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Ersoy, Selin S

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Exploration in red knots

the role of personality in the expression of individual behaviour across contexts

Selin Ersoy

Colophon

The research presented in the thesis was conducted at the Department of Coastal Systems at the NIOZ Royal Netherlands Institute for Sea Research, ‘t Horntje (Texel), The Netherlands, according to the requirements of the Graduate School of Science and Engineering (GSSE), University of Groningen, The Netherlands.

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Exploration in red knots

the role of personality in the expression of individual behaviour across contexts

PhD thesis

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by

Selin Ersoy

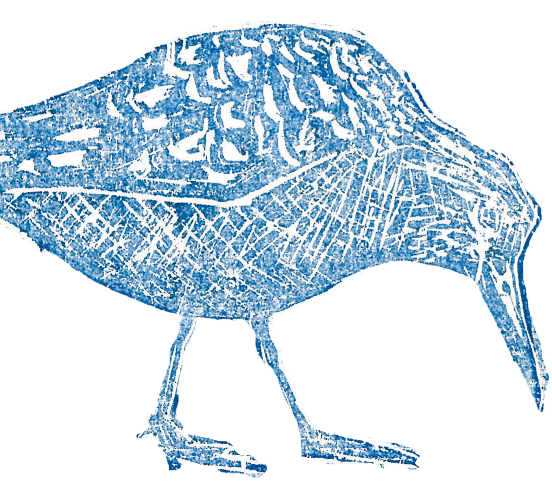
born on 6 June 1990
in Konak, Turkey

Supervisors
Prof. T. Piersma
Prof. A.G.G. Groothuis

Co-supervisor
Dr. A.I. Bijleveld

Assessment Committee
Prof. C. Both
Prof. J.Z. Shamoun-Baranes
Prof. M. Dammhahn

Contents



CHAPTER 1

General Introduction

Selin Ersoy

Intraspecific variation in behaviour

Biological diversity has been explained by mutations and natural (and sexual) selection ever since Darwin (Darwin, 1859). While only the differences between different genus and taxa have been discussed from adaptative perspective at first, it became increasingly popular to discuss the differences between closely related species by the 1960s (Lack, 1961) and different populations of the same species by the 1980s (Endler, 1986). Since the 1990s, it has become possible to study and discus differences between individuals in the same population (Wilson, 1998). However, researchers were still mainly interested in the average behaviour of a population, and intraspecific variation in behaviour was assumed to be ‘noise’ in the data. At the start of the 2000s, it became clear that individual differences in behaviour can be consistent over time and/or across different contexts (e.g., studies under the framework of ‘animal personality’, ’temperament’, or ‘coping style’) and hence, are likely to have consistent ecological and evolutionary consequences (Gosling, 2001; Sih et al., 2004).

Individuals of all ages and sexes show behavioural traits that are consistent over time, but differ across individuals, and affect the expression of behaviours in different situations (hereafter ‘personality traits’; Réale et al., 2007; Stamps and Groothuis, 2010a). Comparative psychologists and behavioural ecologists have shown that animals differ in personality traits, and that it is a common, cross-taxonomic phenomenon in nature (e.g., humans: Costa and McCrae, 1992; mammals: Koolhaas et al., 1999; Réale et al., 2000; birds: Verbeek et al., 1994; reptiles: Cote et al., 2010a; fish: Bell and Sih, 2007; insects: Tremmel and Müller, 2012; crustaceans: Bridger et al., 2015). The most common personality traits reported in the literature are boldness, exploration, dominance, aggressiveness, and sociability (Réale et al., 2010a) and these traits are commonly quantified in laboratory settings where conditions can be controlled and/or manipulated. In some cases, these personality traits correlate with each other in reoccurring patterns (e.g., positive relationship between boldness and exploration) and create ‘behavioural syndromes’ (Sih et al., 2004). Personality traits often also correlate with ecologically relevant behaviours such as social information use (Kurvers et al., 2010), foraging site fidelity (Harris et al., 2019), and habitat use (Boon et al., 2008).

The field of animal personality provides a flexible concept that can explain variation in behaviour even when the behaviour is not ‘optimal’ in some cases (Biro and Stamps, 2008; Réale et al., 2010b). For example, theories based on cost-benefit trade-offs predict that bolder or faster exploring individuals may receive a benefit by outcompeting conspecifics to gain better access to resources, but may also take more risks which makes them more susceptible to predation (Bremner-Harrison et al., 2004; Carter et al., 2010). These theories have been proposed to explain optimization of behaviour from individual level (vs. population level) and describe the “sub-optimal” behavioural tendencies associated with animal personalities (Dall et al., 2004; Dingemanse and Wolf, 2010; Wolf and Weissing, 2010). Different personality traits are expected to represent behavioural phenotypes of equivalent fitness (Wright et al., 2018) and may be expected to show different cost-benefit trade-offs. Therefore, the identification of the variation in consistent behavioural traits, understanding the origin (ultimate cause) of the variation, and how it is maintained (proximate cause) in natural populations should be of high relevance to behavioural ecologists (Hogan, 2017; Laland et al., 2015; Tinbergen, 1963).

Development of personality traits

Even if animals are born and raised under the same conditions, they may still show individual differences in behaviour (Bell et al., 2009; Edenbrow and Croft, 2011; Sinn et al., 2006). For example, genetically identical fish studied in captivity under highly standardized conditions still developed personality traits (Amazon molly, *Poecilia formosa,* Bierbach et al., 2017). How individual differences in personality traits can occur even when every individual (or genotype) is exposed to the same conditions is a question that is still unanswered (Stamps and Groothuis, 2010a; Stamps and Krishnan, 2014, 2017). It has been suggested that individual differences in experience (also reflecting environmental influences) induce positive feedback loops that gradually fix the behaviour of individuals on different developmental trajectories (Dall et al., 2012; Sih et al., 2015). This may be why in the wild, personality traits are found to be more stable in adults than in juveniles (Edenbrow and Croft, 2011; Fratkin et al., 2013; Costa and McCrae, 1994).

An animal’s personality trait can develop during ontogeny as a result of individual experiences (Stamps and Groothuis, 2010a, 2010b). For example, Madagascar hissing cockroaches *Gromphadorhina portentosa* became shyer when they were repeatedly exposed to predator attacks compared to individual with no such experience (McDermott et al., 2014). While studies about the role of experience and learning in developing personality traits has advanced in the last decade (since Stamps and Groothuis, 2010b), it is still unknown how the relation between the genes, epigenetic factors, maternal effects, and personal experiences affect the development of personality (Cabrera et al., 2021).

Feedback between exploration and foraging behaviour

Foraging is essential for most organisms as it directly influences fitness. Individuals can differ in their methods of detecting prey (hereafter 'foraging tactics') if food items induce differences in the behaviours needed to collect them (e.g., Newsome et al., 2009). By foraging for a certain food type, an individual can improve its foraging efficiency to detect, capture, and process this specific food (Heinrich, 1976). The feedback between foraging tactics, food type, and foraging efficiency can create consistent variation in foraging tactics between members of the same population (Luttbeg and Sih, 2010; Sih et al., 2015). The term individual niche specialisation (particularly in terms of behavioural traits associated with foraging behaviour and diet choice) has been used to describe consistent individual variation in resource use (Araújo et al., 2011; Bolnick et al., 2002; Ceia and Ramos, 2015; Odling-Smee et al., 2013).

Animal personality and individual niche specialisation are therefore largely concerned with the same behavioural properties (i.e., among individual consistency) but are applied in different contexts (Bergmüller and Taborsky, 2010; Carneiro et al., 2017; Toscano et al., 2016). For example, exploratory personality (typically measured in open-field test, e.g., Verbeek et al., 1994) may relate to energetic traits (Careau et al., 2008), resource use (Gharnit et al., 2020; van Overveld and Matthysen, 2010) and digestive morphology (Bijleveld et al., 2014; Fürtbauer, 2015). These relationships are likely linked to dietary differences – and thus foraging behaviour – between individuals, and the feedback between foraging behaviour and its dietary outcome is likely to influence the maintenance of exploratory behaviour of an individual.

The spatiotemporal distribution and availability of specific resources can influence the emergence of behavioural traits. Through its role in the expression of a behaviour, the environment influences which behavioural phenotypes are exposed to selection and modified during development (Piersma and van Gils, 2011; West-Eberhard, 2005). This is particularly prevalent when different prey species vary in habitat or behaviour (e.g., Ringler, 1983). For example, passerine birds such as great tits, *Parus major*, select different habitats depending on their chosen prey type, searching for food both on the ground (e.g., nuts) and in the trees (e.g., caterpillars; Hinde, 1952).

Eurasian oystercatchers, *Haematopus ostralegus*, modify their speed of movement when using two different foraging tactics to catch different prey types: visual foraging (quicker movements) to catch worms, *Nereis diversicolor,* and tactile foraging (slower movements) to dig up harder-shelled prey, *Macoma balthica,* (Ens et al., 1996). It is likely that the availability and density of the specific resource at the time that young animals start searching food by themselves influences which behavioural tactic they will be using. Through experience in catching certain prey type, individuals can specialise in a corresponding foraging tactic.

Linking personality traits to movement patterns

Movement as it is expressed at an individual level is a measurable result of many underlying structural, physiological, and behavioural mechanisms, which are triggered by environmental context (Spiegel et al., 2017; pers. com. A. I. Bijleveld). As all animals are mobile at some stage in their lives, to procure food, hide from predators, seek mating opportunities, and migrate between habitats (Heape, 1931), local or global movement patterns are great way to study consistent individual differences across contexts. Studying movement differences between individuals in the wild has become possible with technological advances in bio-logging techniques (Nathan et al., 2022; Shaw, 2020) and movement patterns have been shown to vary within species, within populations, and also within individuals (Shaw, 2020). In fact, studies show that individuals are highly repeatable in their movement patterns so that one could define ‘spatial personalities’ (Stuber et al., 2022). The framework of animal personality and that of movement ecology can complement each other because consistent differences between behaviour can explain how individuals adjust their behaviour in response to spatiotemporal variation in resources (Spiegel et al., 2017; Webber et al., 2020).

Links between personality and movement patterns have been established for boldness and exploration at both small and large scales of space use through theoretical models (e.g., DiNuzzo and Griffen, 2020) and empirical findings (e.g., Schirmer et al., 2019). Foraging-related movement patterns such as site fidelity (Harris et al., 2019), home range size (Michelangeli et al., 2021), and habitat selection (Boon et al., 2008; Leclerc et al., 2016) have been linked to experimentally measured boldness and exploration and they were found to explain how individuals trade off finding new resources and exploiting known resources (Patrick et al., 2017). Experimental studies showed that consistent exploratory behaviour in captivity is also consistent in the field as faster exploring blue tits were more likely to find new feeders in the natal forest than slower exploring blue tits *Cyanistes caeruleus* (Herborn et al., 2010). Dispersal has been linked to personality in multiple studies showing that bolder or faster exploring individuals disperse more readily or further than shyer or slower exploring individuals (e.g., Cote et al., 2010b; Dingemanse et al., 2003). A handful of studies show correlations between personality traits and migratory behaviour; bolder and more explorative individuals were more likely to migrate (partially migrating roach *Rutilus rutilus* Chapman et al., 2011; warblers Mettke-Hofmann et al., 2005) and visit more new sites during migration (great knots, *Calidris tenuirostris*, Chan, 2021). Since exploration as a personality trait is measured by movement traits in controlled settings, it is likely that exploration is associated with movement at both small and large scales in the wild (Bijleveld et al., 2014).

Adaptation to environmental change

From an adaptive perspective, it would be optimal if individuals constantly adjust their behaviour according to current conditions. This could still result in behavioural variation among individuals in the population but without the within-individual consistency in behaviour. However, individual differences in behaviour can have limited flexibility with lower within-individual variation (Réale et al., 2007). This was suggested to be due to the costs of flexibility in a world that changes continuously regardless of an individual's actions or behaviours (Dall et al., 2004). Behavioural responses to changes in the environment are likely to increase the chance of making a mistake or, in case of giving a correct response to a certain situation, take a relatively long time to become established, which can have survival costs for the individual (Dall et al., 2004; Sih et al., 2004).

Consistent among-individual differences in behaviours can help populations respond to changes in the environment through fluctuating selection (Dall et al., 2004; Dingemanse and Wolf, 2010). Studies on animal personality suggest that among-individual variation in behaviour may emerge in the course of evolution (Dall et al., 2012; Nicolaus et al., 2012; Wolf and Weissing, 2010). For example, exploratory individuals are better at locating new food sources (e.g., van Overveld and Matthysen, 2010) and these individuals may be doing better than non-explorers if the environment changes and regular food sources fail (e.g., negative frequency dependent selection; Christie et al., 2018; Kilgour et al., 2018; Wolf and McNamara, 2012). If personality traits evolve jointly with morphological traits, adaptation of personality to environmental change can further facilitate speciation (Dall et al., 2004; Wilson, 1998).

Aims of the thesis

The aim of this thesis was to identify the variation in consistent behavioural traits, understanding the origin of the variation, and how it is maintained in natural populations. (1) To identify the variation in exploration as a personality trait, I investigated the connection between exploration, foraging behaviour, and diet. (2) To understand the origin of the variation in exploration, I investigated how relation between exploration and diet develops during ontogeny. Specifically, I asked if consistency in exploration behaviour in juveniles increases with the amount of foraging experience. (3) To understand how variation in exploration is maintained in natural populations, I investigated individual movement patterns in different contexts in the wild. (4) To understand whether exploration measured in experimental setups could be extrapolated to a larger and more complex context, I investigated the link between exploration and migratory behaviour.

Study system: red knot

The red knot, *Calidris canutus*, is a long-distance migratory shorebird that breeds in the high arctic tundra (latitude 62–80ºN) in June and inhabits intertidal mudflats in temperate and tropical zones during the rest of the year (Piersma, 2007). There are six subspecies of red knot (*rufa, canutus, islandica, piersmai, rogersi, roselaari;* Figure 1) that are distributed around the globe and distinguished by their breeding and non-breeding ranges, and their migratory behaviour (Piersma, 2007). Population sizes vary largely between subspecies (<20,000 to >400,000 individuals; Wetlands International, 2021) but most have declined in numbers in the last decades (Baker et al., 2004; Boyd and Piersma, 2001). These declines are thought to be caused by a phenological mismatch in the timing of breeding due to arctic warming (van Gils et al., 2016) and/or anthropogenically induced habitat changes in the nonbreeding grounds (Rakhimberdiev et al., 2015).

Our research group has been studying red knots for several decades, providing a thorough understanding of the species' diet, habitat preferences, survival rates, migration routes, and behavioural and morphological flexibilities and limitations (Bijleveld et al., 2014; van Gils et al., 2005; Kok et al., 2019; Mathot et al., 2017; Oudman et al., 2016; Piersma et al., 1994). Foraging behaviour and diet has been particularly well studied in red knots: they ingest their prey as a whole, which makes it easy to calculate intake rate (van Gils et al., 2007); shell materials can be found in the droppings after digestion, which allows identification of prey species (Dekinga and Piersma, 1993); and an ultrasonographic method was developed, which allows individual measurements of a digestive organ size (Dietz et al., 1999). In addition, it is possible to keep red knots in captivity, and the experimental shorebird facility at NIOZ Royal Netherlands Institute for Sea Research was designed to conduct experimental studies in controlled settings. Hence, my PhD thesis benefitted immensely from established field methods, data collection, and facilities and extends the work of previous researchers (Bijleveld, 2015; van Gils, 2004; Kok, 2020; Oudman, 2017; Piersma, 1994; Zwarts, 1997).

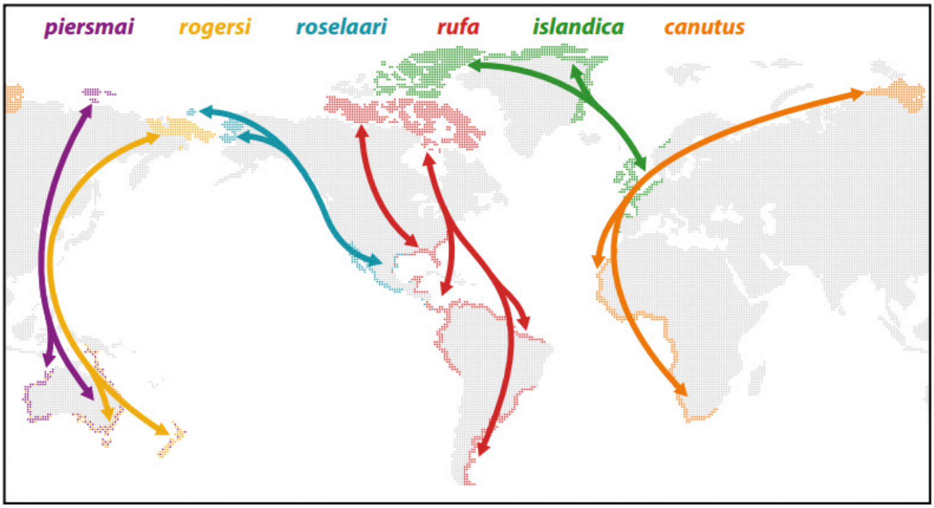


Figure 1. Global distribution of red knots. Each of six subspecies and their general migration routes between breeding and wintering areas are indicated by colour. Figure is from Jesse Conklin (Conklin et al., 2022).

Study population and area: red knots in the Wadden Sea

I studied the *Islandica* subspecies of red knots that breeds in the high Arctic of northern Greenland and north-east Canada and winters in the large mudflat areas of western Europe (Piersma, 2007). I collected field data from August 2018 to October 2020 around the island Griend in the western Dutch Wadden Sea (53°15’N, 5°15’E; Figure 2).

Griend and the surrounding mudflats are used by many shorebird species. Particularly during summer months, right after migration from the breeding grounds, shorebirds use Griend to moult their feathers (Piersma et al., 1993).

While red knots feed mostly on spiders and small insects and sometimes on plant material and insect larvae in the breeding grounds (Delany et al., 2009), red knots mainly use tactile foraging and feed on hard-shelled mollusc species found in intertidal substrates in the wintering grounds (Piersma, 2007). Red knots crush prey items in their muscular stomach called gizzard. Gizzard mass is flexible and increases with decreasing prey quality (Dekinga et al., 2001), which is measured by the ratio between mollusc flesh and shell mass (van Gils et al., 2007). Red knots show high individual consistency in exploration behaviour in captivity (Bijleveld et al., 2014; Kok et al., 2019). Experimentally measured exploration behaviour negatively correlates with gizzard mass (Bijleveld et al., 2014), and individuals with small gizzards have larger space use and travel between the Netherlands, England, and Germany, whereas birds with larger gizzards tend to stay in the Dutch Wadden Sea. Experimental manipulation of gizzard mass does not change individual exploratory behaviour (Bijleveld et al., 2014) nor diet choice (Mathot et al., 2017).

Figure 2. Map of the Wadden Sea. The orange square shows my study area around Griend.

My thesis extends previous studies about exploration behaviour in red knots by Allert Bijleveld, Kim Mathot, and Eva Kok, which were conducted at the experimental shorebird facility at the NIOZ. Thanks to them, measuring exploration of red knots in captivity is well established (Bijleveld et al., 2014; Kok et al., 2019, Figure 3). To be able to identify intraspecific variation in exploration in red knots (Aim 1), I wanted to eliminate the effects of captivity and relate experimentally quantified personalities to individual post-release movement and foraging patterns. Therefore, together with my supervisor Allert Bijleveld, we first adapted the existing experimental setup to be used in the field.

Figure 3. Indoor arena to score exploratory behaviour in captivity. The floor of the unit consists of salt water of 30 cm height and 5 identical sand patches 1m x 1m x 35cm for birds to explore in a room measuring 7m x 7m x 3m.

Exploration assays at the field-site

I used a mobile experimental unit to measure exploratory behaviour under controlled conditions at the field site (Figure 4). The mobile field setup was very similar to the indoor setup at the NIOZ but was smaller (mobile 2m x 2m x 1m, indoor 7m x 7m x 3m). Both the mobile and indoor setup consisted of a sea-water basin and wet sand patches for red knots to “explore”. Before using it for sand patches, we sieved the sand to remove shells and other potential food items to avoid triggering red knots’ searching behaviour. Essentially, our setups resemble an “open-field test” traditionally used to assay exploratory behaviour and where a bird experiences a novel environment for the first time (Hall and Ballachey, 1932; Perals et al., 2017; Verbeek et al., 1994).

Figure 4. Mobile tent setup to score exploratory behaviour at the field site. The floor of the unit consists of sea water of 20 cm height and 4 identical sand patches 61cm x 40cm for birds to explore, tent measures 2m x 2m x 1m.

Thesis outline

In this thesis, I combined personality assays in controlled settings with field observations of foraging tactics, stable isotope for diet analysis and migration timing, and movement tracking to investigate the associations between exploration, foraging, diet, and movement. The chapters of my thesis are organized as self-contained manuscripts that have been or will be submitted to peer-reviewed journals. This inevitably leads to some overlap among the chapters, especially in the methods section of each manuscript. Specifically, my thesis contains the following chapters:

Variation in foraging tactics and diet are usually attributed to differences in morphology, experience, and prey availability. However, personality traits may be linked to foraging strategies because of different energetic cost and gain associated with behaviour and its outcome. In **Chapter 2**, we assessed how exploration measured in controlled settings predicts foraging tactics and diet in the wild. We predicted that faster exploring red knots use faster visual foraging and feed on high quality soft prey (shrimp) while slower exploring red knots use slower tactile foraging and feed on lower quality hard-shelled prey (molluscs).

Behavioural traits that are consistent within, but vary between individuals, can develop through experience during development. Exploration has been shown to associate with foraging strategies and diet, but how these associations emerge during development remains unclear. In **Chapter 3**, we compared repeatability and consistency of exploratory behaviour and diet of juvenile and adult red knots after their arrival from breeding grounds to wintering grounds. We asked whether the experience of juveniles on a marine diet was correlated with consistency of exploratory behaviour. We predicted that juveniles show a more diverse diet and are less repeatable in exploration with larger within-individual and smaller among-individual variation than adult red knots.

To what extent personality traits measured in artificial context can predict movement behaviour in the wild may depend on the environmental cues under natural conditions. Animals that forage both day and night provide a good opportunity to test whether personality-related movement patterns are context dependent such as visual foraging in view of flock mates and the possibility of aerial predation during the day while these threats and cues are absent at night. In **Chapter 4**, we assessed exploration of red knots in controlled settings and then released the same birds with ATLAS transmitters with continuous fine-scale tracking to compare movements during the day and night. We predicted that faster exploring red knots move more within and between foraging patches than slower exploring red knots at night while the differences between individuals according to their exploration score may be absent during the day.

Individuals living in groups can benefit from using social information about foraging opportunities. Interestingly, individuals can differ consistently in how they locate the food (i.e., finding food by themselves or by observing foraging success of others) and this can be linked to their personality traits. In **Box 1**, we present experiments with captive red knots on the relationship between exploration and foraging success. We first assayed exploration of red knots individually in controlled settings and then we tested whether the speed of finding hidden food would differ between individuals according to their exploration and whether the speed of finding food of those individuals would differ when tested individually or in a group. We predicted that faster-exploring individuals are also faster in finding food than slower explorers, both when tested individually and in a group. And we predicted that all individuals regardless of exploration score would find food faster when in a group than tested individually.

Timing and patterns of migration, even within populations that share breeding sites, show large variation between individuals. Arrival timing of red knots in the Dutch Wadden Sea can be related to later departure from the breeding grounds or the number of stopovers used during migration from breeding to wintering grounds. Exploration has been linked to larger scale movement and also may be linked to migration timing in red knots. In **Chapter 5**, we investigated the link between red knots' post-breeding arrival timing in the Dutch Wadden Sea and exploratory behaviour. Because males take care of the broods after hatching, we predicted that females arrive earlier than males. We predicted that faster (vs. slower) exploring red knots arrive later in the Wadden Sea because they are expected to use stopovers in different locations before arriving to the wintering grounds.

In **Chapter 6**, the General Discussion, I summarise the main findings from the previous chapters and link them to individual behavioural differences in general. I discuss some of the main conclusions from different perspectives and limitations of my study. I also discuss what new ideas may emerge from this thesis and suggest directions for future studies.

Acknowledgements

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CHAPTER 2

Exploration speed in captivity predicts foraging tactics and diet in free-living red knots

Selin Ersoy, Christine E. Beardsworth, Anne Dekinga, Marcel van der Meer, Theunis Piersma,
Ton G. G. Groothuis, Allert I. Bijleveld

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Abstract

Variation in foraging tactics and diet are usually attributed to differences in morphology, experience, and prey availability. Recently, consistent individual differences in behaviour (personality) have been shown to be associated with foraging strategies. Bolder or more exploratory individuals are predicted to have a faster pace-of-life and offset the costs of moving more or in risky areas, with higher energetic gains by encountering profitable foraging opportunities and prey. However, the relationship between personality, foraging, and diet is poorly understood. We investigated how exploratory behaviour in red knots *Calidris canutus* is associated with foraging tactics and diet by combining laboratory experiments, field observations, and stable isotope analysis. First, we developed a mobile experimental arena to measure exploration speed in controlled settings. We validated the method by repeated testing of individuals over time and contexts. This setup allowed us to measure exploratory personality at the field site, eliminating the need to bring birds into captivity for long periods of time. After releasing birds within days of their capture, we asked whether exploration speed was associated with differences in foraging tactics and diet in the wild. We found that tactile foraging red knots mainly caught hard-shelled prey that are buried in the sediment, whereas visual foraging knots only captured soft preys located close to or on the surface. We also found that faster explorers showed a higher percentage of visual foraging than slower explorers. By contrast, morphology (bill length and gizzard size) had no significant effect on foraging tactics. Diet analysis based on δ15N and δ13C stable isotope values of plasma and red blood cells confirmed our field observations with slower explorers mainly consumed hard-shelled prey while faster explorers consumed more soft than hard-shelled prey. Our results show that foraging tactics and diet are associated with a personality trait, independent of morphological differences. We discuss how consistent behaviour might develop early in life through positive feedbacks between foraging tactics, prey type, and foraging efficiency.

Introduction

Among-individual variation in foraging behaviour and diet has been demonstrated across a wide range of taxa (also called ‘individual niche specialisation’; e.g., birds in Harris et al., 2014; insects in Heinrich, 1976; mammals in Tinker et al., 2007). This variation can be attributed to differences in prey availability and habitat, the cost-benefit ratio of potential prey, and morphological variation among predators (Hinde, 1959; Kerfoot, 1967; Robinson and Holmes, 1982). Collectively, variation in foraging behaviour provides a basis for adaptation and speciation (Dill, 1983; Knudsen et al., 2010; van Valen, 1965), therefore, understanding the factors that cause and maintain among-individual variation in foraging behaviour is an important topic in ecology (Araújo et al., 2011; Bolnick et al., 2003).

