta V_i = V_{i,\text{adults}} - V_{i,\text{juveniles}}$ ). Posterior medians (circles) and credible intervals (50% tick lines, 95% thin lines) estimated from a Bayesian mixed model. Dashed line shows the zero line.

Ersoy & Bijleveld, n.d.; Appendix Fig. A1). A reduction in diet variation from juvenile to adult stage in the Wadden Sea could have four potential nonmutually exclusive explanations. (1) Competition



**Figure 4.** Absolute difference between the two ( $\log_{10}$  cm/s) assays of exploration in juveniles (y axis) in response to the number of days since arrival in the Wadden Sea. Data are from 26 juveniles caught in September 2021.

for food on the Wadden Sea mudflats may be high; juveniles may be pushed out from the mudflats by competitively superior adults, so they search food in alternative places and find different types of food (e.g. Cresswell, 1994). Indeed, a study on the *canutus* subspecies of red knots wintering in Mauritania showed that juveniles feed separately from adults and they do so in more dangerous locations (van den Hout et al., 2014). (2) Food searching is only possible when the water retreats on mudflats and juveniles might be less successful at catching shellfish than adults in the limited period on mudflats. It could, therefore, be that juveniles also search for alternative food during high tide periods. (3) There may be larger variation in the areas used by juvenile red knots and the food that they encounter there (Piersma et al., 1993). (4) Since our study was cross-sectional, it may be the case that the juveniles with the widest variation in diet do not survive until adulthood, thus reducing the variation that we found in adult birds.

Experience during development is expected to influence personality later in life (Balsam & Stevenson, 2021; Groneberg et al., 2020; Patoka et al., 2019). The amount of feedback between the foraging behaviour and its outcome, that is, the foraging experience that juveniles gain in the marine environment, may influence the consistency of exploratory behaviour. We, therefore, expected the amount of time spent in the Wadden Sea would explain the within-individual variation in juvenile exploration. However, juvenile red knots that were tested for exploration soon after arrival on the wintering grounds did not have a higher difference between repeat tests than individuals that were caught and tested later (relative to their own migration date). In our study, we could not catch and test the same juvenile in different time periods to measure the influence of time spent on the mudflats on consistency of exploration. Instead, we collected data from different juveniles at different times after their arrival on the wintering grounds (i.e. on the mudflats, 14–33 days after arrival). Therefore, we could not investigate changes in exploration or variation at the within-individual level and, thus, account for individual variation in learning between juveniles in this study.

In conclusion, larger within-individual variance in exploration scores of juveniles (versus adults), together with their diverse diet in our study, shows that free-living juvenile red knots are likely to practise their foraging strategies in the wild. The feedback they receive between foraging behaviour and its outcome during the

first months on the wintering grounds later develops into consistency in exploratory behaviour. However, precisely when this develops is still unclear because individuals are likely to differ in how fast they apply these feedbacks to their behaviour. Through its role in repeated exposures, the prey environment an individual experiences can mould exploratory behaviour during development.

### Author Contributions

S.E. and A.I.B. conceived the study. S.E., C.E.B. and E.D. collected the data. S.E. analysed the data and prepared the first draft of the manuscript. A.I.B. and C.E.B. helped improve the writing. All authors contributed critically to the drafts and gave final approval for publication.

### Data Availability

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.8349585> (Ersoy et al., 2022).

### Declaration of Interest

None of the authors have a conflict of interest.

