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Ch APt er **8**

More explorative individuals of a long-distance migrant shorebird respond more quickly to collapse in prey stock and have higher breeding success

Ying-Chi Chan, T. Lee Tibbitts, Chris J. Hassell & Theunis Piersma



Abstract

Movement and information use strategies are identified as key factors influencing the ability of animals to adapt to human-induced global changes. These strategies are found to correlate with personality traits measured under standardized laboratory environments. Here we examine how personality differences might underlie differences between individuals in coping with ongoing rapid environmental changes in Great Knots (*Calidris tenuirostris*), an endangered long-distance migratory shorebird threatened by loss and degradation of their main coastal refuelling sites halfway between their Northwest Australian nonbreeding area and their eastern Russian mountain tundra breeding grounds. Although the number of sites visited during migration did not correlate with individual exploratory tendencies, birds that were more explorative visited proportionally more new sites during southward migration. At a main staging site where the prey stock of the birds had collapsed, explorative individuals moved on to other staging sites sooner. Explorative individuals, compared with non-explorative individuals, arrived earlier on breeding sites and tended to stay longer there, the latter suggesting successful reproduction. We propose that explorative individuals are better at acquiring environmental information, enabling them to respond faster to environmental changes e.g. sudden food declines. Moving to alternative sites enables them to fuel up faster, and thus arrive earlier on breeding sites which, in turn, helps them to breed successfully. Accordingly, variation in exploratory tendencies within a population could be key to adaptive capacity to rapid human-induced environmental changes in long-distance migratory shorebirds. Survival costs associated with being explorative would constrain their ability to cope.

Introduction

The ability to respond to novel and changing environmental conditions by genetic adaptation, phenotypic plasticity, or range shifts, is critical to the persistence of all organisms, especially in the current world where they are exposed to human-induced global changes (Gienapp et al. 2008). For mobile animals, movement is a core response mechanism enabling individuals to exploit new habitats, from which population patterns in the form of range shifts can eventually emerge. In face of the worldwide declines in many migratory animals (Harris et al. 2009, Vickery et al. 2014, Clemens et al. 2016, Rosenberg et al. 2019), understanding the limits of movement responses to environmental changes will enable a deeper understanding of the causes of decline and allow predictions of the fate of populations under a changing environment.

Movement responses are limited by physical constraints, such as the energetic costs to move long distances; by time constraints, since movements must still fit in the annual cycle of events like breeding, migration and moulting; and by cognitive constraints, such as the animal's ability to acquire and interpret information about resources in the environment. With relevant information, an animal can move *strategically*, reaching the most profitable habitats with the lowest energetic and time costs of moving (Winkler et al. 2014). For a migratory animal, this can lead to fitness consequences directly (via an increase in survival) and indirectly by carry-over effects to later seasons, e.g. using higher quality non-breeding habitat can lead to higher reproductive success during the breeding season (Marra et al. 1998, Harrison et al. 2011, Senner et al. 2015).

Individuals may vary in the effort they put into gathering information and in the types of information gathered: they can collect information on the environment themselves ('personal information') or do it by observing the behaviour of others ('social information'; Danchin et al. 2004). Individuals can also use environmental information differently by attributing different values to personal and social information and to past and more-recent information when making decisions. Since the information use strategy that maximizes an animal's success varies between situations, optimality theory predicts that animals should be flexible and be able to attribute different values to personal and social information depending on circumstances (Rendell et al. 2011). However, a growing body of evidence suggests that animals have rather fixed information use strategies, e.g. some individuals are consistently more likely to use social than personal information (Beauchamp 2001, Kurvers et al. 2010, Trompf & Brown 2014, Bijleveld et al. 2015). Studies of linkage between information use strategies and animal personality, i.e. repeatable individual behavioural differences (Smit & van Oers 2019), reveal that information use strategies could be linked functionally to other traits which reduces the scope of flexibility.

One personality trait particularly relevant to information use is the tendency to explore. Individual-level variations in this behavioural trait have been studied in natural populations of a variety of taxa (e.g. Cummins & Walsh 1976, Perals et al. 2017, for a review see Bell, Hankison & Laskowski 2009). Exploratory tendency is measured in