Among-individual variation in foraging behaviour, such as in methods of detecting prey (hereafter foraging tactics), can develop during ontogeny through differences in experience. This is particularly prevalent when different prey species vary in habitat or behaviour (e.g., Ringler, 1983). By foraging for a certain food type, an individual can improve its foraging efficiency to detect, capture, and process it (Heinrich, 1976). This feedback between foraging tactics, food type, and foraging efficiency can create consistent variation in foraging behaviour between members of the same population (O’Brien et al., 1989). Among-individual variation in foraging tactics is often attributed to morphological differences, such as feeding apparatus. For example, proboscis length is negatively related to diet diversity in multiple species of bumblebee (Goulson and Darvill, 2004). Additionally, shorter-billed oystercatchers *Haematopus ostralegus* (Durell et al., 1993) and bar-tailed godwits *Limosa lapponica* (Zwarts, 1985) forage on prey closer to or on the surface, whereas longer-billed individuals find prey buried in the sand (reviewed in Durell, 2000). Variation in morphology of the gut has also been related to diet choice (Piersma et al., 1999). In brachyuran crabs, for example, stomach volume is inversely correlated with diet quality (Griffen and Mosblack, 2011).

Foraging behaviour and diet can also be associated with “consistent among-individual differences in behaviour” (also known as personality, behavioural syndromes, or temperament, Gosling, 2001; Sih et al., 2004; Toscano et al., 2016). For example, shyer wandering albatrosses *Diomedea exulans* (showing little response to a novel object) have larger foraging patches that they exploit for longer period of time than bolder individuals (Patrick et al., 2017). Shyer barnacle geese *Branta leucopsis* scrounge on the food discoveries of bolder geese (Kurvers et al., 2010). Faster exploring great tits *Parus major* have also been shown to search food in different areas and move greater distances in search of prey (van Overveld and Matthysen, 2010) and faster exploring blue tits *Cyanistes caeruleus* are more likely to find new feeders in the wild (Herborn et al., 2010). According to the pace-of-life framework, explorative and bolder individuals in the "fast" pace-of-life are expected to be less risk aversive, behave less cautiously, and have higher energy expenditure (Réale et al., 2010). The increased energy expenditure of exploratory and bold individuals (reviewed in Careau et al., 2008) could be compensated by an increased energy gain associated with their foraging behaviour. For example, even though there is a high energetic cost to exploration (Careau and Garland, 2012), individuals are also more likely to encounter profitable foraging opportunities and high-quality prey types (e.g. Herborn et al., 2010). High cost of exploration and boldness may then have potentially high foraging gain (Bell and Sih, 2007; Brydges et al., 2008). How variation in diet and foraging tactics relate to personality is poorly understood and studying this in free-living animals can help us to understand the causes and consequences of personality traits (Araújo et al., 2011; Réale et al., 2010; Wolf and Weissing, 2012).

The red knot *Calidris canutus* is a useful model system to study the relationship between individual foraging tactics, diet, morphology, and exploratory personality. On the mudflats, red knots are known to be mollusc specialists and mainly use tactile foraging to find hard-shelled prey buried in the sediment, such as edible cockles *Cerastoderma edule* (Piersma et al., 1998). Field observations show that red knots can also opportunistically feed on high quality soft prey located on the surface, such as brown shrimp *Crangon crangon* (Zwarts et al., 1992). Although the specific foraging tactic used to capture soft prey has not been reported for red knots, other shorebird species use visual foraging for this prey type (reviewed in Durell, 2000). Under laboratory conditions, individual red knots are consistent in their exploration of a novel environment (Bijleveld et al., 2014; Kok et al., 2019). Following the pace-of-life framework, we may expect that more exploratory red knots eat more high-quality prey and thus use different foraging tactics. Indeed, more exploratory knots have been shown to have smaller gizzards (muscular stomach) indicating a higher quality diet (Bijleveld et al., 2014). However, a direct link between personality and diet has not yet been demonstrated.

Here, by combining laboratory experiments, field observations, and stable isotope analyses, we ask whether faster exploring red knots eat more high-quality prey than slower explorers, and whether this coincides with the use of different foraging tactics. We first developed a method to measure exploration speed in a controlled setting at the field site shortly after catching, removing the need to transport birds to indoor facilities and keeping them in captivity for longer periods (as in previous studies of this species Bijleveld et al., 2014; Kok et al., 2019). We were then able to catch, assay exploratory personality, and release red knots within a few days after capture (with a WATLAS transmitter, Beardsworth et al., 2021; Bijleveld et al., 2021). Shortly after their release, we tracked and re-sighted the same individuals on the mudflats, video-recorded their behaviour to later calculate the percentage of tactile or visual foraging tactics. We then investigate whether foraging tactic use was related to exploration speed, gizzard size, and bill length, and predicted that faster exploring knots use more visual foraging, have smaller gizzards, and/or shorter bills. We also investigated the relationship between exploration speed and diet using isotope analysis based on δ15N and δ13C stable isotope values from blood samples and predicted that isotopic signatures of faster exploring red knots reflect more soft prey in the diet than slower explorers. To assess the changes in diet over time, we compared isotopic signatures of blood plasma that integrate diet across ca. 14 days and of red blood cells that integrate diet signatures across ca. 45 days (Klaassen et al., 2010).

Materials and Methods

Study site and animals

We studied the *islandica* subspecies of red knots *Calidris canutus* which breeds in the high Arctic of northern Greenland and north-east Canada and winters in the large mudflat areas in western Europe (Piersma, 2007). We collected field data from September 2018 to October 2019 in the western Dutch Wadden Sea (53°15’N, 5°15’E) and conducted laboratory experiments at the experimental shorebird facility in the NIOZ Royal Netherlands Institute for Sea Research (53°00’12”N, 4°47’23”E). All necessary permits to catch, handle, tag, test, and keep red knots were granted to the NIOZ by the Dutch law and regulation under protocol number NIOAVD8020020171505.

Captures, sampling, housing, and personality tests

In total, 283 adult red knots were caught during four catching events between 14 August - 19 September 2018, and 1 August - 6 September 2019 in new moon periods by means of mist netting in the western Dutch Wadden Sea. Red knots were given a numbered metal ring for individual identification and their biometrics were measured (e.g., bill length). From the brachial vein a small blood sample (~30 µL) was taken for stable isotope analysis. Blood samples were separated into plasma and red blood cells by centrifugation (12min, 7000rpm) and pipetted into separate glass vials and immediately stored in a freezer at the field site. At NIOZ, samples were stored at -20 ºC until further analysis. These samples were used to determine the stable carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) from plasma and red blood cells separately. 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 x 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. Red knots which arrived recently in the Wadden Sea from Arctic breeding grounds with a terrestrial isotopic signature (Dietz et al., 2010) were excluded from these diet analyses ($N_{excluded}$=23 from plasma, $N_{excluded}$=46 from red blood cells).

The stable isotope ratios of the food sources from the study area were taken from Waddensleutels program that samples intertidal macrofauna across the Dutch Wadden Sea (Christianen et al., 2017). To discriminate the relative contribution of different prey items in the analysis, we grouped hard-shelled prey (common cockle*,* Mean ± SD: δ15N, 11 ± 1.38; δ13C, –18.69 ± 1.26, *N*=341 and Baltic tellin *Limecola balthica,* Mean ± SD: δ15N, 11.08 ± 2.5; δ13C, –16.03 ± 2.06, *N*=151) as well as soft prey (brown shrimp*,* Mean ± SD: δ15N, 12.78 ± 1.04; δ13C, –14.9 ± 1.93, *N*=119 and polychaete worm *Nephtys hombergii,* Mean ± SD: δ15N, 14.24 ± 1.43; δ13C, –14.86 ± 0.82, *N*=39). By comparing the stable isotope compositions of the plasma and red blood cells with that of potential food items, we were able to analyse the relative contributions of different food items to the diet of birds.

Gizzard size was measured by A.D. using an ultrasound scanner (model Aquilla, Pie Medical Benelux, Maastricht, The Netherlands) as described by Dietz et al. (1999). Measurements of gizzard width and height (cm) were taken to estimate gizzard size in grams using formula -1.09+3.78*(height*width, Bijleveld et al., 2014). Gizzard size was measured within 1 day after capture to be indicative of a bird's organ mass while free-living (Dekinga et al., 2001). Right after ultrasound measurements, the birds were moved to temporary outdoor aviaries of 2m x 0.75m x 0.4m (LxWxH) made of linen with a net floor covered in dried hemp (Hemparade). These aviaries were placed outside on natural sand/grass and provided with *ad libitum* food (live and dried mealworms) and water (freshwater and seawater). Group sizes in the aviaries were between 8 to 12 birds.

Exploratory personality was measured as response to a novel environment in two different setups: 1) a new method to measure exploration speed within 24 hr after capture in the field-based mobile arena, and 2) an established method to measure explorative behaviour of captive red knots in the lab-based indoor arena (Bijleveld et al., 2014).

Mobile arena

To score the exploration speed of captive red knots at the field site, we used a pyramid shaped mobile unit of 2m x 2m x 2m (referred to as "mobile arena"; Suppl. Fig. S1). The floor of the unit consists of seawater of 20 cm depth in which four identical trays with wet sand (61cm x 40cm x 25cm) were situated. Birds could explore these artificial patches in which no food was offered. A GoPro (Hero Black) camera was mounted at the ceiling to record the movement trajectories at 2 frames s^{-1} and another GoPro (Hero+) camera recorded behaviour from the side at 30 frames s^{-1} (Suppl. Video S1). To standardise the procedure and motivate birds equally for the personality tests (like Bijleveld et al., 2014), we placed them individually into a holding pen without access to food. After 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, 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 by excluding speeds higher than 200 cm/s. An individual's exploration speed was calculated as the average speed during each 20 min trial. An example video with tracks can be found in Suppl. Video S2.

We investigated the repeatability of the exploration speed measured in the mobile arena to validate its consistency over time and context. At the field site, we tested 57 birds twice in the mobile arena with on average 5 days in between tests (range 3-7 days). Thirty of these birds were then brought into longer-term captivity at NIOZ for establishing long-term repeatability. At NIOZ, these birds were housed in flocks of 14 individuals in aviaries measuring 4m x 2m x 2.5m lined with white Trespa foil (Trespa International B.V. Weert, The Netherlands). They were provided with running saltwater along a coated concrete surface, as well as a stretch of sand covered with 5 cm water. The birds were fed *ad libitum* with trout-feed pellets (Produits Trouw, Vervins, France) and had unlimited access to saltwater and freshwater for drinking and bathing. Because of health problems that developed in captivity (Milot et al., 2014), a few birds were not used in all of the long-term measurements. To investigate the long-term repeatability in exploration speed measured in the mobile arena, we tested birds for a third time within 136 days after first capture on average (range 135-137 days, N=29), and for a fourth time within 176 days after first capture on average (range 175-177 days, N=25, Table S1). These repeated measurements in captivity were conducted in the mobile arena and with identical settings as to those at the field site (i.e., with a 2-hour acclimation period, inside the pyramid-shaped arena).

Indoor arena

To investigate if exploration speed as measured in the mobile arena was comparable to the well-established method measuring exploratory behaviour of captive red knots (Bijleveld et al., 2014; Kok et al., 2019), we additionally tested 24 red knots in the established method (from now on it will be referred to as “indoor arena”; Table 1, Suppl. Fig. S2). Indoor arena measurements were conducted 43 days after capture when red knots have adjusted to their captive conditions. The experimental arena in this method measured 7m x 7m x 3m and was filled with 30 cm seawater. Five similar trays 1m x 1m x 35cm were filled with wet sand and placed above the water surface for the birds to explore. The trays that contained no food were placed approximately 90 cm from the walls. Experimental birds were isolated, and food was removed 2 h before the tests started. Five minutes before the testing, the bird was introduced into a side aviary adjacent to the experimental arena. The side aviary leads into the experimental arena through a sliding door that can be opened and closed remotely via a pulley mechanism. After the door was opened, the bird either flew themselves or after 5 min, it was gently herded into the experimental arena. Individual trials lasted 20 min. A GoPro Hero+ camera was fitted such that it recorded the behaviour from the side. An observer, who was blind to the birds’ previously measured exploratory behaviour, watched the video recordings of each trial in slow speed and recorded the time that the focal bird spent exploring (probing and walking) using *Cowlog* event coding software (Pastell, 2016). For more details on the experimental procedure see Bijleveld et al. 2014.

To compare measures of exploration between the mobile and indoor arena, exploration in the mobile arena was scored as mean speed and exploration in the indoor arena was scored as proportion of time spent on walking and probing (following the established method from earlier studies Bijleveld et. al., 2014, Kok et al., 2019). To compare how well speed correlates with behaviour, we additionally scored exploration as the proportion of time spent probing and walking as well as mean speed for 75 red knots from their first trial in the mobile arena.

Foraging behaviour in the field

To investigate how exploration speed relates to the use of different foraging tactics, we caught and tested 126 red knots one time in the mobile arena in the summer of 2019. Right after the personality tests, red knots were released with unique combinations of colour rings and with a time-of-arrival (WATLAS) radio-tag weighing ~4g (approximately 3% of red knot body mass) to retrieve their locations in the Wadden Sea (Beardsworth et al., 2021; Bijleveld et al., 2021). The tagged birds were located through a website (www.nioz.nl/watlas) where the location of the tagged birds could be seen on a map in real-time. Observers approached the flock of red knots (up to ~200m) and searched for the focal bird with a 10x40 Swarovski telescope. Once the focal bird was found, observers filmed the bird using a video camera (Sony Camera A6000) attached to the scope. Focal birds were filmed for 20 min or up to the moment they flew away. Observations of foraging behaviour were conducted during the low-tide period when large mudflat areas are available for red knots to forage. In total, recordings were collected from 38 different individuals. The distribution of the exploratory scores of these individuals can be seen in comparison with all birds exploratory scores in Suppl. Fig. S3.

The videos were processed with event logging software *Boris* (Friard and Gamba, 2016). Before starting the behavioural coding, the list of videos was randomized. To prevent observer bias, the observer was blind to the bird's exploratory score. The ethogram in which all relevant behaviours are described can be found in Supplementary Table S1. In the field, red knots spend 74% of their time foraging on the mudflats during low-tide periods (Suppl. Fig. S4). For the foraging tactic analysis, we restricted the analysis to the periods when the birds were actively foraging, so visual and tactile foraging added to 100% of the foraging time. We defined two types of foraging tactics: ‘tactile foraging’ when a bird is probing continuously with the bill into the substrate (Piersma et al., 1998), and ‘visual foraging’ when a bird is scanning the area in front of it and pecking at items seen on the substrate surface (Barbosa, 1995, see Suppl. Video S3). In cases that we could identify the ingested prey (N=136), we categorized it as hard-shelled prey ($N_{\text{hard-shelled}}$=73, e.g., cockles or Baltic tellins) or soft prey (N_{soft}=63, e.g., brown shrimp or polychaete worms) to investigate the relationship between foraging tactics and diet.

Table 1. Controlled experiments and field observations were collected from red knots. Two different approaches were followed in two different field seasons. We validated the mobile experimental arena in 2018 with repeatedly testing wild caught birds at the field site short term (first two repeats within 5 days ± 2.2 after capture) and then in captivity long term (third and fourth repeat within 176 days ± 1 after capture). We additionally tested 24 of these birds in the indoor arena. In 2019, wild caught red knots were tested in the mobile arena and immediately after released back to their natural habitat and tracked to record their foraging tactics in the field.

Year	Location	**At the field site**			**In captivity**			**In the field**
	Treatment	Catch	Mobile arena 1st Repeat	Mobile arena 2nd Repeat	Mobile arena 3rd Repeat	Mobile arena 4th Repeat	Indoor arena	Foraging observation
2018	Number of birds	111	111	57	29	25	24	-
	Repeatability short term (5 days ± 2.2)		R = 0.7, 95% CI (0.56, 0.82)					
	Repeatability long term (176 days ± 1)		R = 0.54, 95% CI (0.4, 0.66)					
2019	Number of birds	173	126	-	-	-	-	26

Statistical analysis

All data analyses were carried out in R statistical software v. 4.0.3 (R Core Team, 2013). We analysed the exploration personality of N_{2018}=111 and N_{2019}=126 individuals in N_{2018}=246 and N_{2019}=126 experimental trials (Table 1). Red knots that swam in the arena for more than 10 consecutive min (N_{mobile}=14, N_{indoor}=6) were removed from the arena because of welfare concerns for the bird (i.e., the risk of drowning or difficulty to thermoregulate with wet feathers), and its data excluded from the study. In the field, some videos had poor quality (due to distance between observer and the bird, and weather conditions) and the behaviour could not be scored. Therefore, these videos were excluded from the analysis. Final sample size for analysing the foraging tactics was N=32 videos from N=26 individuals. We were not able to calculate individual repeatability of foraging tactics because too few individuals had more than one recording (N=6). In those cases, we averaged recordings for each individual and weighted with the video length.

After checking for collinearity, overdispersion, and model assumptions (homogeneity and normality of residuals), we formulated four models using the *lme4* package. First, a linear mixed-effects model to quantify repeatability of exploration speed measured in the mobile arena. We used mean speed as the response variable, the number of the repeated measure as a fixed effect and individual identity as a random effect. Mean speed was log10 transformed to meet normality assumptions. Adjusted repeatability *R* was calculated with the *rptR* package (among-individual variance divided by the total phenotypic variance) and confidence intervals and significance were calculated with parametric bootstrapping (Nakagawa and Schielzeth, 2010). Second, a linear mixed-effects model to compare the individuals' scores in the mobile arena (as log10 mean speed) and the indoor arena (as logit proportion of time spent walking and probing behaviour). We used behaviour in the indoor arena as the response variable and the speed in the mobile arena as a fixed. Third, a linear mixed-effects model to compare speed with behaviour using the data from the first trial in the mobile arena. We used the logit proportion of time spent walking and probing behaviour as the response variable and the log10 of mean speed as a fixed effect. Fourth, we ran a quasibinomial generalized linear model with logit link function to test the effects of bill length, gizzard size, and exploration speed (log10 mean speed cm/s) measured first time in the mobile arena on the response variable percentage of foraging tactics that were visual observed from the videos taken in the field. To investigate whether a particular foraging tactic (tactile and visual) resulted in ingesting certain prey types (soft and hard-shelled), we ran a non-parametric Chi-square test.

The relative contribution of potential prey types (soft and hard-shelled) to the diet of individual red knots was estimated using an isotopic Bayesian mixing-model programmed in the R-package MixSIAR (Stock and Semmens, 2016). For the diet analysis, we decided to use the Bayesian approach, because Bayesian models estimate diet contributions while accounting for variability in both prey and consumer isotope data (Moore and Semmens, 2008; Parnell et al., 2010). Furthermore, continuous fixed effects (in our case, exploration speed) can be implemented in the model using the MixSIAR package (see Stock et al., 2018 for further details). The MixSIAR model combines three different datasets and requires input of at least two stable isotopes (here $\delta^{15}N$ and $\delta^{13}C$) of a consumer, its prey, and a diet-tissue trophic discrimination factor. We used $\delta^{13}C$ and $\delta^{15}N$ of blood plasma (and red blood cells in separate analysis with identical parameters Suppl. Figs S8-S9) of red knots and as prey sources, we used mean and standard deviation of $\delta^{13}C$ and $\delta^{15}N$ from groups of hard-shelled and soft prey. We did not measure discrimination factors ourselves therefore, we used general discrimination factors (for avian plasma: $\Delta^{15}N$: 2.82 ± 0.14‰ and $\Delta^{13}C$: –0.08 ± 0.38‰; red blood cells: $\Delta^{15}N$: 2.25 ± 0.2‰ and $\Delta^{13}C$: –0.2 ± 0.39‰ Caut et al., 2009). These values (Fig. 2.a) were then used to construct MixSIAR models with first exploration speed (log10 mean speed cm/s) measured in the mobile arena as a continuous fixed effect. We checked for convergence diagnostics and set the model to run for 100,000 iterations with 3 chains and discarded the first 50,000 iterations.

Results

Exploration speed measured in the mobile arena one day after catching was highly repeatable within 7 days at the field site (R = 0.7, 95% CI (0.56, 0.82), $P< 0.01$, $N = 57$; Table 1). Long-term repeatability in the mobile arena was also high within three trials in 136 days (R = 0.6, 95% CI (0.44, 0.73), $P< 0.01$, $N = 29$), and within four trials in 176 days (R = 0.54, 95% CI (0.4, 0.66), $P< 0.01$, $N = 25$; Table 1). The first exploration speed (log10 mean speed cm/sec) measured in the mobile arena was positively correlated with the proportion of time spent walking and probing measured in the indoor arena 43 days after capture at NIOZ (Intercept = -3.46, Slope = 5.34, $SE = 1.36$, Adj. $R^2 = 0.38$, $P< 0.01$, $N = 24$; Suppl. Fig. S5). Automated scoring of exploration speed (mean speed log10 cm/s) was positively correlated with manual coding of proportion of time spent walking and probing (logit), Intercept = -3.64, Slope = 6.19, $SE = 0.69$, Adj. $R^2 = 0.61$, $P< 0.001$, $N = 75$, Suppl. Fig. S6).

In the field, red knots caught hard-shelled prey only by using tactile foraging (100%) and caught soft prey mostly by using visual foraging (97%) and rarely by tactile foraging (3%, $\chi^2 = 134.35$, $P < 0.01$, Fig. 1.a). The percentage of visual foraging tactics that were observed in the field was positively correlated with the exploration speed measured in the mobile arena: faster exploring red knots showed significantly higher percentage of visual foraging than slower explorers (Table 2; Fig. 1.b). Bill length and gizzard size did not explain the variation in the observed foraging tactics (Table 2).

Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) from plasma and red blood cells were highly correlated (Pearson's r for $\delta^{13}C$= 0.77 and $\delta^{15}N$= 0.68) which indicates consistency in diet over the ca. 14 days before blood sampling to the ca. 45 days before (Klaassen et al., 2010). Results from MixSIAR analysis using plasma that integrates diet from the past ca.14 days (Fig. 2) were similar to those using red blood cells that integrates diet from the past ca. 45 days (Klaassen et al., 2010; Suppl. Figs S8-S9). Stable isotope analysis of red knots with measured exploration speed in the mobile arena confirmed our field observations that faster exploring red knots have soft and hard-shelled prey in their diet while slower exploring red knots relied heavily on hard-shelled prey (Fig. 2.b). MixSIAR analysis using plasma showed that on average, red knots proportionally consumed more hard-shelled prey (Median = 0.59, 2.5 % CrI = 0.5, 97.5 % CrI = 0.68) than soft prey (Median = 0.41, 2.5 % CrI = 0.32, 97.5 % CrI = 0.5). The model also predicted the proportion of soft prey as a function of exploration speed. For slower exploring red knots, the model estimate of $p_{\text{hard-shelled prey}}$ is 0.76 (Median, 2.5 % CrI = 0.61, 97.5 % CrI = 0.88) and $p_{\text{soft prey}}$ is 0.24 (Median, 2.5 % CrI = 0.12, 97.5 % CrI = 0.39). For faster exploring red knots, model estimate of $p_{\text{hard-shelled prey}}$ is 0.4 (Median, 2.5 % CrI = 0.22, 97.5 % CrI = 0.58) and $p_{\text{soft prey}}$ is 0.6 (Median, 2.5 % CrI = 0.42, 97.5 % CrI = 0.78). The posterior distributions of model estimates for slower and faster exploring red knots can be found in Suppl. Fig. S7.

Table 2. Effects of exploration speed (log10 mean speed cm/sec), gizzard size, and bill length on the percentage of visual foraging tactics observed in the field. Significance (*p*) is based on Wald statistics under the null hypotheses that the estimate is zero.

Variable	Estimate	SE	*p-value*
Intercept	1.1	4.04	0.81
Exploration speed	2.26	0.65	<0.01
Gizzard size	0.17	0.18	0.37
Bill length	-0.15	0.13	0.27

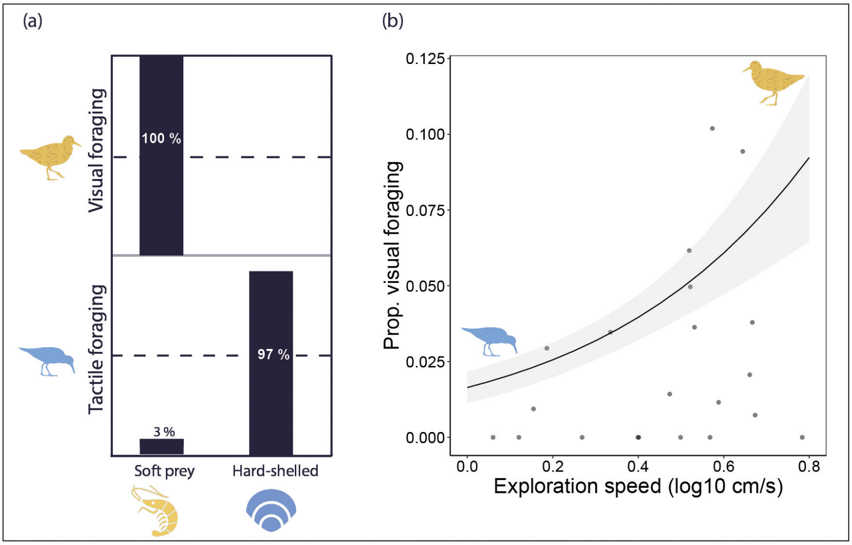

Figure 1. (a) Different foraging tactics (visual and tactile) leads to ingestion of different types of prey (soft and hard-shelled). Knots using visual foraging only ingested soft prey while knots using tactile foraging ingested mainly hard-shelled prey (97%) and rarely soft prey (3%). **(b)** Exploration speed (log10 mean speed cm/s) measured in the mobile arena for the first time (x axis) predicts the percentage of visual foraging observed in the field (y axis). Probabilities and 95 % confidence intervals are predicted by a GLM with quasibinomial error distribution.