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### References

- Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, *14*, 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>
- Araya-Ajoy, Y. G., & Dingemanse, N. J. (2017). Repeatability, heritability, and age-dependence of seasonal plasticity in aggressiveness in a wild passerine bird. *Journal of Animal Ecology*, *86*, 227–238. <https://doi.org/10.1111/1365-2656.12621>
- Balsam, J. S., & Stevenson, P. A. (2021). Agonistic experience during development establishes inter-individual differences in approach-avoidance behaviour of crickets. *Scientific Reports*, *11*, 1–13. <https://doi.org/10.1038/s41598-021-96201-1>
- Bell, A. M., Hankison, S. J., & Laskowski, K. L. (2009). The repeatability of behaviour: A meta-analysis. *Animal Behaviour*, *77*, 771–783. <https://doi.org/10.1016/j.anbehav.2008.12.022>
- Bijleveld, A. I., Massourakis, G., van der Marel, A., Dekinga, A., Spaans, B., van Gils, J. A., & Piersma, T. (2014). Personality drives physiological adjustments and is not related to survival. *Proceedings of the Royal Society B: Biological Sciences*, *281*, Article 20133135. <https://doi.org/10.1098/rspb.2013.3135>
- Bijleveld, A. I. (2015). *Untying the knot: Mechanistically understanding the interactions between social foragers and their prey*. Groningen, The Netherlands: University of Groningen. PhD Thesis.
- Bürkner, P.-C. (2017). brms: An R package for Bayesian multilevel models using stan. *Journal of Statistical Software*, *80*, 1–28. <https://doi.org/10.18637/jss.v080.i01>
- Cabrera, D., Nilsson, J. R., & Griffen, B. D. (2021). The development of animal personality across ontogeny: A cross-species review. *Animal Behaviour*, *173*, 137–144. <https://doi.org/10.1016/j.anbehav.2021.01.003>
- Carlson, B. E., & Tetzlaff, S. J. (2020). Long-term behavioral repeatability in wild adult and captive juvenile turtles *Terrapene carolina*: Implications for personality development. *Ethology*, *126*, 668–678. <https://doi.org/10.1111/eth.13024>
- Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: Characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B*, *365*, 4065–4076. <https://doi.org/10.1098/rstb.2010.0176>
- Cresswell, W. (1994). Age-dependent choice of redshank *Tringa totanus* feeding location: Profitability or risk? *Journal of Animal Ecology*, *63*, 589–600. <https://doi.org/10.2307/5225>
- Delaney, D. M., Hoekstra, L. A., & Janzen, F. J. (2020). Becoming creatures of habit: Among- and within-individual variation in nesting behaviour shift with age. *Journal of Evolutionary Biology*, *33*, 1614–1624. <https://doi.org/10.1111/jeb.13701>
- Dietz, M. W., Spaans, B., Dekinga, A., & Klaassen, M. (2010). Do red knots *Calidris canutus islandica* routinely skip Iceland during southward migration? *Condor*, *112*, 48–55.
- Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, *64*, 929–938. <https://doi.org/10.1006/anbe.2002.2006>
- Dingemanse, N. J., Hertel, A. R., & Royauté, R. (2022). Moving away from repeatability: A comment on Stuber et al. *Behavioral Ecology*. <https://doi.org/10.1093/beheco/arac006>. arac006.
- Dochtermann, N. A., & Royauté, R. (2019). The mean matters: Going beyond repeatability to interpret behavioural variation. *Animal Behaviour*, *153*, 147–150. <https://doi.org/10.1016/j.anbehav.2019.05.012>