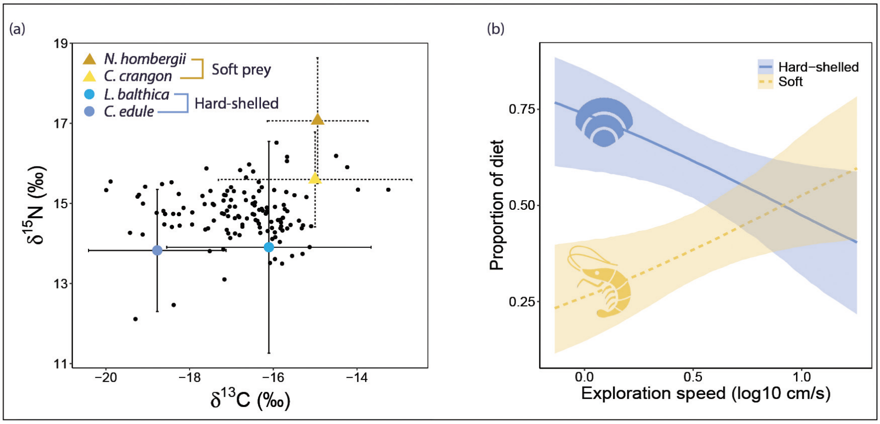

Figure 2. (a) Stable isotope ratios of carbon (δ13C, x axis) and nitrogen (δ15N, y axis) that were used in the MixSIAR diet analysis. Black dots are stable isotope values from the plasma of individual red knots. Stable isotope values of prey items are shown with mean ± SD as soft and hard-shelled prey. **(b)** Diet proportions estimated using individual plasma stable isotope samples with MixSIAR (y axis) as a function of exploration speed (log10 mean speed cm/s, x axis) showing that slower explorers depend upon hard-shelled prey while faster explorers consume both soft and hard-shelled prey. Lines depict posterior medians, and shading displays the 95% Bayesian credible intervals.

Discussion

We found that slower explorers use only tactile foraging and eat mainly hard-shelled prey, while faster explorers use both tactile and visual foraging tactics and consume both soft and hard-shelled prey. We show that exploration speed was highly repeatable over time and in different contexts for wild-caught red knots. Bill length and gizzard mass did not explain differences in the use of foraging tactics. Our results demonstrate a direct link between personality traits, foraging tactics, and diet, independent of morphological differences (Fig. 3).

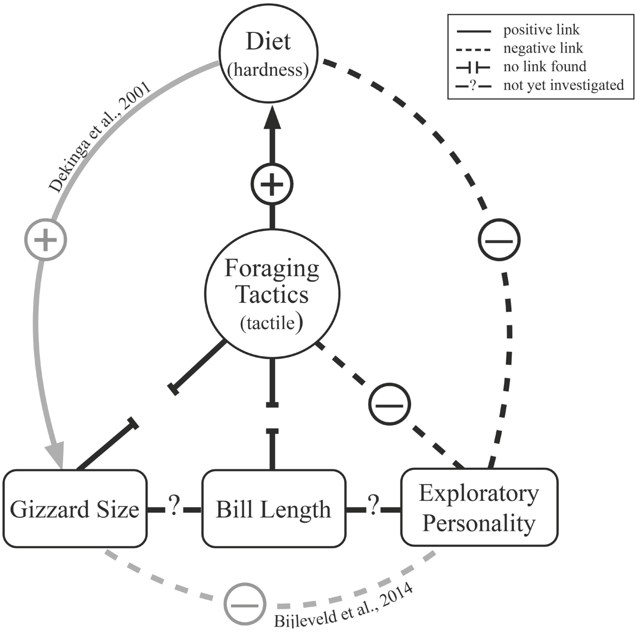

Figure 3. Conceptual diagram showing the links between foraging tactics, diet, exploratory personality, gizzard size, and bill length. Positive and negative symbols indicate the relationship. Arrows indicate the direction. If the link is found in a different study (indicated in grey), the original study is referred.

Previous research on red knots foraging on mudflats has shown that red knots are mollusc specialists that mainly feed on hard-shelled prey that are buried in the sand and found by touch rather than sight (Piersma et al., 1998). In accordance with this, we observed that red knots primarily relied on tactile foraging, however faster exploring birds also used visual foraging that resulted in combined diet of soft and hard-shelled prey. Soft prey, such as shrimp, have higher energetic value and lower digestive processing costs than hard-shelled prey (van Gils et al., 2003) but catching soft prey requires more active visual foraging and handling these prey takes longer than hard-shelled prey (van Gils et al., 2005). By adding soft prey in the diet, faster exploring knots may offset the higher energetic cost of their movement with higher quality soft prey gain in a foraging context. While we did not investigate energy expenditure, our finding that exploration speed in red knots was correlated with prey quality matches with the pace-of-life literature and warrants further study.

During foraging, faster explorers used visual foraging up to 10% of the time. Yet stable isotope analysis predicted that the amount of soft prey in the diet of the fastest exploring birds could reach up to 60%. This discrepancy between video observations in the field and diet analysis by stable isotopes could be explained in two ways. Firstly, finding individuals in the field was difficult (N=26 re-sightings out of 126 individuals for which we had blood samples for isotope analysis), and there was a tendency to resight slower red knots more often in the wild (as seen in Suppl. Fig. S3). Individuals with a higher exploratory personality have been shown to cover more ground when foraging in other species, such as great tits (van Overveld and Matthysen, 2010). Since our observations were conducted on a large intertidal mudflat, if faster explorers change location more frequently or forage further from land, they may be less likely to be observed. From the video observations, we may therefore have underestimated the percentage of visual foraging used in the population. Secondly, while spending small amounts of foraging time searching for soft prey, the contribution of energetically rich soft prey to the birds' total biomass intake, and thus isotopic signal, could be proportionally much larger (van Gils et al., 2007).

Individual differences in morphology are often associated with the use of different foraging tactics (Barbosa and Moreno, 1999; Hespenheide, 1973). In our study, however, bill length was not associated with the percentage of foraging tactic use. This is similar to findings from a study on great knots *Calidris tenuirostris,* which showed that bill length was not related to diet, however birds that ate softer prey had smaller gizzards (Zhang et al., 2019). We expected that birds that spent more time using the visual foraging tactic, thus with a higher proportion of soft prey in their diet, would also have smaller gizzards (Dekinga et al., 2001; Fig. 3). Contrary to our predictions, we did not find an association between small gizzard size and the percentage of visual foraging tactic use. This may be because even faster exploring individuals, with the highest percentage of visual foraging, still consumed on average 40% hard-shelled prey based on the stable isotope analyses.

Likewise, the slower exploring birds also consumed 24% soft prey. Perhaps these mixed diets were large enough to reduce individual differences in gizzard size.

While many personality studies show repeatable behaviour between contexts in controlled conditions, few studies (e.g., Fraser et al., 2001; Harris et al., 2019) show a link between the behaviour measured in standardized experiments and behaviour in the wild (Carter et al., 2013). We showed that exploration speed is repeatable between contexts in controlled artificial conditions (notably without food), and that it correlates with ecologically relevant foraging tactics in the wild. Exploration speed and foraging tactics may be correlated because different foraging tactics themselves are associated with different movement speeds (Barbosa, 1995). In red knots, tactile foraging with continuous probing of the sediment is a relatively slow behaviour. In contrast, using a visual foraging tactic can involve quick scanning of the surface, which results in faster movement. Our standardised measurement of exploration speed as a personality trait therefore closely relates to foraging movement, which can be an inherent part of these foraging tactics. However, we show that exploratory movement in controlled conditions was repeatable in the absence of food. Moreover, the slow explorers often stood still during the trials and did not probe more than fast explorers (Suppl. Video S1), which indicates that the standardised measure of exploration does not directly reflect probing behaviour as measured in the field. Interestingly, exploration speed predicts probing behaviour in the field. This suggests that foraging tactic itself is repeatable regardless of the environmental variation. Indeed, the correlation between isotopic signatures of plasma and red blood cells suggests consistency in diet, but whether foraging tactic itself is repeatable is unknown. To clarify the repeatability and thus flexibility of foraging tactics in the field with environmental variation, future studies should aim to repeatedly observe the same free-living individuals.

Our results raise the question of where and how the consistent individual differences originate. Among-individual variation could, for example, arise from differences in environmental influences or experience between individuals (Stamps and Groothuis, 2010). Especially the positive feedback between behaviour, learning, and increased efficiency can gradually set individuals on different developmental trajectories and thus cause consistent individual differences in behaviour (Sih et al., 2015). There are, for instance, studies indicating that the prey environment experienced during early life, shapes an individual’s foraging tactics (e.g., Heinsohn, 1991; Slagsvold and Wiebe, 2007). Competition between conspecifics is suggested to be a major factor affecting diet specialisation, foraging tactics, and the emergence of personality traits (Bergmüller and Taborsky, 2010). When competition for food is high, conspecifics can, for instance, reduce the amount of conflict by feeding on different types of food (e.g., Parent et al., 2014). Through positive feedback between learning to detect, catch, and process food, this differentiation in diet can favour behavioural consistency and maintain among-individual variation. When, to what extent, and by which mechanisms consistent individual differences develop during ontogeny needs to be studied further and will likely provide interesting insights into the origin and maintenance of among-individual variation between the members of the same population.

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Data Availability Statement

Data is available at the Dryad Digital Repository: doi: 10.5061/dryad.vmcvdncts (Ersoy et al., 2022).

Authors’ Contributions

SE and AIB designed the study. SE collected and analysed the data. SE drafted the first version of the manuscript. All authors contributed to writing of the final manuscript. None of the authors have a conflict of interest.

Supporting Information

Figure S1: Mobile arena to score exploration speed at the field site. The floor of the unit consists of sea water of 20 cm height and 4 identical sand patches 61cm x 40cm x 25cm for birds to explore.

Figure S2: Indoor arena to score exploratory behaviour in captivity. The floor of the unit consists of salt water of 30 cm height and 5 identical sand patches 1m x 1m x 35cm for birds to explore in a room measuring 7m x 7m x 3m.

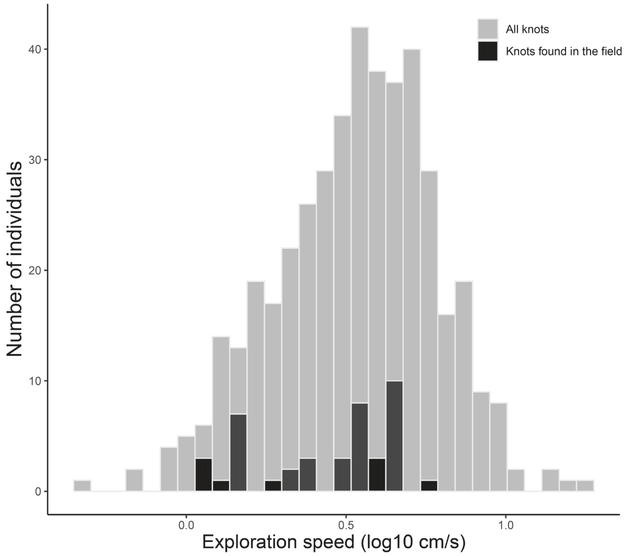


Figure S3: Histogram of individuals with measured exploration scores. The distribution of the exploratory scores of individual red knots which were followed in the field (in yellow) and all red knots with exploratory score (in grey).

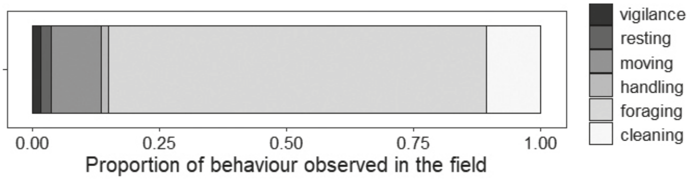


Figure S4: All observed behaviours in the field. Observed behaviours from low tide field observations: foraging 74%, cleaning 11%, moving 0.9%, resting 0.2%, vigilance 0.1%, handling 0.1%.

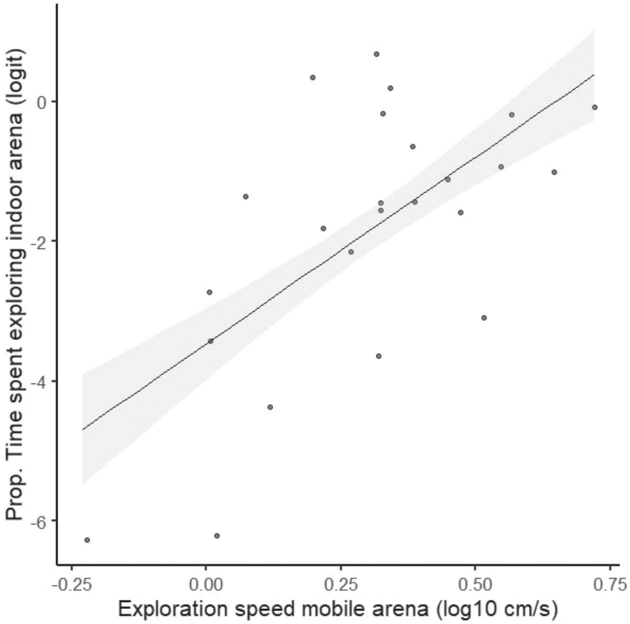


Figure S5: Correlation between mobile and indoor arena. Correlation between the results from the same individuals measured in newly developed mobile method (x axis) on exploration speed (mean speed log10 cm/s) and the established indoor method (y axis) on exploration behaviour (proportion of time spent searching and walking) in red knots. Probabilities and 95 % confidence intervals are predicted by a GLM with gaussian error distribution.

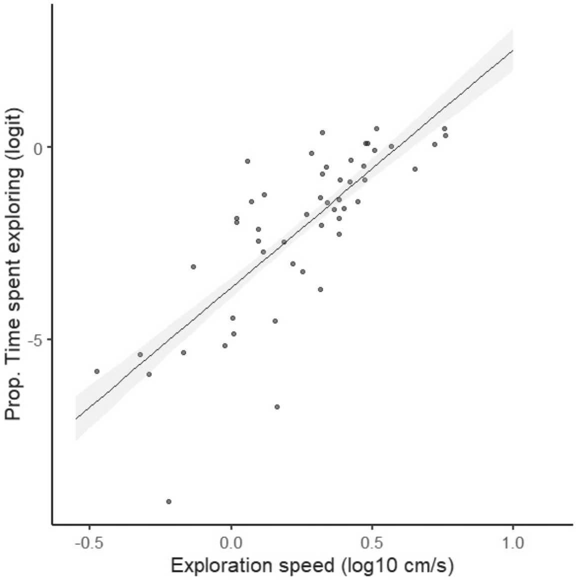


Figure S6: Correlation between speed and behaviour. Correlation between different techniques to score exploration personality on movement scores (mean speed log10 cm/s on the x axis) and behavioural scores (proportion of time spent probing and walking on the y axis). Probabilities and 95 % confidence intervals are predicted by a GLM with gaussian error distribution. y= -3.64 + 6.19 x, R = 0.62.

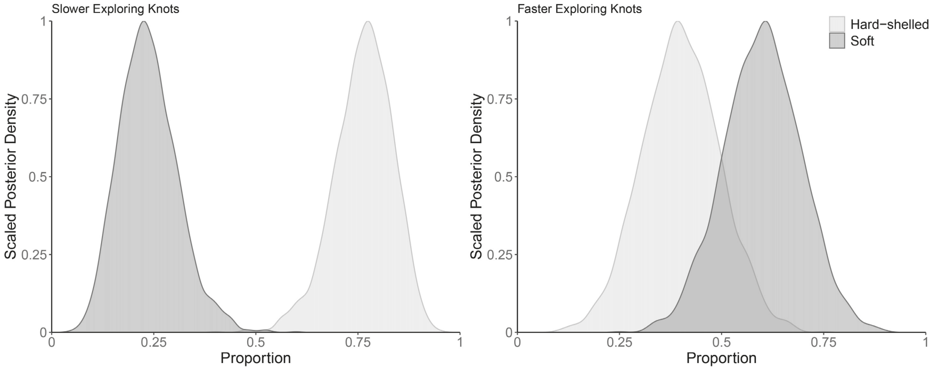


Figure S7: MixSIAR Posterior distribution for plasma. Posterior distribution of model estimates for slower exploring knots (on the left) and faster exploring knots (on the right). Diet estimated from plasma stable isotope samples. For slower exploring red knots, the model estimate of $p_{\text{hard-shelled prey}}$ is 0.76 (Median, 2.5 % CrI = 0.61, 97.5 % CrI = 0.88) and $p_{\text{soft prey}}$ is 0.24 (Median, 2.5 % CrI = 0.12, 97.5 % CrI = 0.39). For faster exploring red knots, model estimate of $p_{\text{hard-shelled prey}}$ is 0.4 (Median, 2.5 % CrI = 0.22, 97.5 % CrI = 0.58) and $p_{\text{soft prey}}$ is 0.6 (Median, 2.5 % CrI = 0.42, 97.5 % CrI = 0.7).

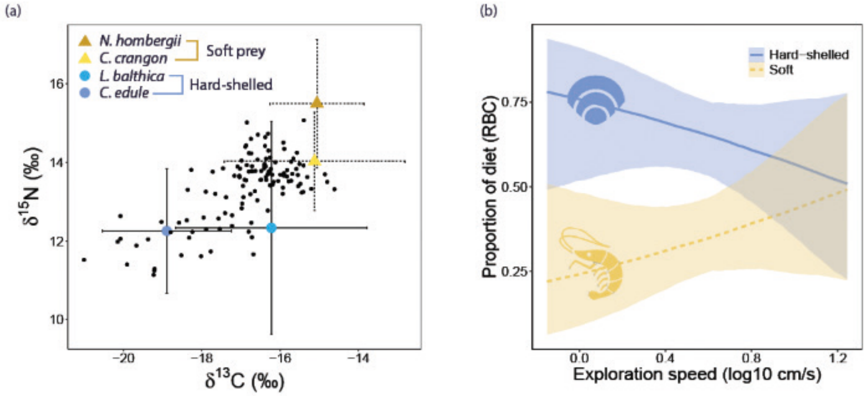


Figure S7: MixSIAR Diet analysis for red blood cell. **(a)** Biplot of carbon (δ13C, x axis) and nitrogen (δ15N, y axis) stable isotope values. Black dots are isotopic signatures of individual red knots from red blood cell. Different prey items plotted on; soft preys (brown shrimp Crangon crangon and polychaete worm Nephtys hombergii) and hard-shelled preys (cockle Cerastoderma edule and balthic tellin Limecola balthica). **(b)** Posterior distributions for red knot diet proportions (estimated using blood cell stable isotope samples) as a function of exploration speed (log10 cm/s) measured in the mobile arena for the first time. MixSIAR model predicted that on average, red knots proportionally consumed more hard-shelled prey (Median = 0.67, 2.5 % CrI = 0.56, 97.5 % CrI = 0.75) than soft prey (Median = 0.34, 2.5 % CrI = 0.23, 97.5 % CrI = 0.44). Slower explorers depend upon hard-shelled prey while faster explorers consume both soft- and hard-shelled prey. Proportion of diet estimated from the Bayesian mixing model for isotope analysis MixSIAR. Lines depict posterior means, and shading displays the 95% credible intervals.

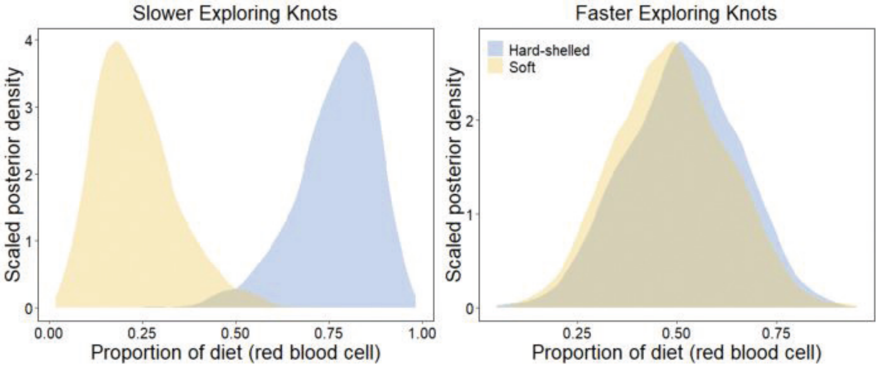


Figure S9: MixSIAR Posterior distribution for red blood cell. Posterior distribution of model estimates for slower exploring knots (on the left) and faster exploring knots (on the right). Diet estimated from red blood cell stable isotope samples. For slower exploring red knots, the model estimate of $p_{\text{hard-shelled prey}}$ is 0.77 (Median, 2.5 % CrI = 0.51, 97.5 % CrI = 0.94) and $p_{\text{soft prey}}$ is 0.23 (Median, 2.5 % CrI = 0.65, 97.5 % CrI = 0.49). For faster exploring red knots, model estimate of $p_{\text{hard-shelled prey}}$ is 0.51 (Median, 2.5 % CrI = 0.23, 97.5 % CrI = 0.79) and $p_{\text{soft prey}}$ is 0.49 (Median, 2.5 % CrI = 0.51, 97.5 % CrI = 0.94).

Table S1: Ethogram of all videos recorded behaviours in the field.

Behaviour	**Description**
Aerial Vigilance	Looking up by tilting the head
Ingesting	Ingesting prey item (cockle/white shellfish, shrimp, worm, not specified)
Kleptoparasitism	Prey item stolen by other bird (common gull, another knot, black-headed gull, other)
Walking	Moving to another location. Can be slow or fast, also on one leg. During foraging only count walking when >2 sec when bird moves in certain direction and head is up > 90° angle
Flying	Taking off by flapping and then moving to another location
Tactile searching	Looking for food buried in the ground, the bill forming a 45° angle with the horizontal, probing in the sand
Visual searching	Looking for food on the surface, head is 45° to 90° angle, head moves actively to look around
Handling	Handling prey items. Prey needs to be visible or obvious ingestion at the end of handling
Social interference from focal bird	Any kind of social interaction from focal bird to another bird
Social interference from other bird to focal bird	Any kind of social interaction from another bird to the focal bird
Resting	Standing still with its head under its feathers, can be on one leg
Standing	Standing on one or two legs with the bill in a 90° angle, without moving, for >2 sec
Preening	Cleaning and/or rearranging its feathers with the bill, by flapping or shaking, scratching with its foot, stretching wings and legs
Ground Vigilance	Head turning side to side with the bill in a 90° angle. Only if >1sec
Bathing	The bird is in the water washing itself
Miscellaneous	Behaviour that does not fit the descriptions above
Out of sight	The bird cannot be seen by the observer

CHAPTER 3

Learning to be a shellfish forager: variation in exploration and diet differ between juvenile and adult red knots

Selin Ersoy, Christine E. Beardsworth, Elif Duran, Theunis Piersma,
Ton G. G. Groothuis, Allert I. Bijleveld

Manuscript

Abstract

Behavioural traits that are consistent within, but vary between individuals, can develop through positive feedback between behaviour and its outcome during development. Exploration, a commonly used personality trait, has been shown to associate with foraging strategies and diet, but how these associations emerge during development remains unclear. Here we compared exploration and diet variances of juvenile and adult red knots *Calidris canutus islandica* that breed on tundra and migrate to spend the nonbreeding season on European intertidal mudflats. Juveniles, having grown up on tundra arthropods, are confronted with intertidal marine prey for the first time when they reach the mudflats. This fact enabled us to ask whether the first experiences of juveniles on a marine diet correlates with development of exploratory behaviour. We conducted repeated tests of exploration from juvenile and adult red knots in controlled settings, and used stable isotope analyses to estimate diet, and the number of days that juveniles had been eating marine invertebrates after arrival from the tundra. We found that juvenile red knots have more diverse diet than adults, and that juveniles are less repeatable in exploration than adults. Increased repeatability from juvenile to adult stage was due to a reduction in within-individual variance, with among-individual variance remaining stable. Time since the switch from a tundra to a marine diet did not explain the within-individual variation in the repeated exploration tests of juveniles, suggesting that plasticity is still available in their first weeks on the wintering grounds. The diversity in diet between juvenile and adult red knots and the decline in within-individual variation in exploration in juveniles support the idea that feedbacks between learning to detect, catch, and process food at an early age can favour consistency in exploration behaviour later in life.

1. Introduction

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) that may affect fitness (Réale et al., 2010; Smith and Blumstein, 2008). How these associations arise is elusive and require studies on their developmental origin. Personality traits have been suggested to reflect genetic variation (Dingemanse et al., 2002; Drent et al., 2003; Van Oers et al., 2004); however, heritability is often found low (Araya-Ajoy and Dingemanse, 2017; Dochtermann et al., 2015; Stirling et al., 2002), illustrating that personality traits develop under the influence of the environment (Groothuis and Trillmich, 2011). For example, genetically identical fish still develop consistent among-individual variation (Amazon molly, *Poecilia formosa,* Bierbach et al., 2017). It has been suggested that differences in experience (also reflecting environmental influences) induce positive feedback loops that gradually fix the behaviour of individuals on different developmental trajectories (Sih et al., 2015; Urszán et al., 2018; Wolf and Weissing, 2012).

Individuals may gradually diverge from one another in behavioural tendencies as they age and have different experiences (i.e., fanning-out pattern, Stamps and 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 and Tetzlaff, 2020). Individual differences in experience and the feedback between behaviour and its outcome are likely to affect this divergence and consistency of behaviour (Stamps and Groothuis, 2010). For example, studies indicate that the prey environment experienced during early life can shape an individual's foraging behaviour (e.g., Heinsohn, 1991; Slagsvold and Wiebe, 2007). Positive feedbacks between learning to detect, catch, and process food can lead to behavioural consistency and divergence (O'Brien et al., 1989). Indeed, foraging behaviour and personality traits such as exploration (magnitude of space use in novel environment) and boldness (approaching to a novel object) has been linked in several studies (e.g., Kurvers et al., 2010; van Overveld and Matthysen, 2010; Patrick et al., 2017). However, how foraging behaviour, diet, and personality interacts during development remains poorly studied.

Repeatability in individual-level traits is the most used measure in animal personality studies. 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 approaches. While comparing repeatability 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 and Royauté, 2019).

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 this is correlated with foraging tactics and diet in the wintering grounds (Ersoy et al., 2022). Slower exploring adult red knots mainly use 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 softer prey (e.g., brown shrimp, *Crangon crangon*) and hard-shelled prey (Ersoy et al., 2022). The links between exploration, foraging tactics and diet makes red knot a good study species to investigate how foraging behaviour, diet, and personality interacts during development.

Red knots breed on the high Arctic tundra of Northern Greenland and Northeast Canada and migrate 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 when the young are independent, and the juveniles leave latest when ca. 35 days old (Nettleship, 1974). Red knot chicks feed only on soft prey such as terrestrial arthropods and larvae that requires visual foraging in their first month of life on the Arctic tundra (Schekkerman et al., 2003). Juvenile red knots encounter hard-shelled benthic prey for the first time in the wintering grounds. Unlike their prey in the Arctic, this prey type requires tactile foraging to detect (Piersma et al., 1998). It is therefore likely that the differences in foraging tactics and diet that we find in adult red knots are determined 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, a study on captive red knots showed that repeatability of exploration did not differ between juveniles and adults, nor significantly increased with age over time (Kok et al., 2019). Juvenile red knots were captured ca. a month after their arrival to the wintering grounds, kept in aviaries in controlled environment, and repeatability was reported from the four repeated assays conducted throughout a year in Kok et al. (2019). Lack of differences in exploration between juveniles and adults could be due to captivity effect (a conclusion by Kok et al., 2019) because juveniles in captivity may have missed the opportunity to practice their foraging strategies in the wild thus receiving no feedback in their behaviour. Therefore, measuring exploration 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 conducted repeated tests of exploration behaviour of juveniles and adults in controlled settings at the field site and used stable isotope analyses of blood cells and plasma to estimate diet in the wild and the number of days that the juveniles were in the Wadden Sea after arrival from the tundra (Dietz et al., 2010). We expected juveniles to try different marine prey types thus show larger variation in diet than adults. We expected juveniles to be less repeatable in exploration with larger within-individual and smaller among-individual variation than adult red knots. Days since the diet switch from tundra to marine may influence the juvenile consistency in behaviour thus, we expected juveniles that were tested for exploration soon after arrival in the wintering grounds would have a higher difference between repeats than individuals that were caught and tested more days post-migration.

2. Materials and Methods

2.1. Capture Events

We used data collected between 2018 and 2021. In all years, we used night-time mist netting for ~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) or adult (>18 months; Prater et al. 1977). We focused on juveniles (young of the year) and adults and did not work with birds that were identified as second calendar year birds (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 section: 2.5 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 for analyses comparing exploration speed between juveniles and adults (see section: 2.5 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 section: 2.3 below). Juveniles from September 2021 were also used in analyses investigating the factors influencing the difference between the exploration test repeats (see section: 2.6 and 2.7 below).

2.2. Stable Isotope Measurements

Blood samples (~80 µL) for stable isotope analyses were taken from individuals during catching event in September 2021. The samples were separated into plasma and red blood cells by centrifugation (12 min, 7000 rpm) and pipetted into separate glass vials and immediately stored in a freezer at the field site. In the lab, 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 x 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. We did not always have enough plasma samples to finalise isotope analysis ($N_{excluded}$= 8; juveniles N_{final}=37, adults N_{final}=44).

2.3. Diet

For the diet comparison between juveniles and adults in the Wadden Sea, we used stable isotope values of $\delta^{13}C$ and $\delta^{15}N$ 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). In this study, 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.

2.4. Short-term captivity

After taking biometric measurements, the birds were moved to temporary outdoor aviaries of 2m x 0.75m x 0.4m (LxWxH) 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 and provided with *ad libitum* food (live and dried mealworms) and water (freshwater and seawater). Group size in the aviaries were between 8 to 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 with unique colour coded rings in the Wadden Sea. All necessary permits to catch, handle, tag, 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.

2.5. Exploratory behaviour

The exploratory behaviour of adults (N = 57 from 2018) and juveniles (N = 67 from 2019, 2020, 2021) was measured after 24 hr in captivity. The assays took place in a field-based arena (see Ersoy et al., 2021 for a detailed description of the method). Briefly, a pyramid shaped mobile unit of 2m x 2m x 2m was filled with seawater (20 cm depth) and contained four identical trays (61cm x 40cm x 25cm) 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^{-1}. To standardise 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 experiments 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 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 log10 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 run 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 (Δ).

2.6. Estimating days since juvenile switch diet from tundra to marine

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 carbon isotope ($\delta^{13}C$) to estimate time since diet switch (Klaassen et al., 2010):

Start and end values were taken from Dietz et al. (2010); the start value indicates where the migration started hence, we took Arctic tundra value ($\delta^{13}C$ = -24.7), and end value indicates where the migration ended accordingly, we took the Wadden Sea value ($\delta^{13}C$ = -14.0). We took the turnover rate value for red knots (λ = 0.046) from Klaassen et al. (2010). We fitted individual carbon isotope ($\delta^{13}C$) values from red blood cells of our juvenile red knots. The result of this function was the days since the diet switch, so to estimate arrival date we subtracted the outcome from the date of capture. Finally, we extracted arrival date from capture date to find the number of days since juveniles' arrival in the Wadden Sea.

2.7. Variation in exploration test repeats in juveniles

We were interested in the factors affecting the absolute difference between the exploration speed (log10 cm/s) measures in juveniles, however we added the data on the real difference between two exploration measures in the Supplementary Material S1. We built a Bayesian linear regression model using *brms* to test whether the absolute difference between the exploration test repeats (log10 cm/s) in juveniles (response variable) can be predicted by the number of days since arrival in the Wadden Sea. We ran the model with 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. 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, 2014).

3. Results

3.1. Does diet differ between juveniles and adults?

The posterior estimates of the standard ellipses that represents the core dietary niche of each group revealed that juveniles (Median 95% CI = 1.5 ‰^{2} (1.07; 2.06)) have larger diet variance than adults (Median 95% CI = 0.88 ‰^{2} (0.76; 1.04), Figure 1). Overlap between the standard ellipse areas of juveniles and adults was high (4.71 ‰^{2}, Ellipse area $_{\text{Juveniles}}$ = 9.37 ‰^{2}, Ellipse area $_{\text{Adults}}$ = 5.36 ‰^{2}). The proportion of juveniles' ellipses overlap with adults was 0.50 and the proportion of adults' ellipses overlap with juveniles was 0.88 (Figure 1).

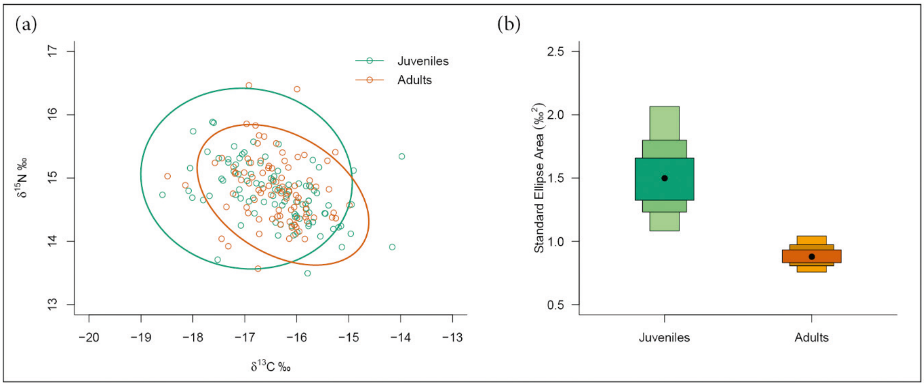


Figure 1. Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of plasma are from juvenile (green) and adult (orange) red knots. (a) Standard ellipses drawn to represent standard ellipse area of each age group. (b) Density plot showing the credible intervals of the Bayesian standard ellipse areas.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

3.2. Do repeatability and variance components of exploration differ between juveniles and adults?

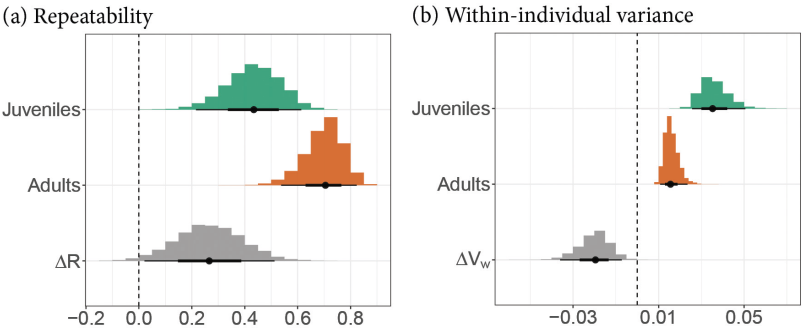
Juvenile and adult groups of red knots did not differ on their overall scores of exploration speed (Table 1, Suppl. Fig S2). Exploration speed of juveniles was less repeatable and had higher within-individual variance than for adults (Table 2, Figure 2). However, there was no difference between adults and juveniles in among-individual variance (Table 2).

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

	Exploration speed (log cm/s)
Predictors	*Estimates (95% CI)*
Intercept	0.55 (0.49 – 0.61)
Age (Juvenile)	-0.04 (-0.14 – 0.04)
Sigma: Age (Adult)	-2.08 (-2.27 – -1.88)
Sigma: Age (Juvenile)	-1.66 (-1.88 – -1.40)
Marginal R^2 / Conditional R^2	0.009 / 0.573

Table 2. Table compares repeatability and variance components in exploration speed by age groups. Magnitude of the difference in variability in between age groups is shown with Δ. Posterior medians and 95% credible intervals estimated from a Bayesian mixed model. Bold font indicates credible intervals do not overlap with zero.

Variance and ratio	**Age groups**		**Difference Δ**
	Juveniles Median (95% CI)	**Adults** Median (95% CI)	**Adult – Juvenile** Median (95% CI)
Repeatability (R)	0.43 (0.23; 0.62)	0.7 (0.55; 0.83)	**0.27 (0.03; 0.52)**
Within-individual variance (V_w)	0.04 (0.02; 0.05)	0.02 (0.01; 0.02)	**-0.02 (-0.04; -0.01)**
Among-individual variance (V_i)	0.03 (0.01; 0.05)	0.04 (0.02; 0.06)	0.01 (-0.01; 0.04)


(a) Repeatability

(b) Within-individual variance

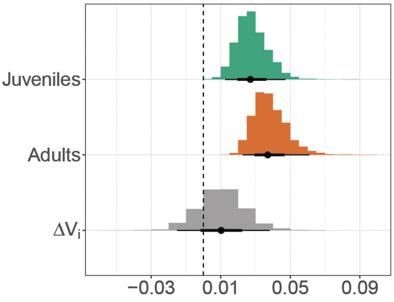

(c) Among-individual variance

Figure 2. Comparison of variance components and ratios of exploration speed between age groups. Posterior distribution of (a) repeatability of age groups (R), the difference in repeatability ($\Delta R = R_{adults} - R_{juveniles}$), (b) within-individual variance of age groups, the difference in within-individual variance ($\Delta V_w = V_{w\_adults} - V_{w\_juveniles}$), (c) among-individual variance of age groups, the difference in among-individual variance ($\Delta V_i = V_{i\_adults} - V_{i\_juveniles}$). Posterior medians and 95% credible intervals estimated from a Bayesian mixed model.

3.3. Do the days since diet switch explain the variation in exploration in juveniles?

The absolute difference between the exploration test repeats differed between juveniles and ranged from 0.01 to 0.66 (Median = 0.18). Estimated number of days since diet switch 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 (Figure 3).

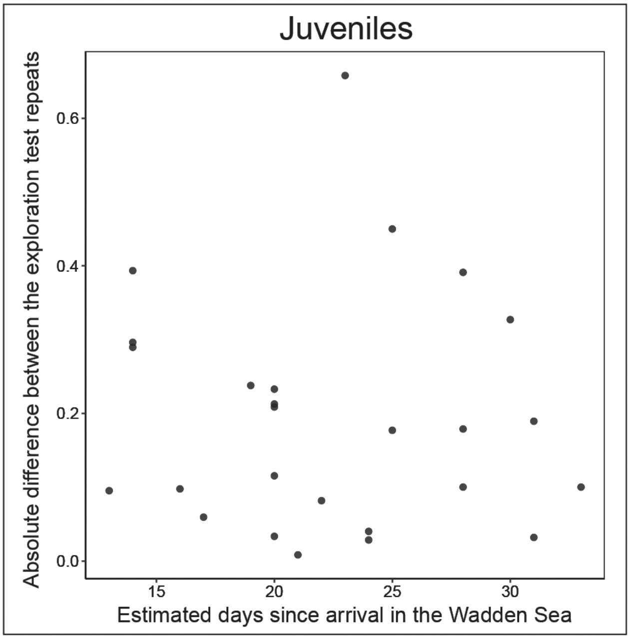


Figure 3. Absolute difference between the two (log10 cm/s) exploration speed measures of juveniles (y axis) in response to the number of days since arrival in the Wadden Sea. Data is from juveniles caught in September 2021.

4. Discussion

In this study, we investigated how foraging behaviour and diet associates with exploratory personality during development. We found that juvenile red knots have more diverse diet than adults, and that juveniles (vs. adults) showed lower repeatability with higher within- but not differing among-individual variation in exploration trait. Number of days since diet switch from tundra to marine areas did not explain the intraindividual variation in the exploration scores for juveniles. We discuss how the feedback between learning to detect, catch, and process food at 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. Thus, the increase in repeatability between juveniles and adults is likely to be 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 and Briffa, 2017 and mosquitofish, *Gambusia holbrooki*; Polverino et al., 2016). The value for repeatability in juveniles ($R = 0.43$) in this study was similar to another study that measured exploratory personality of red knots captured as juveniles then raised and tested in captive conditions over two years period ($R = 0.48$, Kok et al., 2019). In that captivity study, juvenile's repeatability in exploration increased with age from first (juvenile age $R = 0.48$) to 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 this study. A repeatability 0.4 can be considered as a repeatable behaviour in animal personality studies (Baker et al., 2018). Together with this relatively high repeatability of juveniles, and the lack of differences in the among-individual variation between adult and juveniles, we conclude that part of juvenile personality has already developed before we captured them. Thus, development of exploratory personality would have taken place on the tundra breeding grounds or within the first week in the marine areas. However, our findings on the decrease in within-individual variation between age groups shows that experiences that juvenile gain in their first month in the wintering grounds are important and influences the consistency of exploratory behaviour later in life.

We found that within the first month after arriving on the wintering grounds, juveniles are 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 two separate years, unpublished data, Suppl. Figure S3). A reduction in diet variation from juvenile to adult stage in the Wadden Sea could have three potential non-mutual explanations: (1) Competition 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 *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 be that juveniles also search for food during high tide period in atypical locations. (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). Ultimately, survival of those juveniles that eat different types of food may be low.

The amount of feedback between the foraging behaviour and its outcome, i.e., foraging experiences juvenile gain in the marine environment, may influence the consistency of exploratory behaviour. We 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 in the wintering grounds did not have a higher difference between repeats than individuals that were caught and tested more days post-migration. In our study, we did not catch and test the same juvenile in different time periods, instead we collected data from different juveniles that arrived in the wintering grounds in different times. Thus, we did not account for the individual variation in learning between juveniles. Speed of learning through feedback between detecting, catching, and processing food can vary between juveniles, thus the amount of time is needed for behaviour to become consistent may not be the same for all juvenile red knots. For example, young ones mostly learn from watching experienced adults in social foraging animals (Heyes, 1994; Watts, 1985); juvenile red knots that forages in the same flock with adults may be more likely to learn certain foraging strategies faster.

In conclusion, larger within-individual variance in exploration scores of juveniles (vs. adults) together with their diverse diet in our study shows that free-living juveniles are likely to practice their foraging strategies in the wild. The feedback they receive between foraging behaviour and its outcome during the first weeks in the wintering grounds later develops into consistency in both foraging tactics and exploratory behaviour. However, each juvenile is likely to differ in how fast they apply these feedbacks in their behaviour. The environment that the juveniles experience together with the switch from tundra to marine diet may initiate the changes in the foraging behaviour. Through its role in repeated exposures, the environment an individual experiences can mould the behaviour during ontogeny (West-Eberhard, 2005).

Acknowledgements

We thank Natuurmonumenten for permission to conduct this research on Griend. We thank field assistants and volunteers for helping with data collection, in particular, we thank Anne Dekinga, Job ten Horn, Luc de Monte, Calu Noriega Hoyos. We thank Ronald van Bommel and Marcel van der Meer for technical assistance with the stable isotope analyses. We thank the crews of the NIOZ research vessels RV *Navicula* and RV *Stern* for safely transporting us around the Wadden Sea. We thank Raphaël Royauté for directing us to the method that we were able to compare variance ratios of different groups in the same dataset. We also thank Eus de Groot for his observations on juvenile knots foraging on algae. This study was funded by the core funding of NIOZ and the NWO-Veni grant to AIB (VI.Veni.192.051).

Authors' Contributions

SE and AIB designed the study. SE, CEB and ED collected the data. SE analysed the data. SE drafted the first version of the manuscript. All authors contributed to writing of the final manuscript. None of the authors have a conflict of interest.

Supplementary Materials

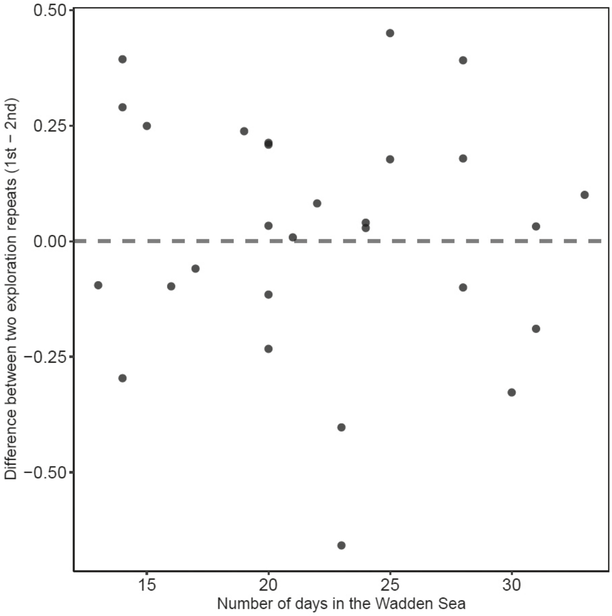


Figure S1. Real difference between two exploration speed (log10 cm/s) measures (y axis), estimated days since arrival in the Wadden Sea. Individual points above zero indicate that juveniles were faster in their first exploration measure than second measure, and values below zero show that juvenile were faster in second exploration measure than first measure.

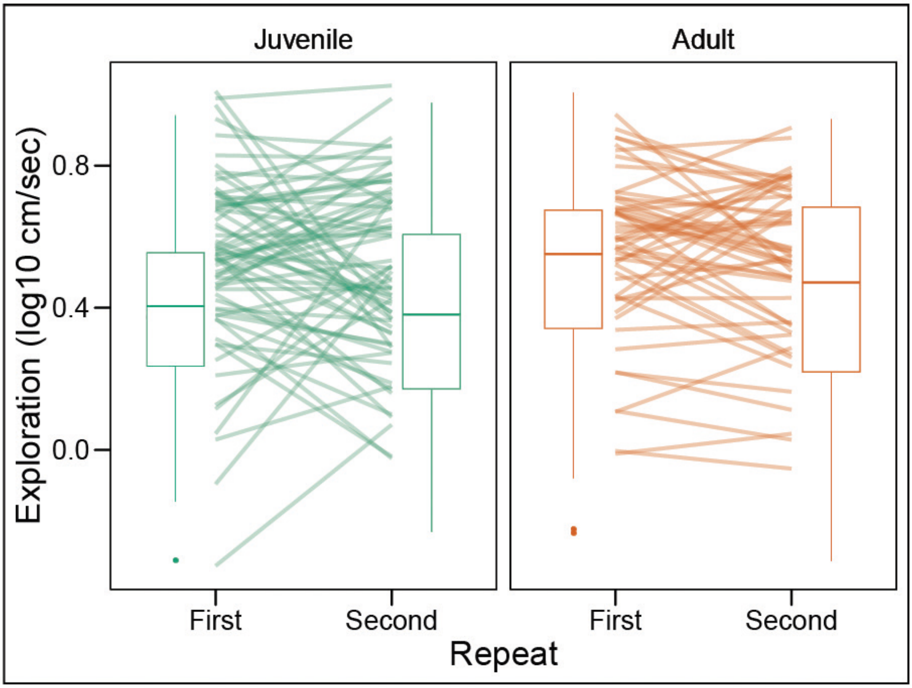


Figure S2. Repeated measurements of exploration speed (log10 cm/sec) on adults and juveniles.

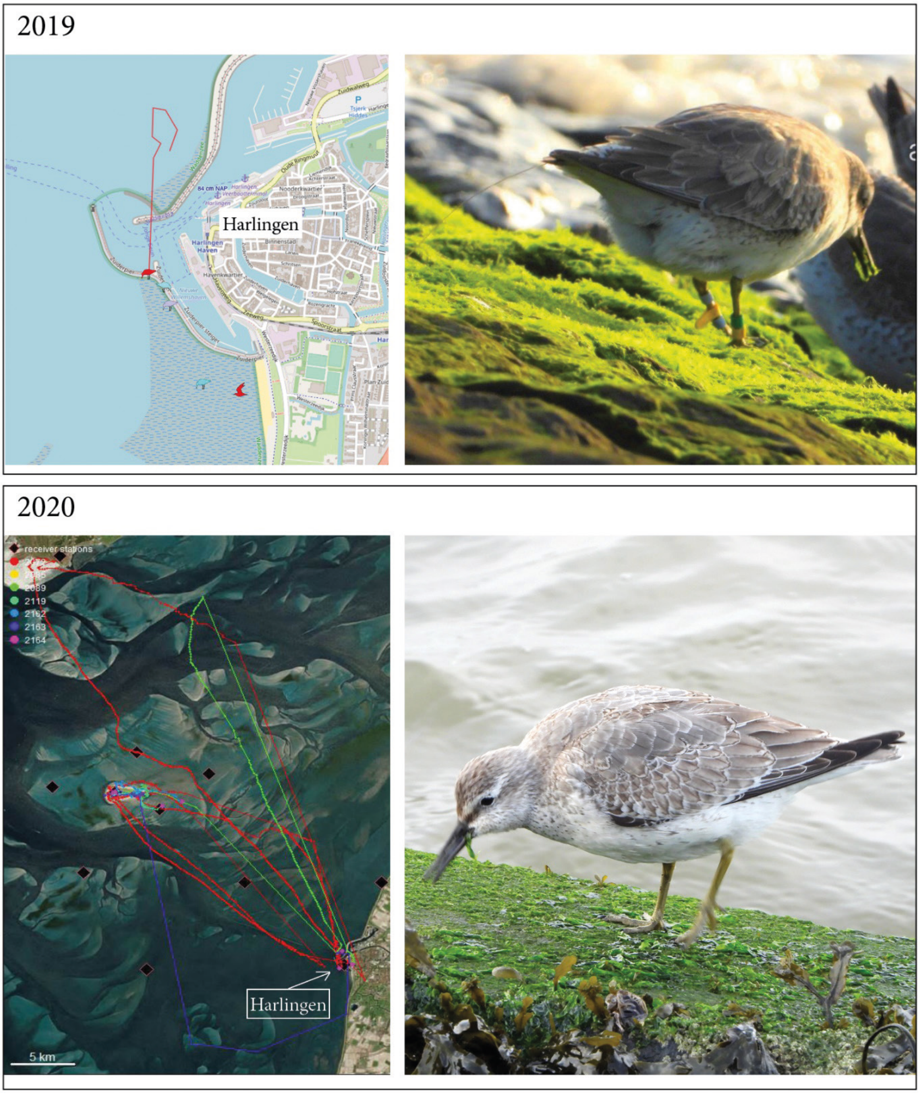


Figure S3. Anecdotal observations from juvenile red knots eating algae on Harlingen harbour in 2019 and 2020. Some juveniles were tagged so we could retrieve their location in the Wadden Sea (left panel). Many thanks to Eus de Groot for taking red knot pictures in Harlingen (right panel).

BOX 1

Slow-exploring red knots benefit from foraging in groups

Selin Ersoy, Aileen Roncoroni, Allert I. Bijleveld

Individuals living in groups can benefit from using social information on foraging opportunities, which may ultimately lead to increased survival rates (Clark and Mangel, 1986). Individuals that live in groups (e.g., schools of fish, flocks of birds) have been shown to locate food through observing conspecifics that results in an increase in their foraging success (Buckley, 1996). Interestingly, individuals can differ consistently in how they locate the food (i.e., finding food by themselves or by observing foraging success by others; reviewed in Valone, 2007). Consistent behavioural traits (also known as personality traits; Verbeek et al., 1994) could be one of the factors associating with individual differences in food finding strategies. For example, faster exploring great tits *Parus major* in controlled settings are more likely to discover new feeders in the natural habitat than slower explorers (van Overveld and Matthysen, 2010) and slower barnacle geese *Branta leucopsis* scrounge on the food discoveries of faster geese (Kurvers et al., 2010b). Faster exploring individuals may be more likely to find food successfully themselves when foraging alone (vs. in a group) while slower explorers may be more successful at finding food in group foraging scenarios (vs. alone). Understanding how exploratory behaviour links to foraging behaviour when foraging in groups could give insights on the individual differences in foraging success (Marchetti and Drent, 2000). Here, we conducted experiments to investigate the relationship between exploratory behaviour and foraging success (i.e., speed of finding food) in group foraging scenarios of captive red knots *Calidris canutus*.

Red knot are shorebirds that forage on patchily distributed shellfish in large groups of up to 15,000 individuals in the wild (Piersma et al., 1993). Red knots can detect the foraging success of conspecifics and scrounge on the food discoveries of others (Bijleveld et al., 2015), however, they do so while avoiding physical encounters with conspecifics (Bijleveld et al., 2012). In laboratory experiments, red knots have been shown to differ consistently in exploratory behaviour (Bijleveld et al., 2014). Exploratory behaviour could be one of the individual behavioural traits that is associated with successful food finding while foraging with conspecifics in group. In laboratory experiments using captive red knots, we asked how the speed of finding hidden food in experimental arena is affected by 1) exploratory behaviour, 2) number of conspecifics, and 3) how these two variables interact.

Fifty red knots of the *islandica* subspecies were captured with mist-nets in the Dutch Wadden Sea near the island of Griend (53°15’N, 5°15’E) in October 2019 and then transported to the shorebird facility in the NIOZ Royal Netherlands Institute for Sea

Research (53°00’12.1 “N, 4°47’23.3“E). We first assayed the exploratory behaviour of red knots in the indoor arena under controlled conditions (with the same method used in Chapter Two, Bijleveld et al., 2014; Kok et al., 2019). In short, we tested the birds inside an arena (7m x 7m x 3m) filled with 30 cm seawater and containing food-free wet sand patches (1m x 1m x 35cm), and we recorded the trials with a camera placed on the ceiling. The individual’s movements were later tracked with an automated tracking software (idTracker, Pérez-Escudero et al., 2014). We calculated the movement speed of the bird. The log10 of the mean speed (m/s) was used as a measure for exploration speed.