- Dochtermann, N. A., Schwab, T., & Sih, A. (2015). The contribution of additive genetic variation to personality variation: Heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*, *282*, Article 20142201. <https://doi.org/10.1098/rspb.2014.2201>
- Drent, P. J., van Oers, K., & van Noordwijk, A. J. (2003). Realized heritability of personalities in the great tit *Parus major*. *Proceedings of the Royal Society B: Biological Sciences*, *270*, 45–51. <https://doi.org/10.1098/rspb.2002.2168>
- Ersoy, S., Beardsworth, C. E., Dekinga, A., van der Meer, M. T. J., Piersma, T., Groothuis, T. G. G., & Bijleveld, A. I. (2022). Exploration speed in captivity predicts foraging tactics and diet in free-living red knots. *Journal of Animal Ecology*, *91*, 356–366. <https://doi.org/10.1111/1365-2656.13632>
- Ersoy, S. & Bijleveld A.I. (n.d.) Feeding observations of juvenile red knots in Harlingen harbour. Unpublished raw data.
- Groneberg, A. H., Marques, J. C., Martins, A. L., Del Corral, R. D., de Polavieja, G. G., & Orger, M. B. (2020). Early-life social experience shapes social avoidance reactions in larval zebrafish. *Current Biology*, *30*, 1–13. <https://doi.org/10.1016/j.cub.2020.07.088>
- Groothuis, T. G. G., & Trillmich, F. (2011). Unfolding personalities: The importance of studying ontogeny. *Developmental Psychobiology*, *53*, 641–655. <https://doi.org/10.1002/dev.20574>
- Heinsohn, R. G. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *American Naturalist*, *137*, 864–881. <https://doi.org/10.1086/285198>
- Hobson, K. A. (2008). Applying isotopic methods to tracking animal movements. In *Terrestrial Ecology* (pp. 45–78). Elsevier.
- Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*, 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Kim, S. L., Tinker, M. T., Estes, J. A., & Koch, P. L. (2012). Ontogenetic and among-individual variation in foraging strategies of northeast Pacific white sharks based on stable isotope analysis. *PLoS One*, *7*, Article e45068. <https://doi.org/10.1371/journal.pone.0045068>
- Klaassen, M., Piersma, T., Korthals, H., Dekinga, A., & Dietz, M. W. (2010). Single-point isotope measurements in blood cells and plasma to estimate the time since diet switches. *Functional Ecology*, *24*, 796–804.
- Kok, E. M. A., Burant, J. B., Dekinga, A., Manche, P., Saintonge, D., Piersma, T., & Mathot, K. J. (2019). Within-individual canalization contributes to age-related increases in trait repeatability: A longitudinal experiment in red knots. *American Naturalist*, *194*, 455–469. <https://doi.org/10.1086/704593>
- Kurvers, R. H. J. M., Prins, H. H. T., van Wieren, S. E., van Oers, K., Nolet, B. A., & Ydenberg, R. C. (2010). The effect of personality on social foraging: Shy barnacle geese scrounge more. *Proceedings of the Royal Society B: Biological Sciences*, *277*, 601–608. <https://doi.org/10.1098/rspb.2009.1474>
- Laskowski, K. L., Bierbach, D., Jolles, J. W., Doran, C., & Wolf, M. (2022). The emergence and development of behavioral individuality in clonal fish. *Nature Communications*, *13*, 6419. <https://doi.org/10.1038/s41467-022-34113-y>
- Masilkova, M., Šlipogor, V., Lima, M. S. G. H., Hadová, M., Lhota, S., Bugnyar, T., & Konečná, M. (2022). Age, but not hand preference, is related to personality traits