We then created an experimental indoor foraging arena (7 m x 3.15 m x 3 m) where food was patchily distributed and hidden in trays (Figure 1). All trays were empty apart from one that was randomly assigned, and individuals needed to search each tray to find the food. We tested each individual by themselves (i.e., number of conspecifics = 0) and with increasing number of conspecifics in group (0 to 3). We ran a total of 200 experimental trials (50 birds x 4 trials). We first tested the birds individually in the experimental arena ($N_{trial} = 50$) and then with other randomly assigned individuals that had exploration speed (log10 cm/s) ranging from -0.15 to 0.93, forming groups of two ($N_{trial} = 50$), three ($N_{trial} = 50$) and four ($N_{trial} = 50$). To eliminate the effect of the time of the day on the experimental results, we randomly assigned the order of trials per day. In the group experiments, we only analysed the focal bird’s behaviour (i.e., not the partners’). The time from the bird to enter the experimental arena until the bird discovered the food patch was defined as “searching time”. In case birds did not search for the food patch or did not find it, experiments were ended after 10 minutes.

To analyse the data of the foraging experiments, we used a linear mixed-effect model using the *lme4* package in R after checking for collinearity, overdispersion, and model assumptions (homogeneity and normality of residuals) (Bates et al., 2011). The response variable was the searching time in seconds and was log10 transformed to meet normality assumptions. We added exploration speed (log10 cm/s) obtained from the exploration assays, number of conspecifics (cont. 0-3), and interaction between the two as fixed effects. To control for repeated measures on individuals, we added ‘focal bird ID nested in group’ and the ‘location ID of the food patch’ as random effects.

Box 1

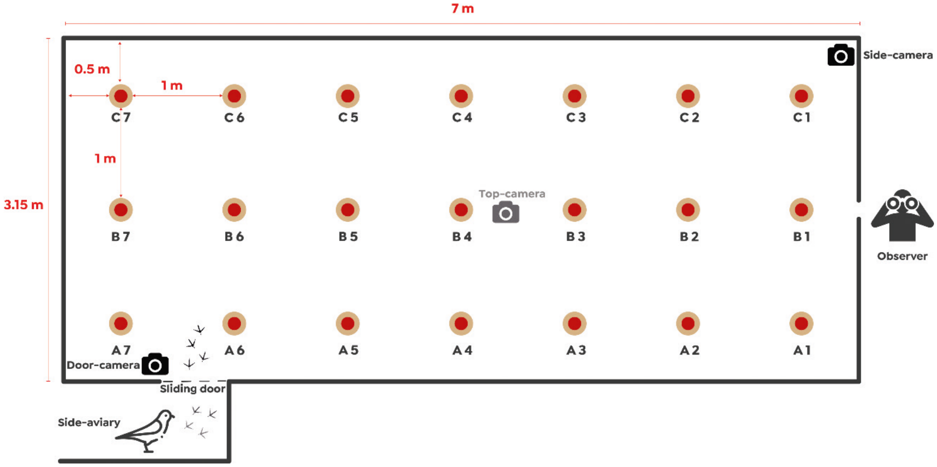


Figure 1: Illustration showing the experimental arena with the location and labels of the food patches. Only one of the patches randomly assigned had food in it. Illustration by Aileen Roncoroni.

We found that, food searching time decreased with increased number of conspecifics in the group (Table 1), showing that all individuals became faster in food-finding when in a group. Slope of food searching time and number of conspecifics was different for different values of exploration speed (Table 1); slope of slow explorers declined, and slope of fast explorers increased with increasing number of conspecifics in the group (Figure 2b). This can be interpreted that the slowest explorers became faster in finding food with increasing number of conspecifics in the group, but that the fastest exploring birds took longer to find food with increasing number of conspecifics in the group (Figure 2).

Table 1. Results from the statistical analysis performed through a linear mixed-effect model investigating the factors explaining the food searching time in experiments. Bold font indicates confidence intervals do not overlap zero. ICC is the intraclass correlation coefficient, N indicates sample size.

	Searching time (seconds)
Predictors	*Estimates 95% CI*
Intercept	**1.88 (1.70, 2.06)**
Exploration score (log10 mean speed cm/s)	**-0.52 (-0.93, -0.11)**
Number of conspecifics (cont. 0-3)	**-0.17 (-0.25, -0.09)**
Exploration score: Number of conspecifics (cont. 0-3)	**0.28 (0.07, 0.49)**

Table 1. Continued

	Searching time (seconds)
Predictors	*Estimates 95% CI*
Random Effects	
Residual	0.15
Among-BirdID	0.08
Among-Food location	0.03
BirdID nested in group	0.01
ICC	0.39
N_{BirdID}	50
$N_{Food\ location}$	14
Observations	200
Marginal R^2 / Conditional R^2	0.079 / 0.436

This study provides insights on how foraging success of single individuals can be influenced by the presence of other individuals in a way that depends on their personality. Faster exploring red knots were fast at finding food when tested alone but slower explorers became faster with increasing number of conspecifics in group. Taking together, our results suggests that the relation between personality and foraging success is not fixed but depends on the foraging context (Marchetti and Drent, 2000). Faster exploring individuals that are better at finding food may attract slower individuals in their foraging areas that may increase competition for food. However, faster explorers may also gain greater benefits from being in group because foraging in a group reduces predation risk (Elgar, 1986). Individuals with different personalities may therefore have different costs and benefits associated with their different tactics that nevertheless result in overall equally successful strategies.

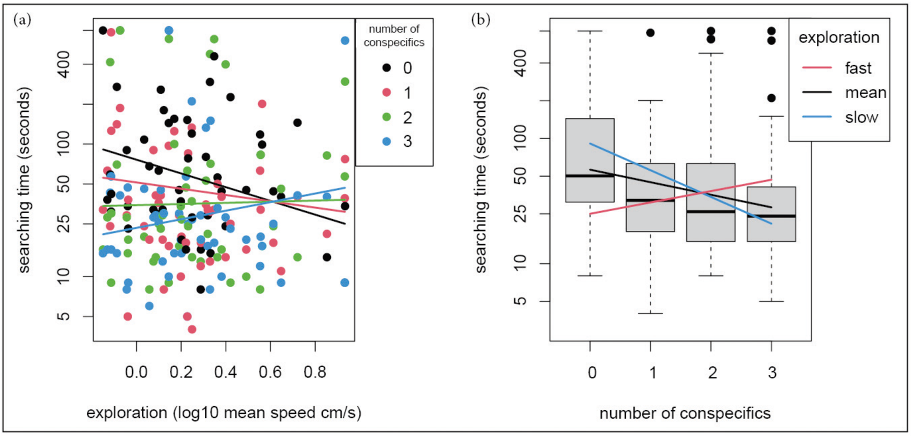


Figure 2. Exploration speed (log10 cm/s) interacting with number of conspecifics (0-3) predicts food-searching time (in seconds). (a) For red knots tested individually (number of conspecifics = 0, slope of black line), faster explorers found food in less time than slower explorers. With the increasing number of conspecifics (1, 2 and 3, slopes of red, green, and blue lines, respectively), slower explorers found food in less time than faster explorers. (b) Continuous exploration score is separated into three groups for visualisation purposes only: 20 individuals with higher exploration speeds are labelled as “fast”, 20 with lower exploration speeds are considered “slow”, and the 10 in the middle constitute the mean exploration score of the group. Slope of slow explorers declined, and slope of fast explorers increased with increasing group size.

CHAPTER 4

Free-living red knots show personality-related movements at night, but not during the day

Selin Ersoy, Pratik Gupte, Christine Beardsworth, Allert I. Bijleveld

Manuscript

Abstract

Movement can be a measurable result of behavioural mechanisms that are triggered by the environmental context. Movement patterns can consistently differ across individuals within the same population, and personality traits measured in controlled settings sometimes link to movement patterns in the wild. However, the link between personality and movement is not always evident. This could be because the behaviour of an individual is triggered by environmental factors, such as storms, group foraging or predation risk, and personality-related movement patterns can differ between different contexts. Shorebirds that forage both during the day and the night provides an opportunity to test whether personality-related movement patterns differ between two very different contexts. Whereas daylight provides an abundance of visual cues for foraging opportunities such as flock mates or landmarks, as well as the risk of aerial predation, these are largely absent at night. Differences in predation risk and visual cues between day and night could mean that personality differences are masked by these challenges or conversely, amplified. To test the relationship between personality trait and movement in two different context (day and night), we captured free-living red knots *Calidris canutus* and assayed their exploration speed in controlled settings. We then released the same birds with ATLAS transmitters and investigated their movement within and between residence patches (areas where birds are stationary or walking). We found that red knots are moderately repeatable on their movement speed in residence patches ($R = 0.26$). All red knots moved further between residence patches and had higher within-residence patch duration, distance, and displacement distance, at night compared to daytime. We also found that faster exploring red knots differed in these movement patterns at night more than slower explorers; specifically, faster (vs. slower) exploring knots moved further between residence patches and travelled more, stayed longer, and displaced further in a residence patch at night. The number of residence patches visited per low tide did not differ between day and night, but faster (vs. slower) exploring red knots visited fewer residence patches at night. In contrast, none of the residence patch movement parameters during the day correlated with exploration scores. The differences between day and night may be explained by personality being masked by the abundance of visual cues for foraging opportunities such as flock mates or landmarks, as well as the risk of aerial predation. The absence of threats and cues at night would facilitate the expression of personality-related movement behaviours.

1. Introduction

Animal movement varies from fine-scale foraging movements to larger-scale migratory movements. Movement patterns can differ across individuals within the same population, and this difference is found to be consistent in behaviours such as foraging site fidelity (Harris et al., 2019), distance travelled per day (Hertel et al., 2021), and stopover use during migration (Hasselquist et al., 2017). Consistent differences in behaviour over time and across contexts among individuals within the same species has been studied within the framework of 'animal personality' and has been shown to be a common, cross-taxonomic phenomenon in nature (Réale et al., 2010; Sih et al., 2004). This consistency across contexts is often studied in a laboratory setting, but field data linking personality traits that are assayed in controlled settings to behaviour in the wild are limited (Carter et al., 2013a). This may be because following wild animals in their natural environments can be technologically challenging. In recent years, technological advances in animal tracking have allowed systematic collection of individual movement data (Jetz et al., 2022; Nathan et al., 2022), and advanced spatial analyses have revealed previously unknown processes on individual differences in space use (Webber et al., 2020). However, movement behaviour of an individual in the wild often depends on the environmental context and/or on the accuracy of the movement data. Linking personality traits that are assayed in controlled settings to movement behaviours of free-living animals is therefore an important step in understanding behaviour in the wild (Spiegel et al., 2017).

Experimentally measured personality traits are sometimes found to correlate with movement behaviour in the wild (e.g., Harris et al., 2019; Patrick et al., 2017; Schirmer et al., 2019) but this link is not always evident (e.g., Carter et al., 2013b; Cote et al., 2013; Luna et al., 2019). This could be because individuals usually face different environmental contexts in the wild (e.g., predation, food availability, social dynamics). For example, dispersing mosquitofish *Gambusia affinis* are less social than resident mosquitofish when there is no predation risk, but they do not show personality-related dispersal behaviour when there is a predation risk; then both dispersers and residents show similar personalities (Cote et al., 2013). Visual cues can be an important determinant of the behaviour in the wild such as when animals can see that they are under risk of a predation or when their foraging success depends on reliable social information (Engeszer et al., 2004; Lima and Dill, 1990). For example, shy chacma baboons *Papio ursinus* scrounge on the food discoveries of bold baboons when the food is hidden, but they do not show personality-related foraging decision when they can see the food (Carter et al., 2013b).

Movement can be a measurable result of behavioural mechanisms that are triggered by the environmental context and thus, provides a good opportunity to test whether personality traits that are assayed in controlled settings are context-dependent in the wild. Shorebirds that forage both during the day and the night offer a possibility to test whether personality-related movement patterns differ between two very different contexts. Whereas daylight provides an abundance of visual cues for foraging opportunities such as flock mates or landmarks, as well as the risk of aerial predation, these are largely absent at night. The red knot *Calidris canutus islandica* is a migratory shorebird that breeds in the high Arctic of northern Greenland and north-east Canada and winters in the mudflats of the Wadden Sea in western Europe (Piersma, 2007). Under laboratory conditions, red knots differ consistently among individuals in their exploratory behaviour (Bijleveld et al., 2014; Ersoy et al., 2022; Kok et al., 2019) and exploratory movement speed is repeatable over time in controlled settings ($R = 0.67$, Ersoy et al., 2022). Faster exploring red knots eat higher quality, soft prey and have a smaller gizzard muscle (Bijleveld et al., 2014; Ersoy et al., 2022). Red knots with smaller (vs. bigger) gizzards have shown to move larger areas such as between England, Germany, and Netherlands (Bijleveld et al., 2014) thus, faster (vs. slower) exploring individuals may be expected to use larger space in the wild.

In the Wadden Sea, there are two low tide periods per day (24 h 50 m). On the mudflats, red knots forage in large groups (up to flocks of 15,000 individuals, Piersma et al., 1993) on a highly heterogeneous and patchily distributed prey (Bijleveld et al., 2016; Kraan et al., 2009, 2010; Oudman et al., 2018). Red knots mainly forage on buried hard-shelled prey which they find by touch while probing the sediment (van Gils and Piersma, 1999). When a prey is detected, they briefly handle and swallow it whole (Suppl. videos from Ersoy et al., 2022 and Bijleveld et al., 2015). During foraging, they can observe each other and detect the foraging success of conspecifics (Bijleveld et al., 2015). Besides gathering information about food patches, foraging in large groups also brings safety in case of predator attacks such as from peregrine falcons *Falco peregrinus* (Piersma et al., 1993). In line with previous research, we may expect personality to influence movement parameters (Bijleveld et al., 2014). However, this might depend on the environmental context. Red knots may behave similarly during the day, regardless of personality score. This is because red knots forage with very large numbers of flock mates who are unlikely to share the same personality score thus, dampening the effect of personality on movement parameters. Equally, when a predator is present, all individuals may react similarly (Cote et al., 2013) to avoid being singled out by a predator (Page and Whitacre, 1975) thus, masking the effects of personality on movement parameters. However, reduction in light levels during the night may mean that red knots might not be able to use flock mates as indicators of foraging possibilities and predation risk is low because peregrine falcons are not active during the night. Thus, the absence of these environmental drivers at night may amplify the effect of personality on movement parameters at night.

In this study, we tested the relationship between a personality trait and movement parameters in two different context (day and night). First, we captured free-living red knots *Calidris canutus* and assayed their exploration speed in a controlled setting. We then released the same birds with ATLAS transmitters and investigated their movement during the day and the night. Residence patches represent areas where the birds are stationary or slow moving (i.e., between flight movements; Barraquand and Benhamou, 2008) and therefore indicating potential foraging activity during low tide. We specifically looked at movement within and between residence patches. As red knots show high repeatability in their movement speed in captivity (Ersoy et al., 2022), we also expected high repeatability in movement speed within residence patches (Stuber et al., 2022). We investigated how the experimentally measured personality trait – exploration speed – interacts with day and night residence patch movement parameters. We predicted that faster exploring red knots would move more frequently and larger distances during low tide than slower exploring red knots. We attempted to assay this by assessing different temporal and spatial scales of movement; specifically, displacement and total distance travelled within a residence patch, duration of residence, number of residence patches visited and displacement distance between residence patches. We expected this effect to be more prominent at night than during the day.

2. Materials and Methods

2.1. Study system

We collected data from red knots in three field seasons during August to October in years 2018 to 2020 on Griend mudflats in the western Dutch Wadden Sea (53°15’N, 5°15’E). For this study, in total 250 adult red knots were caught through mist-netting during 7 catching attempts in the new moon nights of August 2018 (N= 38), September 2018 (N= 70), August 2019 (N= 27), September 2019 (N= 13), October 2019 (N= 62), August 2020 (N= 8), and September 2020 (N= 32). Red knots were given a numbered metal ring for individual identification and their biometrics were measured. They were then moved to temporary outdoor aviaries of 2m x 0.75m x 0.4m (LxWxH) made of linen with a net floor. These aviaries were placed on natural sand/grass ground and provided with *ad libitum* food (live and dried mealworms) and water (freshwater and seawater). Group sizes in the aviaries were between 8 and 12 birds.

2.2. Exploratory behaviour

Exploratory personality was measured in a field-based mobile arena to measure exploration speed within 24hr after capture with identical method published in Ersoy et al (2022). The birds that were caught in 2018 and 2019 were also used in Ersoy et al. (2022). To score the exploration speed of red knots at the field site, we used a pyramid shaped mobile arena of 2m x 2m x 2m. The floor of the unit consists of seawater of 20 cm depth in which four identical trays with wet sand (61cm x 40cm x 25cm) were situated. Birds could explore these artificial patches in which no food was offered. A GoPro (Hero Black) camera was fixed to the ceiling to record the movement trajectories. To standardize the procedure and motivate birds equally for the personality tests, we placed them individually into a holding pen without access to food for 2 hours prior to the experiment. After 2 hours, we started the experiments by gently placing the bird on the sand patch in the experimental unit. Individual trials lasted 20 minutes per bird.

To calculate exploratory movement of individuals from videos recorded by the ceiling camera, 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 minutes that each bird spent in the mobile arena. Exploration speed is calculated as mean speed between consecutive positions (cm/s) per trial. Errors in the video-based position tracking were filtered out by excluding unrealistic speeds higher than 200 cm/s.

After measuring individual exploration, red knots were released on Griend mudflats (where they were captured before) during the low tide period at the end of the day with unique combinations of colour rings and with ATLAS tags (Toledo et al., 2022) weighing 4.4 g (ca. 3.3% of red knot body mass) to retrieve their locations in the Wadden Sea (Beardsworth et al., 2022; Bijleveld et al., 2021; Nathan et al., 2022). All necessary permits to catch, handle, tag, test, and keep red knots were granted to the NIOZ by the Dutch law and regulation under protocol number NIOAVD8020020171505.

2.3. Tracking movement

We used the Wadden Sea ATLAS (Advanced Tracking and Localization of Animals in real-life Systems) tracking system (hereafter WATLAS, Bijleveld et al., 2021) to track red knots on Griend, an important shorebird roosting and foraging site (Piersma et al., 1993). WATLAS is a regional-scale, high-throughput movement tracking system that focuses on the mudflats surrounding Griend. WATLAS comprises an array of receivers that continuously detect tag transmissions. When a transmission is detected, the receiver records the arrival time. These arrival time measurements are sent to a centralized server where location estimates can be computed when at least three receivers detect the signal (see Bijleveld et al., 2021 for further details on WATLAS; and Weiser et al., 2016 for similar systems). In our study, the tags transmit every three seconds in 2018 and every six seconds in 2019 and 2020, and birds were localized as long as they were within the receiver array.

We removed localizations recorded in the 24 hours immediately following release, to prevent the stress of capture and experimentation from biasing further analyses. We first subsampled 2018 data in six seconds to bring these to the same tracking interval as 2019 and 2020 data. To exclude errors in the localization data, we pre-processed these following a protocol we had developed in our study system and for high-throughput animal tracking generally (Beardsworth et al., 2022; Gupte et al., 2022). Briefly, we first targeted large-scale errors and filtered out localizations where the error estimate (provided by the WATLAS system) in the x axis (VARX) and the y axis (VARY) was less than 5000, and where movement speed between localizations was > 30 ms^{-1}. We then accounted for fine-scale errors by taking a 5-point moving median of the x and y coordinates.

2.4. Residence patch identification

We used the tracking data (localization every six seconds) to identify residence patches for our birds (Barraquand and Benhamou, 2008; Bijleveld et al., 2016; Gupte et al., 2022). We calculated residence patches per bird between two consecutive high tides if it had > 100 localizations. Three or more localizations within a 75m buffer of each other and lasting two minutes were classified as a residence patch. For situations with missing localizations, residence patches were additionally differentiated if the speed between consecutive localizations was above 3 m s^{-1}, or if the gap between localizations lasted longer than 180 minutes. For each residence patch, we then computed the following metrics: the median coordinates, the entry and exit coordinates, their associated absolute times, the number of localizations, the duration, and the distance travelled within each patch (as summed distance between localizations) and the linear displacement distance in a patch (from entry to exit localization). Example figure showing residence patches in a map can be found in Suppl. Fig. S1.

Observational study data showed that red knots spend ~ 80% of time foraging when mudflats are exposed (Ersoy et al., 2022). In this study, we used residence patches only from periods when mudflats were exposed and available for foraging, which corresponded to water levels below 50 cm NAP (hereafter called 'low tide', Suppl. Fig. S2). We used the water-level data that is recorded by Rijkswaterstaat at West-Terschelling harbour (53.361 N, 5.216 E). Because of the distance from this location to our study site Griend (12.3 km), we added a 30 min offset to the water level. To investigate the movement difference between day and night context, we additionally selected residence patches that started and ended in day or night only, excluding the twilight period. Day and night were assigned using the *solarpos* function from the *maptools* (v1.0-2) R package to calculate the position (in degrees) of the sun in relation to the horizon (>0 = day; <-18 = night) at Griend.

2.5. Data analysis

We analysed residence patch data from 186 red knots that were assayed in exploratory behaviour and released with WATLAS tags (Suppl. Fig. S3) between mid-August to late-October in study years 2018, 2019, and 2020 around Griend area in the Dutch Wadden Sea. We have identified in total 46,206 residence patches (28,341 in 2018, 3,892 in 2019, and 3,943 in 2020) with a mean of 248 residence patches per bird (*Median* = 149, *Min* = 22, *Max* = 1033). In all years, nights were shorter than days, which resulted in a lower number of residence patches at night than during the day. Specifically, number of low tides at night was $N_{tide\_2018}=81$, $N_{tide\_2019}=115$, $N_{tide\_2020}=90$ and during the day was $N_{tide\_2018}=103$, $N_{tide\_2019}=146$, $N_{tide\_2020}=111$. The numbers of individuals tracked at night were $N_{birdID\_2018}=68$, $N_{birdID\_2019}=76$, $N_{birdID\_2020}=45$ and during the day was $N_{birdID\_2018}=71$, $N_{birdID\_2019}=92$, $N_{birdID\_2020}=55$. The mean duration of residence patches at night was 67 min and during the day was 45 min. Individuals did not differ in the number of localizations between day and night according to their exploration speed.

We first investigate whether foraging-related movement speed of an individual is repeatable. We used mean speed per low tide as response variable to make the repeatability of movement behaviour comparable to our exploration measurements in controlled settings (mean speed of 20 min trial). We built a mixed model with *gaussian* distribution and response variable was log10 transformed prior to the analysis to fit normality assumptions. To measure the repeatability from mixed model, we added Bird ID as random effect and night/day ratio and the mean water level of the tide as fixed effects. None of the Bird ID was repeated in different years. Repeatability (*R*) was calculated by dividing among-individual variation by the sum of among- and within-individual variation (Nakagawa and Schielzeth, 2010). We report how both within-individual (i.e., residual) and among-individual variance components contributed to the overall repeatability.

We then examined how an experimentally measured personality trait – exploration speed – predicts residence patch movements of free-living red knots during low tide using mixed models with *gaussian* distribution. In all models, we controlled for available area for foraging on the mudflats because the available area the birds can go to on intertidal mudflats changes depending on the water level and the height of the location. To calculate the available area, we used the bathymetry data (includes information about the depths and shapes of underwater terrain) for our study area (Griend) from Rijkswaterstaat, we then counted the number of raster cells (20x20 m), which reflected the total available area exposed and available for foraging (Suppl. Fig. S2). We controlled for day and night period differences (as nights were always shorter than days in our sampling periods) with adding ratio between length of night over length of day as a covariate. We corrected for tide status (‘incoming’ or ‘outcoming’) as all birds are pushed by the water to the beach with incoming tide when water level increases, but this tidal force on birds’ movement is absent in outgoing tide when water level decreases. We additionally assumed that localization measurements taken from the same individual, tide and year are more similar to each other than expected by random, i.e., they are not independent. Therefore, we added the factors ‘Bird ID’, ‘Tide ID’, and ‘Year’ as random effects.

Model 1, we fitted multivariate mixed effect model with multiple response variables (within-residence patch parameters: distance in patch (m), duration in patch (min), displacement distance in patch (m)). Response variables were log10 transformed prior to the analysis to fit normality assumptions. The three behaviours were on different scales (distance and displacement distance in metres, residence duration in minutes). For better model fitting we scaled the behaviours, meaning that we centred each variable at its mean value and standardize it to units of one phenotypic standard deviation. Exploration speed measured in experimental setup (log10 mean speed cm/sec) interacting with day-night status (categorical; 'day' or 'night') in addition to available area, night/day ratio, and tide status (categorical; 'incoming' or 'outgoing') were added as explanatory variables together with random factors (Bird ID, Tide ID, Year). To estimate the correlation between response variables on the Bird ID level, we specified in the model that all varying effects of Bird ID should be modelled as correlated.

Model 2, displacement distance between residence patches (m) was calculated as the linear distance travelled from exit to entry localizations of consecutive residence patches was fitted as a response variable and was log10 transformed prior to the analysis to fit normality assumptions. Exploration speed measured in experimental setup (log10 mean speed cm/sec) interacting with day-night status (categorical; 'day' or 'night') in addition to night/day ratio were added as explanatory variables together with random factors (Bird ID, Tide ID, Year).

Model 3, number of residence patches visited per low tide was calculated by counting the number of residence patches of a bird visited per low tide and correcting for the total duration of residence patches that bird was tracked in that low tide. The number of patch visits was log10 transformed prior to the analysis to fit normality assumptions. Exploration speed measured in experimental setup (log10 mean speed cm/sec) interacting with day-night status (categorical; 'day' or 'night') in addition to available area, night/day ratio, and tide status (categorical; 'incoming' or 'outgoing') were added as explanatory variables together with random factors (Bird ID, Tide ID, Year).

We fitted all models using R package *brms* (Bürkner, 2017) based on the Bayesian software *Stan* (Carpenter et al., 2017; Stan Development Team, 2018). We run the models using two Markov chains for 5,000 iterations with 1,000 burn-in iterations, with a warmup of 5,000, and a thinning interval of 4. Given that response variables were transformed prior to the analysis, we used uninformative default priors on all parameters.

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 4.2.1 (R Core Team, 2014). We additionally ran *post hoc* comparisons for the interaction terms 'Exploration speed: Day/Night' using *emmeans* R package (Length, 2022).

3. Results

Individual repeatability of mean speed in a residence patch was 0.26 (0.18, 0.32 95%CI), among-individual variance 0.07 (0.06, 0.07 95%CI) and within-individual (i.e., residual) variance was 0.20 (0.19, 0.21 95%CI).

Model 1 with within-residence patch movement parameters (distance (m), duration (min), displacement distance (m) in a residence patch, Table 1) showed that at the population level, individuals had higher values at night than during the day, and that day-night movement revealed an interaction with exploration speed that was measured in captivity. Specifically, a *post hoc* comparison showed that at night, faster exploring red knots moved further, stayed longer, and displaced further within a residence patch than slower exploring red knots (Figure 1). In contrast, individuals that differed in exploration speed in captivity did not differ in within-residence patch movement parameters during the day. The area available on mudflats predicted the displacement distance within a residence patch (positively) but did not predict distance travelled and duration in a residence patch. During outgoing tide, red knots travelled further and stayed longer but displaced shorter in a residence patch than incoming tide. The correlation analysis between three response variables on the individual level showed that distance and duration in a residence patch are positively correlated while displacement in a residence patch did not correlate with other response variables.