- in common marmosets *Callithrix jacchus*. *Royal Society Open Science*, 9, Article 220797. <https://doi.org/10.1098/rsos.220797>
- Nettleship, D. N. (1974). The breeding of the knot *Calidris canutus* at Hazen Camp, Ellesmere Island. *Journal Polarforschung*, 44, 8–26.
- O'Brien, J. W., Evans, B. I., & Browman, H. I. (1989). Flexible search tactics and efficient foraging in saltatory searching animals. *Oecologia*, 80, 100–110. <https://doi.org/10.1007/BF00789938>
- O'Dea, R. E., Noble, D. W. A., & Nakagawa, S. (2022). Unifying individual differences in personality, predictability and plasticity: A practical guide. *Methods in Ecology and Evolution*, 13, 278–293. <https://doi.org/10.1111/2041-210X.13755>
- Osborn, A., & Briffa, M. (2017). Does repeatable behaviour in the laboratory represent behaviour under natural conditions? A formal comparison in sea anemones. *Animal Behaviour*, 123, 197–206. <https://doi.org/10.1016/j.anbehav.2016.10.036>
- Patoka, J., Kalous, L., & Bartos, L. (2019). Early ontogeny social deprivation modifies future agonistic behaviour in crayfish. *Scientific Reports*, 9, 8–12. <https://doi.org/10.1038/s41598-019-41333-8>
- Patrick, S. C., Pinaud, D., & Weimerskirch, H. (2017). Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *Journal of Animal Ecology*, 86, 1257–1268. <https://doi.org/10.1111/1365-2656.12724>
- Pérez-Escudero, A., Vicente-Page, J., Hinz, R. C., Arganda, S., & de Polavieja, G. G. (2014). idTracker: tracking individuals in a group by automatic identification of unmarked animals. *Nature Methods*, 11, 743–748. <https://doi.org/10.1038/nmeth.2994>
- Piersma, T. (2007). Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology*, 148, 45. <https://doi.org/10.1007/s10336-007-0240-3>
- Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P., & Wiersma, P. (1993). Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the Western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research*, 31, 331–357. [https://doi.org/10.1016/0077-7579\(93\)90052-T](https://doi.org/10.1016/0077-7579(93)90052-T)
- Polverino, G., Cigliano, C., Nakayama, S., & Mehner, T. (2016). Emergence and development of personality over the ontogeny of fish in absence of environmental stress factors. *Behavioral Ecology and Sociobiology*, 70, 2027–2037. <https://doi.org/10.1007/s00265-016-2206-z>
- Prater, A. J., Marchant, J. H., & Vuorinen, J. (1977). *Guide to the identification and ageing of Holarctic waders*. BTO, Tring.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Schekkerman, H., Tulp, I., Piersma, T., & Visser, G. H. (2003). Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. *Oecologia*, 134, 332–342. <https://doi.org/10.1007/s00442-002-1124-0>
- Sheppard, C. E., Inger, R., McDonald, R. A., Barker, S., Jackson, A. L., Thompson, F. J., Vitikainen, E. I. K., Cant, M. A., & Marshall, H. H. (2018). Intragroup competition predicts individual foraging specialisation in a group-living mammal. *Ecology Letters*, 21, 665–673. <https://doi.org/10.1111/ele.12933>
- Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., & Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology & Evolution*, 30, 50–60. <https://doi.org/10.1016/j.tree.2014.11.004>
- Slagsvold, T., & Wiebe, K. L. (2007). Learning the ecological niche. *Proceedings of the Royal Society B: Biological Sciences*, 274, 19–23. <https://doi.org/10.1098/rspb.2006.3663>
- Stamps, J. A., & Biro, P. A. (2016). Personality and individual differences in plasticity. *Current Opinion in Behavioral Sciences*, 12, 18–23. <https://doi.org/10.1016/j.cobeha.2016.08.008>
- Stamps, J. A., & Frankenhuis, W. E. (2016). Bayesian models of development. *Trends in Ecology & Evolution*, 31, 260–268.
- Stamps, J. A., & Groothuis, T. G. G. (2010). The development of animal personality: Relevance, concepts and perspectives. *Biological Reviews of the Cambridge Philosophical Society*, 85, 301–325. <https://doi.org/10.1111/j.1469-185X.2009.00103.x>
- Stirling, D. G., Réale, D., & Roff, D. A. (2002). Selection, structure and the heritability of behaviour: Selection, structure and heritability. *Journal of Evolutionary Biology*, 15, 277–289. <https://doi.org/10.1046/j.1420-9101.2002.00389.x>
- Tariel, J., Plénet, S., & Luquet, E. (2020). How do developmental and parental exposures to predation affect personality and immediate behavioural plasticity in the snail *Physa acuta*? *Proceedings of the Royal Society B: Biological Sciences*, 287, Article 20201761. <https://doi.org/10.1098/rspb.2020.1761>
- Toscano, B. J., Gownaris, N. J., Heerhartz, S. M., & Monaco, C. J. (2016). Personality, foraging behavior and specialization: Integrating behavioral and food web ecology at the individual level. *Oecologia*, 182, 55–69. <https://doi.org/10.1007/s00442-016-3648-8>
- Urszán, T. J., Garamszegi, L. Z., Nagy, G., Hettyey, A., Török, J., & Herczeg, G. (2018). Experience during development triggers between-individual variation in behavioural plasticity. *Journal of Animal Ecology*, 87, 1264–1273. <https://doi.org/10.1111/1365-2656.12847>
- van den Hout, P. J., van Gils, J. A., Robin, F., van der Geest, M., Dekinga, A., & Piersma, T. (2014). Interference from adults forces young red knots to forage for longer and in dangerous places. *Animal Behaviour*, 88, 137–146. <https://doi.org/10.1016/j.anbehav.2013.11.020>
- Van Oers, K., Drent, P. J., De Goede, P., & Van Noordwijk, A. J. (2004). Realized heritability and repeatability of risk-taking behaviour in relation to avian personalities. *Proceedings of the Royal Society B: Biological Sciences*, 271, 65–73.
- van Overveld, T., & Matthysen, E. (2010). Personality predicts spatial responses to food manipulations in free-ranging great tits *Parus major*. *Biology Letters*, 6, 187–190. <https://doi.org/10.1098/rsbl.2009.0764>
- Wilson, A. J. (2018). How should we interpret estimates of individual repeatability? *Evolution Letters*, 2, 4–8. <https://doi.org/10.1002/evl3.40>
- Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27, 452–461. <https://doi.org/10.1016/j.tree.2012.05.001>