Model 2 on displacement distance between patches (Table 1) showed that individuals travelled further between patches at night than during the day, and that day-night movement revealed an interaction with exploration speed measured in captivity. Specifically, a *post hoc* comparison showed that at night, faster exploring red knots moved further between residence patches than slower exploring red knots (Figure 2). In contrast, individuals that differed in exploration speed in captivity did not differ on the displacement distance between patches during the day. During outgoing tide, red knots travelled further between residence patches than incoming tide.

Model 3 on number of residence patches visited per low tide (Table 1) showed that day-night movement revealed an interaction with exploration speed measured in captivity. Specifically, a *post hoc* comparison showed that at night, faster exploring red knots visited smaller number of residence patches than slower exploring red knots. In contrast, individuals that differed in exploration speed in captivity did not differ on the number of residence patches visited per tide during the day (Figure 2).

Table 1: Results for the effects of exploration speed interacting with day-night, available area, tide status, and night/day length ratio on distance travelled (m), duration (min), and displacement distance (m) within residence patch (Model 1), and exploration speed interacting with day-night, available area, tide status, and night/day length ratio on the displacement distance travelled between patches (Model 2), and exploration speed interacting with day-night and night/day length ratio on number of patch visits per low tide (Model 3). *Post hoc* comparison shows marginal means of linear trends and *contrasts* which shows general contrasts of factor levels. Bold font indicates 95% Bayesian Credible Intervals does not overlap zero.

	Model 1			Model 2	Model 3
	Distance in residence patch (log10 m)	**Duration in residence patch (log10 min)**	**Displacement in residence patch (log10 m)**	**Displacement between residence patches (log10 m)**	**Number of residence patches visited (log10 n per low tide)**
	Estimate *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*
Population-Level Effects:					
Intercept	-0.06 (-0.24, 0.13)	-0.10 (-0.50, 0.22)	0.11 (-0.24, 0.43)	**2.30** **(1.97, 2.50)**	**0.39** **(0.16, 0.60)**
Exploration speed (log10 cm/s)	-0.03 (-0.10, 0.04)	-0.02 (-0.09, 0.04)	-0.04 (-0.14, 0.05)	-0.01 (-0.04, 0.02)	0.04 (-0.02, 0.09)
Day-Night [night]	**0.34** **(0.29, 0.39)**	**0.35** **(0.30, 0.40)**	**0.58** **(0.54, 0.64)**	**0.16** **(0.14, 0.19)**	0.00 (-0.03, 0.03)
Night/day ratio	-0.07 (-0.16, 0.02)	-0.03 (-0.11, 0.05)	-0.07 (-0.17, 0.02)	-0.04 (-0.08, 0.01)	-0.01 (-0.09, 0.07)
Area available (scaled)	0.00 (.000, 0.01)	-0.02 (-0.03, -0.02)	0.05 (0.05, 0.06)	0.00 (0.00, 0.01)	
Tide status [outgoing]	**0.12** **(0.11, 0.14)**	**0.20** **(0.19, 0.22)**	**-0.18** **(-0.19, -0.16)**	**0.05** **(0.05, 0.06)**	
Exploration speed (log10 cm/s) : Day-Night [night]	**0.14** **(0.06, 0.22)**	**0.10** **(0.02, 0.19)**	**0.11** **(0.02, 0.19)**	**0.06** **(0.02, 0.10)**	**-0.11** **(-0.16, -0.05)**

Table 1. Continued

	Model 1			Model 2	Model 3
	Distance in residence patch (log10 m)	**Duration in residence patch (log10 min)**	**Displacement in residence patch (log10 m)**	**Displacement between residence patches (log10 m)**	**Number of residence patches visited (log10 n per low tide)**
	Estimate *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*
Group-Level Effects:					
Bird ID (Number of levels: 186)					
Explained variance (sd)	0.09 (0.07, 0.11)	0.07 (0.06, 0.09)	0.1 (0.08, 0.12)	0.04 (0.03, 0.05)	0.05 (0.04, 0.06)
cor(distance in patch, displacement in patch)	-0.03 (-0.31, 0.23)				
cor(distance in patch, duration in patch)	**0.57** **(0.37, 0.72)**				
cor(displacement in patch, duration in patch)	-0.06 (-0.35, 0.23)				
Tide ID (Number of levels: 410)					
Explained variance (sd)	0.14 (0.13, 0.16)	0.15 (0.14, 0.17)	0.17 (0.16, 0.19)	0.09 (0.08, 0.10)	0.15 (0.14, 0.16)
Year (Number of levels: 3)					
Explained variance (sd)	0.14 (0.03, 0.44)	0.22 (0.04, 0.75)	0.24 (0.04, 0.95)	0.11 (0.02, 0.57)	0.15 (0.02, 0.75)
Family Specific Parameters:					
Residual variance (sigma)	0.97 (0.96, 0.97)	0.95 (0.94, 0.95)	0.96 (0.95, 0.96)	0.43 (0.43, 0.43)	0.34 (0.34, 0.35)
Explained variance by predictors					
Conditional R^2	0.06 (0.05,0.06)	0.07 (0.07, 0.08)	0.10 (0.09, 0.10)	0.07 (0.07, 0.08)	0.18 (0.16, 0.19)

Table 1. Continued

	Model 1			Model 2	Model 3
	Distance in residence patch (log10 m)	**Duration in residence patch (log10 min)**	**Displacement in residence patch (log10 m)**	**Displacement between residence patches (log10 m)**	**Number of residence patches visited (log10 n per low tide)**
	Estimate *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*	*Estimate* *95% CI*
Post hoc comparisons of estimated means					
Exploration speed (log10 cm/s) ~ Day	-0.03 (-0.09, 0.02)			-0.01 (-0.05, 0.02)	0.03 (-0.01, 0.09)
Exploration speed (log10 cm/s) ~ Night	**0.08** **(0.01, 0.17)**			**0.05** **(0.03, 0.09)**	**-0.07** **(-0.13, -0.02)**
Contrasts					
Day - Night	**-0.12** **(-0.12, -0.04)**			**-0.06** **(-0.01, -0.02)**	**0.11** **(0.06, 0.12)**

4. Discussion

Our study showed that red knots in the field are moderately repeatable on their movement speed within residence patches (*R* = 0.26). Compared to movement patterns during the day, at night all red knots travelled further, stayed longer, and displace further within and between residence patches. We found that the differences in movement patterns between faster and slower exploring red knots as measured in captivity were particularly pronounced during the night. Specifically, faster exploring knots travelled further, stayed longer, and displaced further within residence patches with further displacement distance between residence patches at night than slower explorers. Faster exploring red knots visited fewer residence patches at night than slower exploring knots while slower explorers did not differ in number of residence patched visited between day and night. During the day, individual exploration scores did not explain variation in movement parameters.

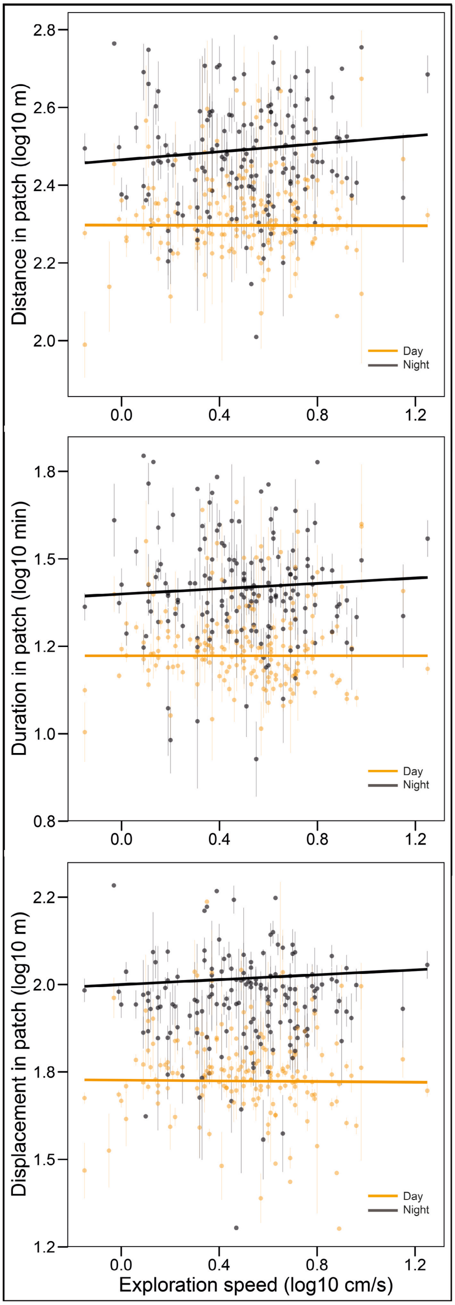


Figure 1: Exploration speed measured in controlled settings (log10 cm/s) interaction with day-night on the distance travelled (upper figure), duration (middle figure), and displacement distance (lower figure) within a residence patch. At night, faster exploring red knots travelled longer, stayed longer, and displaced further in a residence patch than slower exploring knots. Individuals with different exploration score did not differ in their movement behaviour during the day. The figure shows raw data with smoothed conditional mean lines provided by R package *ggplot2*.

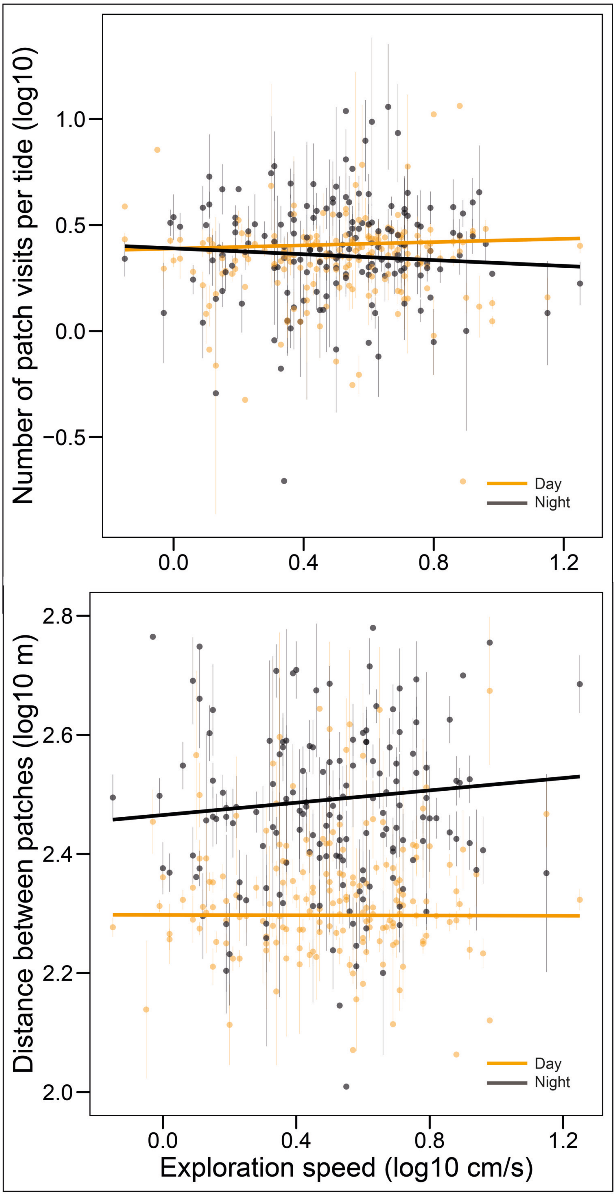


Figure 2: Exploration speed measured in controlled settings (log10 cm/s) interacting with day-night on the number of residence patches visited per low tide (upper figure) and displacement distance travelled between patches (lower figure). At night, faster exploring red knots visited less patches and travelled longer between residence patches than slower exploring knots. Individuals with different exploration score did not differ in their movement behaviour during the day. The figure shows raw data points with smoothed conditional mean lines provided by R package *ggplot2*.

Personality traits may be more consistent in standard experimental setups where conditions are controlled but in the wild, animals can show flexible behaviour in response to changing environmental cues (McElreath and Strimling, 2006). For example, under predation risk, animals may show flexible behaviour and abandon their personality-related behaviours (Cote et al., 2013). Particularly, for red knots that forage on open mudflats where they cannot use cover, it may be safer to move with the group than alone under predation risk (Beauchamp, 2014; Eccard et al., 2021). Therefore, personality-related movements may be masked under predation risk in red knots. Additionally, group living animals may have social cues available that influences where and how individuals move (Carter et al., 2013b; van de Waal et al., 2013). Red knots may be more likely to follow each other during foraging because they can observe the foraging success of their conspecifics (Bijleveld et al., 2015). We found that individuals are repeatable on their movement speed in the wild (mean speed in patch per low tide $R = 0.26$) but repeatability was not as high as it was found in captivity (mean speed in 20 min experiments $R = 0.67$, Ersoy et al., 2022) indicating environmental (including social) factors may mask the expression of personality in the wild. In this study, we could not control for environmental and social variation to investigate individual consistency in the wild (Williams and Safi, 2021). In fact, explained variation (R^2) in all our models was very low indicating that there are large amounts of variation we could not account for. This could potentially be explained by the presence of conspecifics and/or predation risk during foraging.

Many shorebirds follow the tidal cycle and forage during low tide both day and at night (Gaston, 2019; Mc Neil and Rodriguez, 1996). Since they mainly feed on macrozoobenthic organisms that live under the sand and are found by touch rather than sight, many shorebirds are little affected by the diel cycle. However, like other movement studies on shorebirds (e.g., Burton and Armitage, 2005; van Gils and Piersma, 1999; Jourdan et al., 2021), we found that red knots move on the ground more at night than during the day. This could be because moving large distances at night may be risky as they may not be able to see and use landmarks or other individuals to find a profitable foraging area. Additionally, the presence and activity of predators such as peregrine falcons *Falco peregrinus* that hunt small shorebirds – including red knots –may decrease the amount of movement of red knots during the day (vs. night) as those falcons are usually not active at night (Rejt, 2001). The absence of threats and cues at night could therefore explain the differences in movement behaviour between day and night, and further amplify or mask the expression of individual behaviour.

It has been suggested that individuals show behavioural flexibility in foraging behaviour in the wild when they can see and use information on food patches, but personality influences foraging decisions where the visual cues are missing (Carter et al., 2013b). For example, an experimental study on chacma baboons showed that shy individuals are more likely to scrouge on the food discoveries of bold individuals when the food is hidden in experimental arena, but personality does not affect foraging decisions under natural foraging conditions where individuals can collect visual cues in the environment (e.g., seeing where the fruits are on the tree; Carter et al., 2013b). In an experimental setup where the food was hidden, slower (vs. faster) exploring red knots found food slower when they were tested individually but became faster in group foraging scenarios (*Box 1* in this thesis), suggesting that red knots use social cues to find food while foraging in group, but they rely on their personality-dependent foraging decisions when social information about food patch is missing (when tested alone). This may manifest in day and night foraging movement differences in the wild, as we found that red knots do not differ in their movement patterns during the day (when social information on food patch quality is available or when predators are active) but they do show personality-related movement patterns at night when visual cues are likely to be missing.

Faster exploring individuals have been shown to move larger distances when foraging compared to slower exploring individuals in other species (e.g., great tits *Parus major*; van Overveld and Matthysen, 2013; bullhead *Cottus perifretum*; Kobler et al., 2009). In line with other studies, we found that faster (vs. slower) exploring red knots move larger distances at night as they travelled longer within a patch and further within and between residence patches. Our results suggest that exploration measured in captivity relates to exploration in the wild at night, thus predicting the distance moved in the wild at night. Accordingly, we expected faster exploring red knots would visit higher number of patches visited per tide which we did not find any support for. In contrast, we found the opposite of what we expected during night-time movements, where faster exploring red knots visited less patches. This could be because hopping patch to patch may be energetically costly or risky at night therefore, faster explorers may prefer to explore more on the ground than moving between patch to patch. Investigating how faster exploring red knots trade-off between exploring on the ground and exploring between patches may provide interesting opportunities for future research.

In conclusion, our results suggest that personality may emerge in the absence of cues such as when tested alone in experimental setups or when foraging at night with low visibility, and that personality may be masked when individuals respond to cues in their environment such as when foraging with conspecifics or under predation risk (Carter et al., 2013b; McElreath and Strimling, 2006). A control for social and ecological environment would elucidate to what degree the exploration of an individual is consistent across different contexts and to what degree it is influenced by changing environmental cues.

Acknowledgements

We thank Natuurmonumenten for permission to conduct this research on Griend. We thank all volunteers and students for helping with data collection. Particularly, we thank Anne Dekinga, Job ten Horn, Luc de Monte, Roeland Bom, Emma Penning, and Benjamin Gnep for help building the array of receivers and maintaining WATLAS throughout the season. We thank Ran Nathan, Sivan Toledo, Frank van Maarseveen, Bas Denissen and many others for their help designing and maintaining the WATLAS tracking system. We thank Ton G. G. Groothuis for discussions on the personality across contexts, and his valuable comments on the manuscript. We also thank Theunis Piersma and Franjo Weissing for discussions on the early stage of the study. PRG was supported by an Adaptive Life Grant by the Groningen Institute for Evolutionary Life Sciences. This study was funded by the core funding of NIOZ and the NWO-Veni grant to AIB (VI.Veni.192.051).

Authors' Contributions

SE, PRG, CEB and AIB conceived the study. SE conducted personality experiments and with AIB tagged the individuals. PRG and AIB developed the residence patch calculations from movement data. SE analysed the data. SE drafted the first version of the manuscript. All authors contributed to writing of the final manuscript. None of the authors have a conflict of interest.

Supplementary Materials

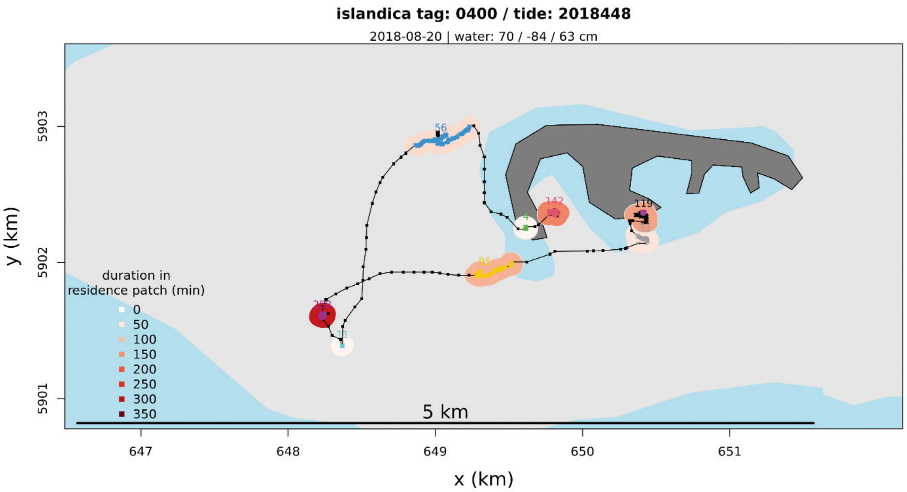


Figure S1: Example map from an individual red knot shows the residence patches used in low tide period around the Griend mudflats. Tracking starts when bird is roosting during high tide period (pink patch, duration 142 min), moves through southwest of the island and ends on high tide roost (black patch, duration 119 min). For our analyses, we excluded the high tide roosting period.

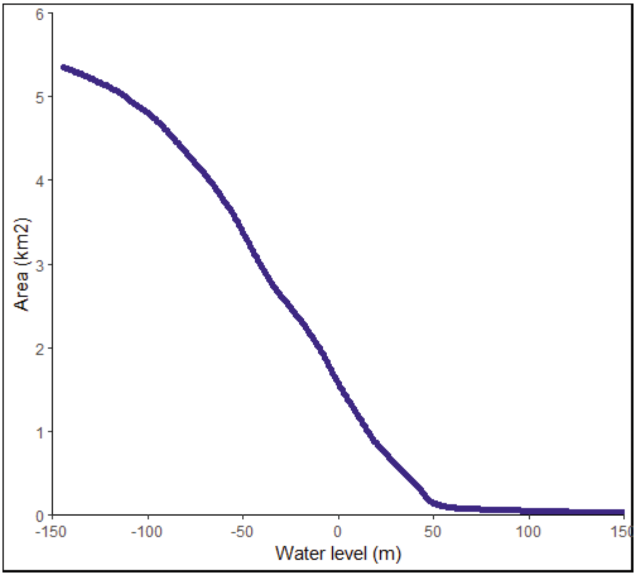


Figure S2: We used residence patches only during low tide periods when mudflats were exposed for foraging, which corresponded to water levels below 50 cm NAP. To calculate the area available (y axis), we used the bathymetry data for our study area (Griend) from Rijkswaterstaat and summed the number of 20x20 m aster cells that were available at certain water levels (x axis).

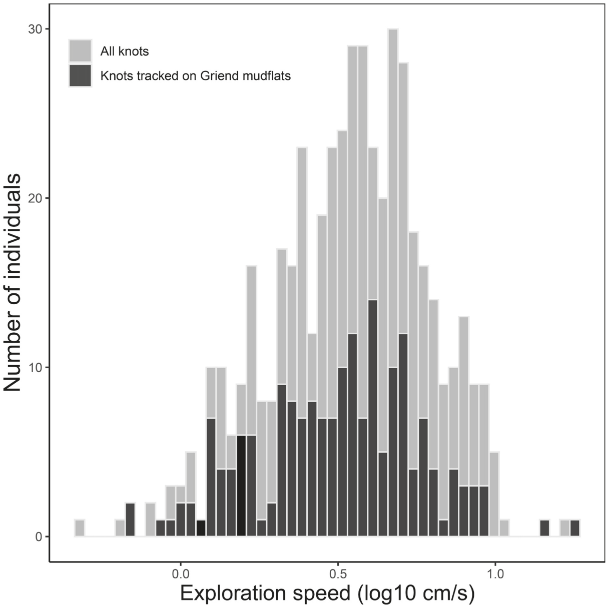


Figure S3: Histogram of individuals with measured exploration scores. The distribution of the exploratory scores of individual red knots which were tracked with WATLAS on Griend mudflats (in yellow) and all red knots with exploratory score (in grey).

CHAPTER 5

When slow explorers can be fast: personality-related differences in post-breeding arrival of red knots in the Wadden Sea

Selin Ersoy, Ton G. G. Groothuis, Theunis Piersma, Allert I. Bijleveld

Manuscript

Abstract

Timing and patterns of migration, even within populations that share breeding sites, show large variation between individuals. Variation in migration timing can have important carryover effect such as early arrival to the wintering sites can be related to advantageous position in roost site and territories, and earlier primary moult helps individuals to gain their flight efficiency earlier and escape ‘predator wave’ in autumn. Whether personality might explain part of this individual variation in migration timing has received little attention. We studied the post-breeding migration timing of red knots *Calidris canutus islandica* that breed in the High Arctic and asked whether arrival timing in the Dutch Wadden Sea was related to exploration speed (a personality trait). Red knots start primary moult in their wintering range, and that earlier primary moult helps avoid predation from peregrines that arrive in autumn. An individual’s exploration speed was assayed in temporary confinement days after capture in the Wadden Sea, and arrival date to the Wadden Sea was estimated with isotope measurements of blood that was sampled right after catching. We validated the arrival dates estimated from isotopic signatures with the progress of primary moult. Because males take care of the broods after hatching, we also investigated differences in arrival timing between the sexes. As predicted, we found that moult scores of primary feathers were correlated with estimated arrival dates, and that females arrived in the Wadden Sea ca. 10 days earlier than males. Arrival timing was also correlated with exploration speed: faster exploring red knots arrived two weeks later than slower exploring red knots. Sex and exploration speed did not show an interaction with arrival date. Individuals that arrive earlier to the wintering grounds are also likely to be early in moulting. Early moulting in summer could help individuals to escape “predation wave” in autumn. Therefore, advantage of arriving earlier to the wintering grounds would represent a carryover effect.

Introduction

Migration timing and patterns do not only vary among species, but also within species. Long-term tracking data show great diversity, with individuals having their own timing and/or use of staging sites (e.g., Senner et al., 2019; Stanley et al., 2012; Vardanis et al., 2011). Variation in migration timing can have important seasonal carryover effect such as early arrival to the non-breeding sites can be related to advantageous position in roost site and territories (Harrison et al., 2011; Leyrer et al., 2012) and earlier primary moult lower the consequences on predation danger of the decreased flight efficiency due to moulting thus helps individuals to escape predator attacks (van den Hout, 2009; Piersma et al., 1993a). Ecological factors and individual differences have an effect on this variation (Jonzén et al., 2006; Walther et al., 2002), however, the behavioural mechanisms influencing migration timing remain to be elucidated (Knudsen et al., 2011). In view of personality-related differences in movement patterns (Chapman et al., 2011; Dingemanse et al., 2003; Kobler et al., 2009), personality traits (consistent among-individual differences in behaviour), might also explain some of the variation in migration timing of an individual.

Personality traits such as exploration (magnitude of space use in a novel environment) or boldness (propensity to take risk) 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 new feeding places (bullheads *Cottus perifretum* Kobler et al., 2009, 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). A handful of 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 (partially migrating roach *Rutilus rutilus* Chapman et al., 2011; warblers Mettke-Hofmann et al., 2005). Explorative great knots, *Calidris tenuirostris*, compared to non-explorative individuals, visited more new 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 use more staging sites thus differ in migration timing (Bijleveld et al., 2014).

The Red knot *Calidris canutus* is one of the migratory shorebird species that breed in the Arctic tundra, and uses 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). The *islandica* subspecies spends most of the nonbreeding season on the extensive intertidal flats of the Wadden Sea and other European estuaries (Quaintenne et al., 2011). During northward migration most of the 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 can skip Iceland as a potential refuelling site and migrate nonstop from the tundra breeding grounds to the Wadden Sea (Dietz et al., 2010; Kok et al., 2020). If they use Iceland to stage during southward migration, the average staging time is 12-15 days (Dietz et al., 2010; Wilson and Morrison, 1992). Upon arrival to the wintering grounds, like the Wadden Sea, red knots switch their diet from tundra arthropods to marine shellfish (Piersma et al., 1993b). Within days after arrival, they also start moulting their primary feathers (Dietz et al., 2010, 2013) and that earlier primary moult helps avoid predation from peregrines that arrive in autumn (van den Hout, 2009; Piersma et al., 1993a).

Here, we asked whether arrival timing of migratory red knots in the Dutch Wadden Sea was related to exploration behaviour. We first estimated arrival time (i.e., days after switching from a tundra to marine diet) based on isotope values from blood samples and we validated our arrival time estimation with primary moult start date. Second, we investigated how arrival time differs among individuals with different exploratory personality. We predicted that exploratory individuals would use more staging sites during migration and thus arrive to the Dutch Wadden Sea later than slower explorers. Lastly, because males take care of the broods after hatching (Nebel et al., 2000; Whitfield and Brade, 1991), we investigated whether males arrive in the Wadden Sea later than females.

Materials and Methods

Catching, sampling, housing

During two catching events in the western Dutch Wadden Sea (53°15’N, 5°15’E) on14 August and 10-13 September 2018 (new moon periods), 131 adult red knots were caught by means of mist netting. 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). To obtain a primary moult score (ranging between 0 and 50), the ten 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 (12min, 7000rpm) and pipetted into separate glass vials and immediately stored in a freezer at the field site. In the laboratory, samples were stored at -20 ºC until analysis. These samples were used to determine the stable carbon and nitrogen isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) from plasma and red blood cells separately.

Right after measurements, the birds were moved to temporary outdoor aviaries of 2m x 0.75m x 0.4m (LxWxH) made of linen with a net floor. These aviaries were placed on natural sand/grass ground and 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 2m x 2m x 2m (referred to as “mobile arena”; see (Ersoy et al., 2022) for detailed explanation of the setup). The floor of the unit consists of seawater of 20 cm depth in which four identical trays with wet sand (61cm x 40cm x 25cm) were situated. Birds could explore these artificial patches in which no food was offered. To standardise the procedure and to motivate birds equally for personality assays, we placed them individually into a holding pen without access to food for two hours. 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 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 3 locations. Exploration speed is calculated as a bird’s mean speed (cm/s) per trial.

Right after exploratory assays, all red knots were released back into their natural habitat with unique combinations of colour rings. All necessary permits to catch, handle, tag, test, and keep red knots were granted to the NIOZ by the Dutch law and regulation under protocol number NIOAVD8020020171505.

Isotope analysis

At NIOZ Royal Netherlands Institute for Sea Research, blood samples were freeze-dried 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 x 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.

Estimation of arrival date in the Wadden Sea

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 carbon isotope ($\delta^{13}C$) to estimate arrival date (i.e., time since diet switch, Klaassen et al.,2010):

Start and end values were taken from Dietz et al. (2010); the start value indicates where the migration started hence, we took Arctic tundra value ($\delta^{13}C = -24.7$), and end value indicates where the migration ended accordingly, we took 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 (Suppl. Figure S1). The result of this function is the days since the diet switch, so to estimate arrival date we subtracted the outcome from the date of capture. Finally, we transformed arrival dates to continuous days since January 1st.

Estimation of moult start date

Because red knots need their flight feathers for migration, adults moult their primary feathers after arrival to their wintering grounds in the Dutch Wadden Sea (Dietz et al., 2013). They start moulting both wings from their first primary feather to the last (tenth) primary feather. To estimate the date at which primary moult started, we selected birds with active moult on their first primary feather (N=46). We back-calculated the date at which the first primary moult started using the primaries scored by observer, capture date, and moult duration for the first primary feather. We used different values for different sexes because female red knots are heavier and larger than males, resulting in more feather mass to replaced and thus affecting moult duration (females 16 ± 1.9 days, males 15 ± 2.5 days for first primary feather; values are taken from Dietz et al., 2013). We transformed first primary moult start date to days since 1 January.

Statistical analysis

We excluded one adult male for which the arrival date was more than 60 days before capture, suggesting that either he did not leave the Wadden Sea for a migration to the Arctic, or there was a mistake in the isotope analysis. To validate our arrival date estimation based on isotope analyses, we first formulated a linear regression model to test whether days since first primary feather moult predicts the estimated arrival day to the Wadden Sea. Then, to investigate the factors influencing arrival date, we formulated generalised linear models using the *lme4* package (Bates et al., 2015). After checking for collinearity, overdispersion, and model assumptions (homogeneity and normality of residuals), we fitted a mixed model with gaussian error distribution to investigate the effects of sex (categorical; male or female), exploration speed (log10 mean speed cm/s) and the interaction between the two on the estimated arrival day to the wintering grounds in Wadden Sea. All data analyses were carried out in R statistical software v. 4.2.1 (R Core Team, 2013).

Results

The number of days since the start of first primary feather moult was correlated with the estimated arrival day in the Wadden Sea (Intercept 95 % CI = -20.02 (-91.6 – 51.6), Estimate 95 % CI = 1.05 (0.72 – 1.38), $R^2 = 0.46$; Figure 1). Red knots started moulting their first primary feathers within five days after arrival in the Wadden Sea (Figure 1).

Red knots arrived in the Wadden Sea between 11 July and 24 August. Females arrived ca. 10 days before males (Table 1). Estimated arrival day in the Wadden Sea was associated with exploration speed (log10 cm/s); fastest exploring red knot predicted to be arrived 14 days later than slowest exploring red knot (Table 1, Figure 2b). The statistical model did not reveal significant interaction between exploration speed and sex. To check the robustness of our results, we additionally ran the model without individuals with extremely low (< -0.1) and high (> 1.2) exploration speed (log10 cm/s). However, results did not change, and we present the results without these individuals in Suppl. Table S1 and Figure S3.

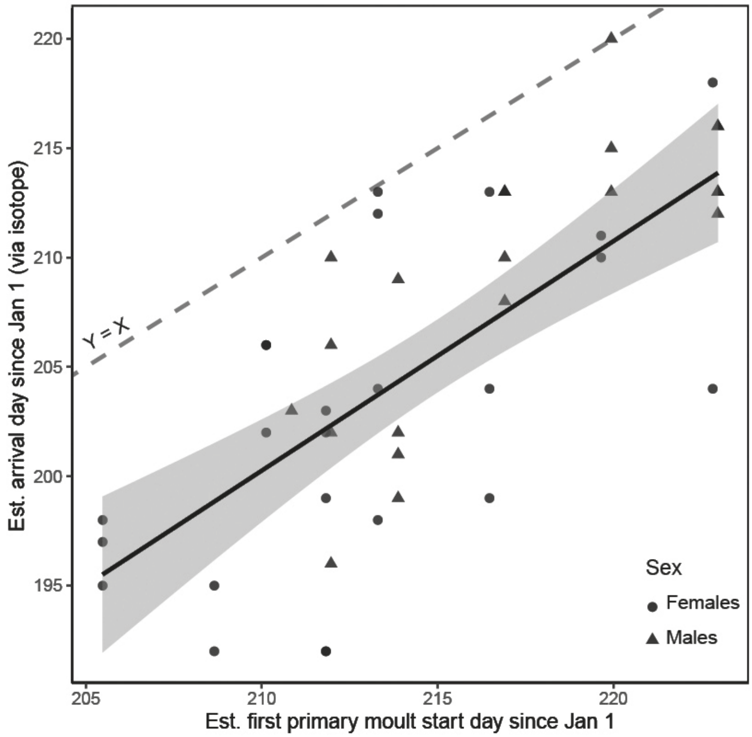


Figure 1. Relationship between arrival date and start of primary moult. The start of moult was calculated from observed primary moult scores (x-axis) that correlated with estimated arrival day to the Wadden Sea based on carbon isotope δ13C (y-axis). Each dot depicts a different individual. Dashed line shows slope =1 and intercept =0. Probabilities and 95 % confidence intervals are predicted by a GLM with gaussian error distribution.

Table 1. Effects of exploration speed (log10 mean speed cm/sec), sex, and the interaction of the two on the estimated arrival day (day number since January 1st) in the Wadden Sea. Bold font indicates confidence intervals do not overlap with zero.

Predictors	Estimates	95% CI
Intercept	203.37	**195.31 – 211.43**
Exploration speed	14.34	**0.86 – 27.82**
Sex (Male)	10.49	**0.91 – 20.06**
Exploration speed * Sex	-7.46	-23.47 – 8.60
R^2	0.134	

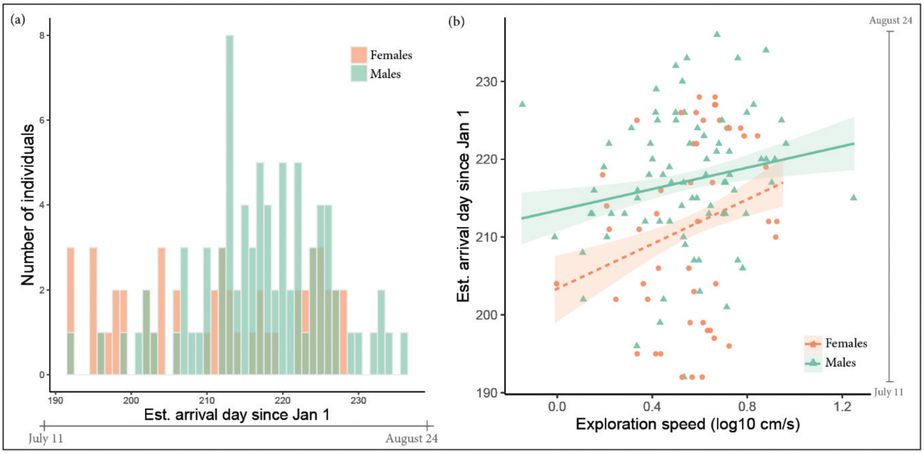


Figure 2. (a) Histogram of number of red knots on their estimated arrival date (January 1st is day 1). Colours indicate females and males. (b) Exploration speed (log10 mean speed cm/s) measured in the mobile arena (x axis) predicts the estimated arrival date to the Wadden Sea based on carbon isotope d13 of their blood (y axis). Females (orange) arrive earlier than males (green). Probabilities and 95 % confidence intervals are predicted by a GLM with gaussian error distribution. Note that interaction effect is non-significant.

Discussion

In this study, we investigated whether post-migration arrival timing of red knots in the Dutch Wadden Sea was related to exploratory behaviour. Red knots start primary moult in their wintering range thus, we first validated arrival day estimated from isotopic signatures with the start of the primary moult. In line with previous studies, we found that females arrived in the Dutch Wadden Sea earlier than males. Arrival timing was also predicted by exploration speed where faster exploring red knots arrived later than slower exploring red knots. Sex and exploration speed did not show an interaction with arrival date.

Individuals within the same species show large variation in the timing of migration, but the underlying causes often remain unclear. Later arrival to the wintering grounds can be caused by later departure from the breeding grounds, or by the amount of staging site use during migration (e.g., Trierweiler et al., 2014; Vardanis et al., 2011). Our finding on the sex differences in migration timing (also shown by Dietz et al., 2010) can be explained by the late departure from breeding grounds; female red knots are expected to arrive earlier because they leave the breeding grounds right after the chicks are hatched, whereas males care for the chicks until independence (Whitfield and Brade, 1991). Our finding that faster exploring individuals - independent of sex - arrived later than slower explorers can also be caused by greater length of stays and/or more use of staging sites. Red knots show flexibility in their staging site use on the way from breeding to wintering grounds, and if they use staging, they stay 12-15 days (Dietz et al., 2010). Fastest exploring red knot arrived 14 days later than slower explorers on the moulting grounds in the Wadden Sea, which is in the range of expected delays if additional stops are made. Since exploration as a personality trait is closely related to space use and visiting different areas (e.g., van Overveld and Matthysen, 2010), faster exploring red knots might use more staging sites during migration than slower explorers, which would postpone arrival on the wintering grounds. To investigate whether later arrival is caused by later departures from breeding grounds or by visiting more staging sites en route remains to be studied, e.g., by GPS-tracking birds of different personalities on their migration.

Many shorebirds moult their feathers right after they arrive to the marine wintering habitats (as in our findings and other studies Dietz et al., 2010). The gap in the wing during moult effects flight efficiency, and actively moulting birds may be more vulnerable to aerial predation (Hedenström, 2003). Indeed, migration timing in sandpipers is associated by the presence of their predators, peregrine falcon *Falco peregrinus* (Lank et al., 2003). In the Dutch Wadden Sea, the number of peregrine falcons tend to show a steep increase from 15 September onwards (van den Hout, 2009). Since red knots need ca. 70 days to moult their feathers fully (Dietz et al., 2013), earlier arrival of slower explorers in the Wadden Sea provides less overlap between moulting and the presence of peregrines. While faster exploring individuals have been shown to be less risk aversive and behave less cautiously than slower explorers in other studies (reviewed in Réale et al., 2010), how our faster-exploring late-arriving red knots deal with consequences on predation danger of the decreased flight efficiency due to moulting warrants further study.

By combining experimental approaches measuring personality with methods estimating arrival timing from isotope values, we tested whether exploration speed measured in a standardised setup could be extrapolated to a larger and more complex context like migratory behaviour. This study suggests that personality of an individual can explain part of the variation in the post-breeding migration timing. However, it remains to be studied how this timing difference is related to later departures form the breeding grounds and staging site ecology. As many migratory species are experiencing anthropogenic (including climatic) changes (Both, 2010; van Gils et al., 2016; Knudsen et al., 2011; Sillett et al., 2000), understanding the factors effecting migratory timing and patterns of individuals might help us understanding species adaptation to environmental changes (van Gils et al., 2016; Lisovski et al., 2021; Piersma and Lindström, 2004; Wikelski and Tertitski, 2016).

Acknowledgements

We thank Natuurmonumenten for using the field station on Griend and to conduct our study on the island. Skipper Dirk de Boer and his mates enabled regular supply with groceries from Terschelling. Furthermore, we thank the crews of the NIOZ research vessels RV *Navicula* and RV *Stern* for transport of people and equipment from and to Griend. We thank all the volunteers and students helped during data collection and stable isotope analysis. In particular, we thank Anne Dekinga, Luc de Monte, Job ten Horn, Marcel van der Meer and Ronald van Bommel. We thank Thomas Lameris with his help on arrival date estimation. This study was funded by the core funding of NIOZ and the NWO-Veni grant to AIB (VI.Veni.192.051).

Authors' Contributions

SE and AIB designed the study. SE collected and analysed the data. SE drafted the first version of the manuscript. All authors contributed to writing of the final manuscript. None of the authors have a conflict of interest.

Supplementary Materials

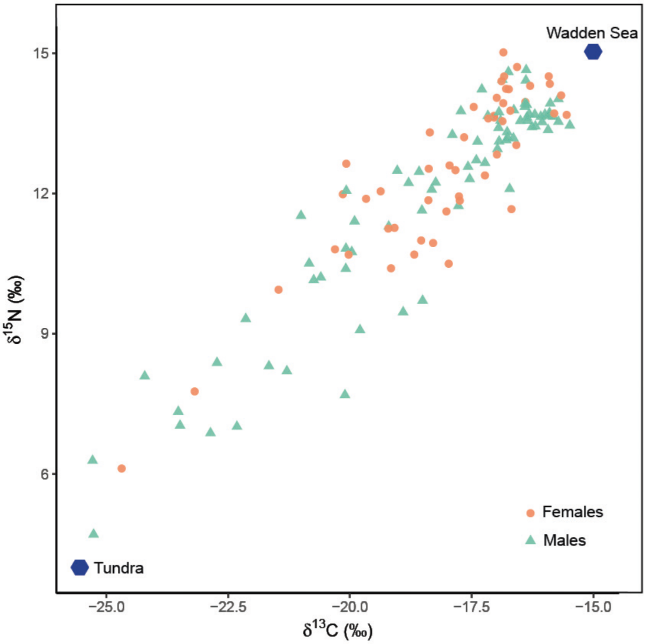


Figure S1. Stable isotope ratios of carbon (δ13C, x axis) and nitrogen (δ15N, y axis) in red blood cells that were used in the analyses. Tundra and Wadden Sea expectations are indicated with blue hexagons.

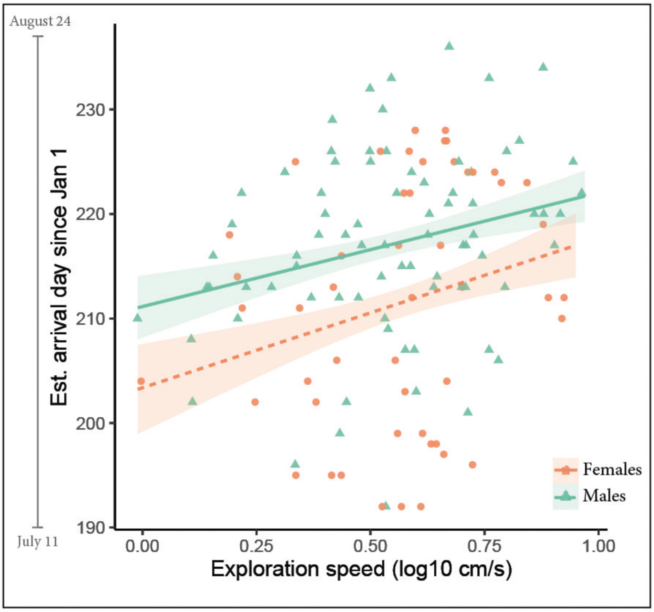


Figure S2. Analysis without the outliers (exploration speed < -0.1,> 1.2 Exploration speed (log10 mean speed cm/s) measured in the mobile arena (x axis) predicts the estimated arrival date to the Wadden Sea based on carbon isotope d13 of their blood (y axis). Females (orange) arrive earlier than males (green). Probabilities and 95 % confidence intervals are predicted by a GLM with gaussian error distribution. Note that interaction effect is non-significant.

Table S1. Results of the analysis without the outliers (exploration speed < -0.1,> 1.2). Effects of exploration speed (log10 mean speed cm/sec), sex, and the interaction of the two on the estimated arrival day (day number since January 1st) in the Wadden Sea.

Predictors	Estimates	95% CI
Intercept	203.37	195.36 – 211.38
Exploration speed	14.34	0.94 – 27.74
Sex (Male)	8.22	0.60 – 18.03
Exploration speed * Sex	-3.41	-19.95 – 13.12
R^2	0.149	

CHAPTER 6

General Discussion

Selin Ersoy

In this thesis, I attempted to identified individual differences in consistent exploratory behaviour in relation to foraging behaviour and diet, how exploration may develop during ontogeny and is maintained in wild populations, and what could be the movement consequences of the individual differences in exploration. To do so, I put laboratory experiments, field observations, stable isotope analysis, and movement tracking to task. In this final chapter, I make links to the previous chapters and discuss some of the main conclusions from different perspectives, rather than repeating the discussion sections of each chapter. While I acknowledge the limitations and shortcomings of my thesis, I also suggest what new ideas may emerge from it. In some places, I question the definition of potentially controversial key concepts in animal personality research and suggest directions for future studies.

What is exploration?

Exploration and boldness are the most studied personality traits (Réale et al., 2007) but are perhaps the traits that have the most overlapping definitions in the literature. Exploration is defined as "the action of searching information about a novel environment" (Verbeek et al., 1994) and is commonly assayed as the amount of movement an individual shows in "open-field test" (developed by Hall and Ballachey, 1932). Boldness is defined as "the propensity to take risks in novel situations" and is commonly assayed as individual's response to novel objects and novel environments (Brown and Braithwaite, 2004; Carter et al., 2012; Dingemanse et al., 2004). When exploration and/or boldness are measured in a novel environment test, results of the behavioural assays may reflect the same behaviour. In my experiments, red knots were assayed in a novel environment. I calculated exploration as the movement speed of an individuals in the experimental arena. However, I also observed that individuals with a slower exploration speed mainly stood on a patch and looked around (behaviours indicative of shyness or anxiety) while faster explorers showed various kinds of active behaviour including hopping between patches, walking, and running within patches, and both tactile (slow probing) and visual (fast scanning of surface) foraging behaviours. Therefore, it is likely that exploration and boldness in red knots are correlated when individuals are tested in a novel environment.

Exploration and foraging behaviour – two sides of the same coin?

Originally, exploration in a novel environment was suggested to demonstrate the adjustment of an individual to a novel environment (Verbeek et al., 1994) and exploration and foraging were considered as two different concepts. However, it has become increasingly common to link the concept of exploration to those of foraging and resource selection (e.g., Bijleveld et al., 2014; Coomes et al., 2022; van Overveld and Matthysen, 2010, Chapter 2). In many studies using an open-field test, the experimental arena resembles a natural foraging habitat to stimulate wild animals to "explore". For example, in studies investigating exploratory behaviour in great tits *Parus major*, tree branches were placed in an experimental arena (e.g., Verbeek et al., 1994), and in fish, open and vegetated spaces were provided in an experimental tank (e.g., Jones and Godin, 2010; Mazué et al., 2015). In my study, I used sand patches arranged in a sea water basin to study exploration behaviour in red knots (Chapter 2, following Bijleveld et al., 2014; Kok et al., 2019). Because of the nature of the experimental methods – i.e., structures are related to foraging habitat, despite no food being provided – exploration and foraging behaviour may be linked directly if the selection of specific food resources is the cause for variation in exploratory behaviour (Ingram et al., 2018). For example, hopping between tree branches may indicate resource-independent exploratory behaviour in great tits but could also be a proxy for foraging for caterpillars on tree branches in the wild (Cowie, 1977; Verbeek et al., 1994).

In Chapter 2, we found that slower exploring red knots (measured in experimental arena) mainly use tactile foraging in the wild, while faster exploring red knots use both tactile and visual foraging. In the experiments, slower exploring red knots (measured as speed of movement) did not show tactile foraging behaviour but stood on a patch and looked around (it may be caused by their anxiety or shyness during experiments), while faster exploring red knots showed visual and tactile foraging behaviour. The result from slower explorers would indicate that slowness/shyness may be an inherent trait, making individuals slow/shy across different contexts, thereby indirectly connecting exploration and foraging behaviours; the result from faster explorers suggests that exploration and foraging behaviours are more directly related. Whether the two behaviours are directly or indirectly connected, I suggest these exploration and foraging are related concepts, and that they can overlap depending on the (experimental) context.

The connection between exploration and foraging behaviour could be driven by the physical activity level of an individual. According to the pace-of-life framework, fast exploring individuals in the “fast” pace-of-life are expected to have higher energy expenditure (Réale et al., 2010). The increased energy expenditure of fast explorers (reviewed in Careau et al., 2008) could be compensated by an increased energy gain associated with a foraging behaviour that provides high-energy food. For example, fast exploring individuals have high energetic cost (Careau and Garland, 2012) and are more likely to encounter profitable foraging opportunities and high-quality prey types (e.g., blue tits *Cyanistes caeruleus*; Herborn et al., 2010). High cost of exploration may then have potentially high foraging gain (Bell and Sih, 2007; Brydges et al., 2008). Indeed, we found that faster exploring visual foraging red knots mainly feed on high quality soft prey (Chapter 2). This feedback between the foraging behaviour and its successful outcome with high quality prey could explain how individuals maintain consistent individual variation in exploration with corresponding high levels of energy expenditure in the wild.

The development of exploration in a social context

If exploratory behaviour develops during ontogeny as a result of continuous interactions with the environment, I expected that the longer juvenile red knots practice their foraging strategies on the mudflats, the more consistent their exploratory behaviour may become. While we found that juvenile red knots have higher within-individual variation in exploration than adults, indicating that juveniles were still developing the personality trait, the number of days already spent in the Dutch Wadden Sea did not increase the consistency in juvenile exploratory behaviour (Chapter 3). Unfortunately, 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 in the wintering grounds (i.e., on the mudflats, between 14 to 33 days after arrival). Therefore, I could not account for individual variation in learning between juveniles in this thesis.

How quickly and which foraging strategy juveniles learn may depend on the social environment during development. In social animals, young ones mostly learn from watching experienced adults (Heyes, 1994; Watts, 1985); and juvenile red knots that forage in the same flock with adults may be more likely to learn certain foraging strategies faster than those that flock with other juveniles. To test the influence of the presence of adults on juvenile foraging strategy and learning speed, one should use an experimental setup to compare (1) a group of juveniles foraging by themselves for soft prey such as shrimp *Crangon crangon* and (2) another group of juveniles foraging by themselves for hard-shelled prey such as cockles *Cerastoderma edule* to (3) a group of juveniles foraging with experienced adults that use visual foraging to catch shrimp and (4) another group of juveniles foraging with experienced adults that use tactile foraging to catch cockles. Which foraging tactics these groups of juveniles will use when they became adults, how fast they learn certain foraging strategies, and how they differ in exploration speed could help to understand the development of exploratory behaviour and the role of social learning during ontogeny in red knots.

What can we learn from repeated measures?

An important aspect of personality traits is that the behaviour in question needs to be repeatedly measured over time and contexts (Réale et al., 2010; Stamps and Groothuis, 2010). However, there are several conceptual problems with repeated measures of an individual in identical experimental setup. First, some personality traits are defined as 'measures taken in a novel environment' such as, exploration of a novel environment and boldness to a novel object/environment. However, once an individual has undergone the first assay, the environment is no longer novel (Carter et al., 2013).

Second, underlying mechanisms of the repeated behaviour may not always be explicit. For example, some individuals are repeatedly active, and others are not active in the same experimental setup. This may be because the behaviour is inherent (as we often think and label it as 'personality trait') but it could also be that individual experience in the first assay influences the behaviour in the next assays. Whichever way an individual behaved in the first assay (active or non-active) may have positive (or not-negative) feedback (e.g., individual is not harmed during experiment). Therefore, if behaving in certain way avoids possible high costs associated with it, an individual may learn that the behaviour it showed in the first assay is a good strategy for that environment. Therefore, it may repeat the same behaviour in the next assay (pers. comm. T. G. G. Groothuis).

Third, an individual's experience in the first assay may increase or decrease its score as measured in the second assay (Box 2). For example, in my experimental setup to assay exploration, no food was provided, but there were sand patches suggesting hidden food in the arena. It is possible that some birds learn during the first assay that there is no food to explore in the arena and therefore change their behaviour and become slower in the second assay. Or some birds may compensate for finding nothing in the first assay by switching strategy and become faster in the second assay (Box 2). To my knowledge, the robustness of results based on repeated measures of personality traits in an identical setup has not been questioned so far. It is possible that these repeated measures tell us more (or something else) than inherent behaviour of an individual.

Box 2. Slower (vs. faster) exploring juveniles on average are more likely to change their exploratory behaviour in repeated tests

Here, I investigated whether the average exploration score of an individual may predict the differences between two exploration measures in juvenile and adult red knots. I used data from 57 adults (Chapter 2) and 67 juveniles (Chapter 3) that were assayed in exploration speed (log10 cm/s) twice with on average 4 days between assays (range: 2-6 days). I built separate linear regression models for juveniles and adults. In both models, I fit the absolute difference between the exploration speed (log10 cm/s) measures as response variable and the mean of the two exploration test repeats as fixed effect.