## Appendix

**Table A1**

Results from analyses comparing juveniles and adults in exploratory behaviour for juveniles in 2019

Predictors	Exploration speed (log cm/s)
	Estimates (95% CI)
Intercept	0.55 (0.49–0.60)
Age (Juvenile)	–0.00 (–0.10–0.10)
Sigma: Age (Adult)	–2.09 (–2.27––1.88)
Sigma: Age (Juvenile)	–1.67 (–1.91––1.37)
Marginal $R^2$ /Conditional $R^2$	0.005/0.59
N	86 (adult = 57, juvenile = 29)

CI: credible interval.



**Table A2**

Comparison of repeatability and variance components in exploration speed by age group for juveniles in 2019

Variance and ratio	Age groups		Difference $\Delta$
	Juveniles median (95% CI)	Adults median (95% CI)	Adult – Juvenile median (95% CI)
Repeatability ( $R$ )	0.44 (0.06; 0.69)	0.71 (0.54; 0.82)	0.27 (–0.03; 0.66)
Within-individual variance ( $V_w$ )	0.04 (0.02; 0.07)	0.02 (0.01; 0.02)	<b>–0.02 (–0.05; –0.01)</b>
Among-individual variance ( $V_i$ )	0.03 (0.00; 0.06)	0.04 (0.02; 0.06)	0.01 (–0.03; 0.04)

Magnitude of the difference in variability between age groups is shown with  $\Delta$ . Posterior medians and 95% credible intervals (CI) estimated from a Bayesian mixed model. Bold font indicates credible intervals do not overlap with zero.

**Table A3**

Results from analyses comparing juvenile and adults in exploratory behaviour for juveniles in 2021

Predictors	Exploration speed (log cm/s)
	Estimates (95% CI)
Intercept	0.55 (0.49–0.60)
Age (Juvenile)	–0.04 (–0.14–0.05)
Sigma: Age (Adult)	–2.08 (–2.26––1.88)
Sigma: Age (Juvenile)	–1.66 (–1.87––1.41)
Marginal $R^2$ /Conditional $R^2$	0.01/0.58
$N$	90 (adult = 57, juvenile = 38)

CI: credible interval.

**Table A4**

Comparison of repeatability and variance components in exploration speed by age groups for juveniles in 2021

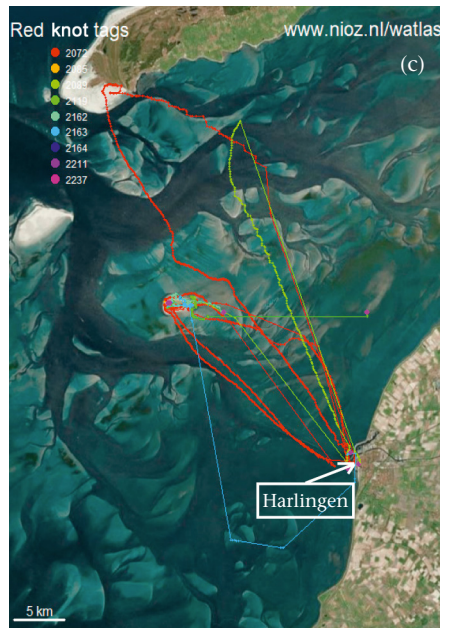
Variance and ratio	Age groups		Difference $\Delta$
	Juveniles median (95% CI)	Adults median (95% CI)	Adult – Juvenile median (95% CI)
Repeatability ( $R$ )	0.44 (0.11; 0.67)	0.71 (0.54; 0.82)	0.26 (–0.02; 0.61)
Within-individual variance ( $V_w$ )	0.04 (0.02; 0.06)	0.02 (0.01; 0.02)	<b>–0.02 (–0.04; –0.01)</b>
Among-individual variance ( $V_i$ )	0.03 (0.01; 0.06)	0.04 (0.02; 0.06)	0.01 (–0.01; 0.04)

Magnitude of the difference in variability between age groups is shown with  $\Delta$ . Posterior medians and 95% credible intervals (CI) estimated from a Bayesian mixed model. Bold font indicates credible intervals do not overlap with zero.

2019



2020



**Figure A1.** (a, c) Locations of tagged juvenile red knots in the Wadden Sea and (b, d) juvenile red knot eating algae in Harlingen harbour in 2019 and 2020. Photo credits: Eus de Groot.