I found that mean exploration speed (log10 cm/s) of adults did not predict the absolute difference between two measures. However, on average slower exploring juveniles were more likely to have different scores from the two exploration measures (*Est. 95% CI* = -0.22 (-0.41, -0.05), Figure 1). This could potentially be explained by adults and faster exploring juveniles being more likely to regulate their behaviour through inner routines whereas slower exploring juveniles may be more open for external cues, to which they adapt their behaviour (DiRienzo et al., 2012; Finger et al., 2016; Monnet et al., 2020).

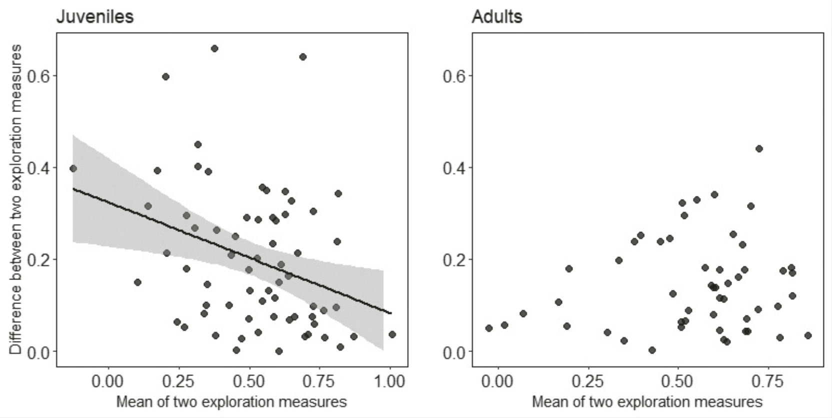


Figure 1. Absolute difference between the two exploration speed measures (log10 cm/s, y axis) of juveniles (on the left) and adults (on the right) in response to the mean of the two measurements of exploration speed (log10 cm/s).

Repeatability and the level of aggregation

Repeatability of a behavioural trait is often measured as a ratio of among-individual variation divided by the sum of among- and within-individual variation. I showed that exploratory movement in controlled conditions was highly repeatable in red knots (mean speed in 20 min experiments $R = 0.67$, Chapter 2). Repeated observations of the foraging behaviour in the field were difficult to obtain, but stable isotopes from blood plasma samples reflecting short term diet (~14 days) and blood cell samples reflecting long term diet (~45 day) were highly correlated (Pearson's r for $\delta^{13}C= 0.77$ and $\delta^{15}N= 0.68$; Chapter 2), suggesting repeatable diet and foraging tactic use in the wild. However, the repeatability of mean movement speed of tide in the wild was much lower (R = 0.26; Chapter 4) than found in captivity, indicating that environmental (including social) factors may mask the expression of personality in fine-scale movement behaviour in the wild.

Studies investigating the repeatability of movement behaviour generally use aggregated data across a certain period (time scale ranges from day to year in spatial personalities; reviewed in Stuber et al., 2022; e.g., daily distance travelled Hertel et al., 2020; weekly home range Villegas-Ríos et al., 2018). So far, the repeatability across classes of spatial behaviour reported in the literature was very high (R= 0.67 – 0.82, meta-analysis from Stuber et al., 2022). Indeed, by aggregating our fine-scale, within-patch (patch = area where birds are stationary or walking, i.e., between flight movements; Chapter 4) movement data into time classes of different length, i.e., per patch, tide, day, and week, I found that the repeatability of individual within-patch movement speed increased and varied considerably: R=0.08 per patch, R=0.26 per tide, R=0.32 per day, and R=0.49 per week (Box 3). This could be because environmental noise is likely to average out in aggregated data such as daily, weekly, or monthly. Under natural conditions, movement patterns can change depending on environmental factors. For example, individuals may move more similarly during a predator attack or during a storm causing low among-individual variation, and it may be difficult to find personality-related movement differences if the time scale of the tracking method is sufficiently detailed to capture those moments.

The observed variation in repeatability between aggregation classes (i.e., patch, tide, day, week) further indicates that repeatability values between different studies on the different levels of aggregation are incomparable. Additionally, changes in repeatability between aggregation classes may well depend on the biology of the species. For example, red knots may be very responsive and their behaviour within a tide may be dictated by environmental factors (e.g., storms, predation risk, foraging in a group; Oudman et al., 2018). During each high tide, red knots are forced to gather at roost sites and in the following low tide, group composition changes and individuals may move differently. This may be the reason why red knots show lower repeatability within a tide than between tides. Species that have more routine-like behaviour such as territorial individuals (e.g., oystercatchers *Haematopus ostralegus*; Bakker et al., 2021) may be less responsive to small scale differences in the environment as they are likely to follow their own individual routines and thus, the repeatability may not differ as much with the level of aggregation (pers. comm. A. I. Bijleveld).

Box 3. Repeatability of movement behaviour increases with the level of aggregation

To investigate the differences in repeatability at different aggregation levels, I used the movement data from three years (2018, 2019, 2020) collected from in a total of 321 red knots that were tracked between August and November in the Dutch Wadden Sea. I aggregated mean movement speed (duration divided by distance travelled) in a residence patch (areas where birds are stationary or walking; Chapter 4) in four different levels (i.e., patch (~minutes), low tide (~6 hours), day, and week), using each as a response variable in mixed models with *gaussian* distribution in the R package *lme4*. Response variables were log10 transformed prior to the analysis to fit normality assumptions. I added Bird ID as random effect and I controlled for year, night/day ratio, and the mean water level of the tide by including them as fixed effects. Tide ID was added as a random effect in models where response variables were mean speed per patch and per low tide. Repeatability was calculated by dividing among-individual variation by the sum of among-individual, among-tide (if added), and residual (i.e., within-individual) variation, respectively (Nakagawa and Schielzeth, 2010).

I found that the repeatability of individual within-patch movement speed increased and varied considerably (Figure B3): R=0.08 per patch, R=0.26 per low tide, R=0.32 per day, and R=0.49 per week. Among-individual variance was 0.00 per patch, 0.01 per low tide, 0.01 per day, 0.02 per week. Residual variance was 0.08 per patch, 0.02 per low tide, 0.01 per day, 0.01 per week.

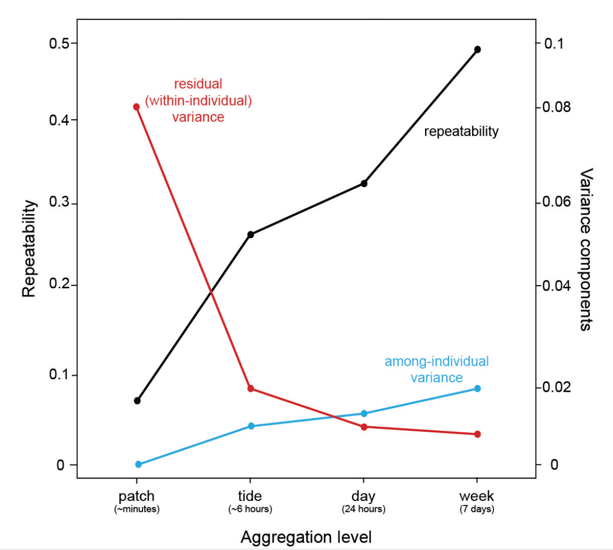


Figure B3. Figure shows the repeatability and variance components of movement speed in residence patch across aggregation levels. Black line shows repeatability estimate, red line shows residual variance, and blue line shows among-individual variance.

Movement outside of the Dutch Wadden Sea

Faster exploring red knots mainly eat higher quality soft prey and have smaller gizzard muscles (Chapter 2, Bijleveld et al., 2014). However, soft prey such as shrimp is available in the mudflats of the Wadden Sea only during summer months and completely disappears in October (van Gils et al., 2005b; Penning et al., 2021). After summer, faster exploring red knots may therefore completely switch to hard-shelled prey or leave the Wadden Sea area to search for soft prey somewhere else. During winter months, red knots with smaller gizzards have been shown to use a larger area in the wild and travel between the Netherlands, England, and Germany, whereas red knots with larger gizzards tend to stay in the Dutch Wadden Sea (Bijleveld et al., 2014). Accordingly, faster and slower exploring red knots can be expected to differ in their large-scale movement patterns during winter (as suggested by Bijleveld et al., 2014).

If faster exploring red knots leave the Dutch Wadden Sea at the end of summer and slower explorers stay in the area over winter, we can expect to find differences in average exploratory behaviour between summer and winter populations of red knots in the Dutch Wadden Sea. To test this, we captured 30 red knots between 6-9 February

2019 and measured their exploration speed in the mobile experimental unit right after the capture. We then compared the group of red knots caught in winter to another group of 71 red knots caught by the end of summer and tested between 12-18 September 2018. We found that red knots that were caught in winter were on average slower exploring than the red knots that were caught in summer (*Est.* = -0.21, *Intercept* = 0.62, *p* <0.01, Figure 1). This preliminary result supports the idea that before winter, faster exploring red knots are more likely to leave the Dutch Wadden Sea than slower exploring red knots. Alternative explanation for the decrease in exploration speed in population level between summer and winter could be that red knots decrease in exploratory behaviour on an individual level, and they all become slower in winter. However, this is unlikely because repeatability of exploratory behaviour measured in experiments are high across summer-winter measurements (Bijleveld et al., 2014; Kok et al., 2019; Chapter 2). It should be noted that we only had one capture event in winter and the sample size in winter (N=30) was lower than in summer (N=71). Increasing the winter sampling size of the red knot population and collecting data across several years would help to make more accurate conclusions.

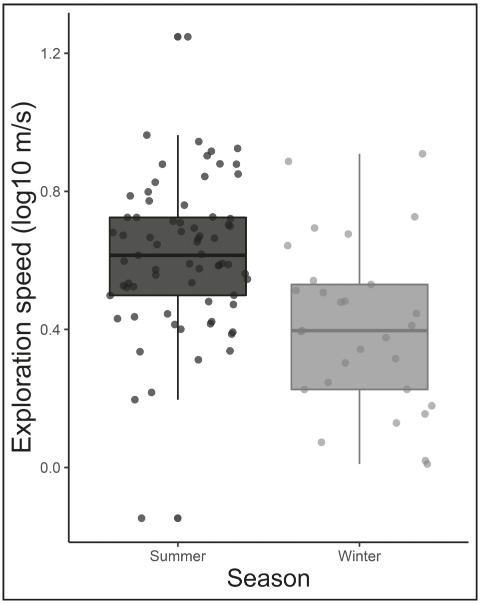


Figure 1. Comparison between groups of red knots caught in summer (N=71; September) and winter (N=30; February) that were assayed in their exploration in mobile unit within days after capture. Boxplot summarizes the distribution of a continuous variable and notably displays the median and standard errors of each group.

Large scale movement may be driven by competition

Fast exploring individuals have been shown to move longer distances in search of food in other species (bullheads *Cottus perifretum* Kobler et al., 2009, blue tits *Cyanistes caeruleus* Herborn et al., 2010). However, it is not clear what drives these fast explorers to move longer distances. Competition between conspecifics may drive displacements of individuals (Bergmüller and Taborsky, 2010). It is possible that faster explorers are less dominant than slow explorers, and by moving elsewhere, they avoid foraging competition in the local group (Bijleveld et al., 2012). While no clear relationship between exploration and dominance in foraging competition can be found in the literature (Dingemanse and de Goede, 2004; Fox et al., 2009; Verbeek et al., 1996), it is possible that slower exploring individuals are more competitive and can capitalise on the benefits associated with foraging in a group. In an experimental setup, we found that slower exploring red knots took longer to find food than faster explorers when they were tested individually, but found food sooner than faster explorers in group foraging scenarios (Box 1). This may suggest that slower exploring red knots use social cues to find food and are more successful at finding food while foraging in a group than when foraging alone. By which social mechanisms individual differences in exploratory behaviour and space use are influenced needs to be studied further and will likely provide interesting insights into the origin and maintenance of among-individual variation between members of the same population.

Conclusion

The work presented in this thesis provides a comprehensive definition of consistent individual differences in exploratory behaviour and gives new insights to understand the origin and maintenance of this behavioural trait in the wild. My findings suggest that experience during ontogeny (i.e., exposure to a certain physical or social environment) can be important for the development of personalities in juvenile red knots. For adults, exploratory behaviour assayed in experimental setups is highly consistent within individuals and can predict a suit of other behaviours in different contexts in the wild. That is, variation in explorative personality type (i.e., slow vs. fast explorer) predicts foraging tactics and dietary choice in the wild. Hence, my work provides a new potential explanation for variation in foraging niche specialisation between individuals in the same population. Exploratory behaviour also relates to variation in movement across different temporal and spatial scales in previously unforeseen ways. Specifically, slow and fast explorers show divergent movement patterns during the day and night and differ in arrival times from migration. This thesis fills a critical gap in the literature to link an experimentally measured personality trait to real-world behavioural strategies and demonstrates the importance of studying personality across contexts. Future challenges will be to (1) apply similar personality research to other taxa to generalise or challenge the findings presented here and in other recent studies and (2) obtain demographic rates (i.e., reproduction and survival) of different personality types to assess their relative contributions to overall population dynamics. Ultimately, understanding the causes, maintenance, and consequences of animal personalities should further our understanding of population responses to environmental change, population and community dynamics, and speciation.

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We are *k*not the same!

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A

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Author contact information

Christine E. Beardsworth
NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems,
PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
Email: christine.beardsworth@nioz.nl

Allert I. Bijleveld
NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems,
PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
Email: allert.bijleveld@nioz.nl

Anne Dekinga
NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems,
PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
Email: anne.dekinga@nioz.nl

Elif Duran
Izmir University of Economics, Department of Psychology, Sakarya Cad. No:156,
Balcova, 65330, İzmir, Turkey
Email: elifduran35@outlook.com

Ton G. G. Groothuis
Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen,
PO Box 11103, 9700 CC, Groningen, The Netherlands
Email: a.g.g.groothuis@rug.nl

Pratik Gupte
Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen,
PO Box 11103, 9700 CC, Groningen, The Netherlands
Email: p.gupte@rug.nl

Selin Ersoy
NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems,
PO Box 59, 1790 AB Den Burg, Texel, The Netherlands

Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen,
PO Box 11103, 9700 CC, Groningen, The Netherlands
Email: selin.ersoy@gmail.com

Marcel T. J. van der Meer
NIOZ Royal Netherlands Institute for Sea Research, Department of Marine Microbiology & Biogeochemistry, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
Email: marcel.van.der.meer@nioz.nl

Theunis Piersma
NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
Rudi Drent Chair in Global Flyway Ecology, Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences (GELIFES), University of Groningen, PO Box 11103, 9700 CC, Groningen, The Netherlands
Email: theunis.piersma@nioz.nl

Aileen Roncoroni
NIOZ Royal Netherlands Institute for Sea Research, Department of Coastal Systems, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands
Email: aileen.roncoroni@gmail.com

Summary

Individuals of all ages and sexes show behavioural traits that are consistent over time, but differ across individuals, and affect the expression of behaviours in different situations (hereafter: personality traits). This consistent behavioural traits have been shown to have consistent ecological and evolutionary consequences. Therefore, identifying the variation in personality traits, understanding the origin of the variation, and how it is maintained in natural populations is important. The work presented in this thesis provides a comprehensive definition of consistent individual differences in exploratory behaviour as a personality trait and gives new insights to understand the origin and maintenance of this behavioural trait in the wild.

We studied red knots (*Calidris canutus islandica*) that breed in the high Arctic of northern Greenland and north-east Canada and winter in the large mudflat areas of western Wadden Sea Researchers has been studying red knots for several decades, providing a thorough understanding of the species' diet, habitat preferences, survival rates, migration routes, and behavioural and morphological flexibilities and limitations. Red knots show high individual consistency in exploration behaviour in captivity, and exploratory personality has been linked to diet choice and space use in the wild. We adapted the existing experimental setup to assay exploration to be used in the field so that we were able to eliminate the effects of captivity and relate experimentally quantified personalities to individual post-release movement and foraging patterns. We combined personality assays in controlled settings with field observations of foraging tactics, stable isotope for diet analysis and migration timing, and movement tracking to investigate the associations between exploration, foraging, diet, and movement in the wild.

To identify the variation in exploration as a personality trait, **Chapter Two** investigates the connection between exploration, foraging behaviour, and diet. We assessed how personality measured in controlled settings predicts foraging tactics and diet in the wild. Combining laboratory experiments, field observations and stable isotope analyses, we found that faster exploring red knots use more visual foraging tactics and eat soft prey while slower exploring red knots rely mainly on tactile foraging and feed on hard-shelled prey.

To understand the origin of the variation in exploration, **Chapter Three** investigated how relation between exploration and diet develops during ontogeny. We compared repeatability and consistency of exploratory behaviour and diet width of juvenile and adult red knots after their arrival from breeding grounds to wintering grounds. We asked whether the amount of time that juveniles on a marine diet was correlated with consistency of exploratory behaviour. We found that juvenile red knots have a more diverse diet, lower repeatability, and larger within-individual variation in exploration than adults, while among-individual variation in exploration did not differ between age groups. Slower (vs. faster) exploring juveniles had larger variance in their exploration repeats however, variation in juvenile exploration tests did not covary with the amount of time that juveniles were on a marine diet in the Wadden Sea.

To understand how personality traits measured in artificial context can predict movement behaviour in the wild, **Chapter Four** investigated personality-related movement patterns in different contexts (day and night) in the wild. We assessed exploration speed of red knots in controlled settings and then released the same birds with ATLAS transmitters to investigate fine-scale movement in the field. We found that faster exploring red knots differed in movement patterns at night more than slower explorers; specifically, faster (vs. slower) exploring knots visited fewer patches but travelled further between the patches, and stayed longer, travelled longer, and displaced further in patches at night. In contrast, movement parameters during the day did not differ between individuals according to exploration scores.

To investigate how individuals living in groups can benefit from using social information about foraging opportunities, **Box 1** investigated the link between personality and foraging success in group foraging scenarios. We conducted experiments to investigate the relationship between exploratory personality and foraging success (i.e., speed of finding food) of captive red knots. We found that faster-exploring individuals were also faster in finding food than slower explorers, when tested individually. All individuals found food faster when in a group than tested individually. However, slower exploring knots became faster in finding food than faster explorers with increasing group size.

To understand whether exploration measured in experimental setups could be extrapolated to a larger and more complex context, **Chapter Five** investigated the link between exploration and migratory behaviour. We studied the post-breeding arrival timing in the Dutch Wadden Sea of red knots and asked whether arrival timing was related to the exploratory behaviour. Because males take care of the broods after hatching, we also investigated differences in arrival timing between the sexes. We found that females arrived in the Wadden Sea earlier than males. Arrival timing was also correlated with exploration speed where faster exploring red knots arrived later than slower exploring red knots. Sex and exploration speed did not show an interaction with arrival date.

In **Chapter Seven**, the General Discussion, I summarise the main findings from the previous chapters and discuss some of the main conclusions from different perspectives. I further question the definition of potentially controversial key concepts in animal personality research and suggest directions for future studies. Finally, this thesis contributes to current and future studies with filling a gap in the literature to link an experimentally measured personality trait to real-world behavioural strategies and demonstrates the importance of studying personality across contexts.

Samenvatting

Individuen van alle leeftijden en geslachten vertonen consistente gedragsverschillen. Deze consistente gedragsvariaties tussen tussen individuen (hierna; 'persoonlijkheidskenmerken') komen tot uiting op verschillende manieren in verschillende situaties en blijken ecologische en evolutionaire consequenties te hebben. Het is daarom belangrijk om niet allen de variatie in persoonlijkheidskenmerken te bepalen, maar ook het ontstaan ervan te begrijpen en te onderzoeken hoe deze individuële variatie in natuurlijke populaties wordt behouden.

Wij bestudeerden kanoeten (*Calidris canutus islandica*) die in het poolgebied van Noord-Groenland en het noordoosten van Canada broeden en overwinteren in de grote slikgebieden van het westelijk deel van de Waddenzee. Onderzoekers hebben kanoeten al tientallen jaren bestudeerd, waardoor er veel informatie beschikbaar is over dieet, voorkeur voor habitat, overleving, migratieroutes, en flexibiliteit en limitaties in gedrag en morfologie. In gevangenschap laten kanoeten laten een hoge individuele consistentie zien in exploratief gedrag. De mate van exploratie is bovendien gerelateert aan dieetkeuze en ruimtelijk gebruik in het wild. Wij hebben een bestaande experimentele opzet aangepast zodat het mogelijk was om exploratie ook te testen in het veld. Op deze manier konden we de effecten van vervoer en langdurige gevangenschap vermijden en de experimenteel bepaalde persoonlijkheid van elk individu vergelijken met ruimtelijk gebruik en foerageerpatronen na vrijlating. We combineerden persoonlijkheidstesten in een gecontroleerde omgeving met veldobservaties van foerageertactieken, stabiele isotopen voor dieetanalyse en de timing van migratie, en volgden ruimtelijk gebruik d.m.v. zendertjes om de verbanden tussen exploratie, foerageergedrag, dieet en ruimtelijk gebruik in het wild te bestuderen.

Om de variatie in exploratie te identificeren als persoonlijkheidskenmerken, onderzoeken we in **Hoofdstuk twee** het verband tussen exploratiegedrag, foerageergedrag, en dieet. We hebben onderzocht hoe persoonlijkheid, gemeten in een gecontroleerde omgeving, foerageertactieken en het dieet in het wild kan voorspellen. Door laboratoriumexperimenten, veldobservaties, en stabiele isotopen analyses te combineren, ontdekten we dat kanoeten met een snellere exploratie-score meer visuele foerageertactieken gebruiken en zachtere prooidieren eten (schaaldieren zoals garnalen en krabbetjes), terwijl kanoeten met een langzamere exploratie-score hoofdzakelijk op de tast foerageren op prooidieren met een harde schaal (schelpdieren zoals nonnetjes).

Om te begrijpen waar de variatie in exploratiegedrag vandaan komt, onderzoeken we in **Hoofdstuk drie** hoe de relatie tussen exploratie en dieet ontstaat tijdens de ontwikkeling (otogenie) van een individu. We hebben de herhaalbaarheid en consistentie van gemeten exploratie gedrag en de variëteit in dieet vergeleken tussen juveniele kanoeten en volwassen kanoeten, nadat zij uit de broedgebieden arriveerden in overwinteringsgebieden. We bekijken of de ervaring met een marine dieet van juveniele kanoeten gecorreleerd is met de consistentie van het gemeten exploratiegedrag. We concluderen dat juveniele kanoeten een grotere verscheidenheid aan prooien eten, een lagere herhaalbaarheid van exploratie laten zien, en een grotere variatie tussen individuen in exploratiegedrag vertonen ten opzichte van volwassen kanoeten. Tegelijkertijd verschilt de variatie in exploratiegedrag tussen individuen van dezelfde leeftijdsgroepen niet. Juvenielen met een langzamere exploratie-score (versus snellere) vertoonden een grotere variantie in de herhalingen van hun exploratie-scores, echter, deze variatie in juveniele exploratie-scores zijn niet gecorreleerd aan de tijd die zij, terugekeerd van de toendra, alin de Waddenzee hebben doorgebracht.

Om te begrijpen hoe persoonlijkheidskenmerken, gemeten in een kunstmatige context, gedrag en bewegingspatronen in het wild kunnen voorspellen, analyseren we in **Hoofdstuk vier** hoe persoonlijkheid is gerelateerd aan bewegingspatronen in verschillende contexten (dag en nacht) in het wild. We beoordeelden exploratie-scores van kanoeten in een gecontroleerde setting waarna we dezelfde vogels uitrustten met een ATLAS-zendertje om nauwkeurig hun bewegingen in het veld te volgen. We zagen dat kanoeten met snellere exploratie-scores ‘s nachts verschillen in bewegingspatronen van kanoeten met een langzamere exploratie-score; in het bijzonder, kanoeten met een snelle exploratie-score bezochten ’s nachts minder voedselgebieden maar legden grotere afstanden af tussen de gebieden, waar ze langer verbleven en langer onderweg naar toe waren. Dit in tegenstelling tot overdag, waarin we geen significante verschillen zagen in bewegingspatronen tussen individuen met verschillende exploratiescores.

Om te onderzoeken hoe individuen die in groepen leven kunnen profiteren van het gebruik van sociale informatie over foerageermogelijkheden, onderzocht **Box 1** de relatie tussen persoonlijkheid en foerageersucces foerageerscenarios in groepen. We hebben experimenten uitgevoerd om de relatie tussen exploratieve persoonlijkheid en foerageersucces (snelheid van het vinden van voedsel) van kanoeten in gevangenschap te onderzoeken. We vonden dat sneller verkennende individuen ook sneller waren in het vinden van voedsel dan langzamere individuen wanneer ze individueel werden getest.

Alle individuen vonden sneller voedsel in een groep dan als ze alleen getest werden. Echter, langzamere verkennende kanoeten werden sneller in het vinden van voedsel dan snellere verkenners met een toenemende groepsgrootte.

Om te begrijpen of exploratie gemeten in experimentele opstellingen geëxtrapoleerd zouden kunnen worden naar een grotere en complexere context, onderzocht **Hoofdstuk vijf** de relatie tussen exploratie en migratie gedrag. We onderzochten de aankomst timing in de Nederlandse Waddenzee van kanoeten na het broeden en vroegen ons af of aankomst timing gerelateerd was aan verkenningsgedrag. Omdat mannetjes voor het broedsel zorgen na het uitkomen hebben we ook het verschil in aankomst timing tussen de geslachten bekeken. We vonden dat vrouwtjes eerder in de Waddenzee aankomen dan mannetjes. Aankomst timing was ook gecorreleerd aan verkenningssnelheid: snellere verkennende kanoeten kwamen later aan dan langzaam verkennende kanoeten. Geslacht en verkenningssnelheid waren niet gecorreleerd met aankomstdatum.

In **Hoofdstuk zeven**, de algemene discussie, vat ik de belangrijkste bevindingen uit de voorgaande hoofdstukken samen en bespreek ik enkele van de belangrijkste conclusies vanuit verschillende perspectieven. Verder zet ik vraagtekens bij de definitie van potentieel controversiële sleutelconcepten in het persoonlijkheidsonderzoek van dieren en suggereer ik richtingen voor vervolgonderzoek. Ten slotte draagt dit proefschrift bij aan huidige en toekomstige studies door het opvullen van een gat in de literatuur om een experimenteel gemeten persoonlijkheidseigenschap te koppelen aan *real-world* gedragsstrategieën en toont het belang van het bestuderen van persoonlijkheid in verschillende contexten.

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