a controlled laboratory setting that fits the particular ecological traits of the study species and usually involves introducing focal individuals to a novel space or object and measuring speed of approaching the novel object and movement within the novel space (Carter et al. 2013). Laboratory-measured exploratory traits have been shown to correlate with exploratory behaviours in the wild at small spatial scales, e.g. in bullheads (*Cottus perifretum*) exploring a novel stretch of stream (Kobler et al. 2009), and in the likeliness of Blue Tits (*Cyanistes caeruleus*) finding new feeders in their resident forests (Herborn et al. 2010). On the relationship between personality and response to environmental change, one study on Great Tits (*Parus major*) manipulated food availability by emptying feeding stations (van Overveld & Matthysen 2010). The more exploratory a Great Tit, the more rapidly it switched to foraging areas further away in response to the food removal. The home ranges remain the same before and after the food removal and do not relate to the birds' personalities. Thus, the observed quick responses appeared to be caused by the larger amount of environmental information that the birds had already acquired before the food removal. In summary, explorative individuals might be better at adapting to rapid environmental change, by a mechanism of a faster response facilitated by a larger amount of environmental information having already been acquired, which could be due to a higher propensity to go into novel environments to collect new information. Following this logic, exploratory personality could be driving species adaptation to the current human-induced environmental changes, such as climate change and habitat destruction. However, given the challenges of following individual animals with measured exploratory tendencies in the wild, no studies have examined this reasoning with empirical data so far.

Here we investigate the influence of exploratory tendency on individuals' responses to a rapid environmental change in a wild species with a declining population. Our study species is the Great Knot (*Calidris tenuirostris*), a long-distance migratory shorebird, which migrates annually along the East Asian–Australasian Flyway from Northwest Australia to the Eastern Russian Arctic and back (Tomkovich 1997, Chan et al. 2019b). It is listed as globally 'Endangered' on the IUCN Red List (IUCN 2017) with low adult survival (Piersma et al. 2016) and continuous population decline (Studds et al. 2017) linked to the loss and degradation of their main fuelling sites along the Yellow Sea coast. By satellite-tracking individuals with measured exploratory tendencies, we first examine whether the most explorative individuals visit the most stopping sites during migration and, during southward migration if they are more likely to visit 'new' sites (i.e. sites not visited during northward migration). Second, we investigate whether more explorative individuals respond faster to environmental changes by capitalizing on a 'natural' experiment – the sharp decline of the most abundant high-quality shorebird prey (the bivalve *Potamocorbula laevis*) at a main staging site of Great Knots (the Chinese side of the Yalu Jiang estuary, Zhang et al. 2018). We hypothesize that among individuals that stage at the Yalu Jiang estuary, the more explorative birds will switch to alternative sites more quickly, enabled by their knowledge on alternative habitats. We further assess if being more explorative leads to better migratory performance by quan-

tifying arrival dates to the breeding grounds, and whether that may lead to fitness advantages in terms of breeding success.

Materials and Methods

Bird capture

In September and October 2014, 2015 and 2016, we captured Great Knots with cannon nets at their primary non-breeding site, the northern beaches of Roebuck Bay, Northwest Australia (17.98°S, 122.31°E). After capture, each bird was measured and individually marked on their tarsi with a unique combination of leg flag and colour-bands. Birds were aged based on plumage characteristics and 20–30 adults were selected per year to be transported to an indoor aviary.

Testing exploratory tendency

In the aviary, birds were housed in groups of 4–5 in cages made with mesh nets (thus all the birds could see each other in the aviary) with *ad libitum* food (mealworms). The birds were acclimatized for at least 24 hours before being tested for exploratory behaviour. Following the 7 × 7 m experimental arena described in Bijleveld et al. (2014), we designed a exploration trial tent of 3 × 3 m, filled with a layer of water of about 12 cm. Four plastic trays of wet sand (with its surface at the same level as the surrounding water) were placed in the tent for the birds to explore (Fig. 8.1). To motivate the birds to



Figure 8.1. Inside view of the 3 × 3 m tent for measuring exploratory tendency in Great Knots (*Calidris tenuirostris*). The tent is filled with a layer of water of about 12 cm, with four plastic trays of wet sand for the bird to explore.

search for food during the trials and to induce standard hunger levels, each focal bird was transported to a waiting cage without food two hours before the start of the trial. The trial lasted 30 mins from the moment that the tent door was closed and the bird had landed on a patch. Trials were conducted between 5:30–9:30 and 15:30–17:30, avoiding the hottest time of the day.

All trials were recorded on video and later analysed with the BORIS software (Friard & Gamba 2016), allowing accurate estimation of time budgets. We recorded the following behaviours: ‘searching for food’ (include walking and probing), ‘standing’, ‘preening’, ‘flying’, ‘swimming’ and ‘bathing’. We also recorded when the bird was on which patch (i.e., which tray). We quantified exploration by the fraction of total time spent in searching behaviour while on a patch, a metric first used by Bijleveld et al. (2014) as a measure of exploratory tendency. Prior to the current study, we tested our tent set-up in an aviary and experimental facility on Texel, the Netherlands in 2013 using Red Knots (*C. canutus*, a sister species of Great Knots). We tested the same individuals in both the 7 × 7 m arena used in Bijleveld et al. (2014) and in the 3 × 3 m tent, and exploratory tendency between both settings were strongly correlated ($r_{19} = 0.642$, $P = 0.001$). We also found high repeatability between 1st and 2nd trials ($R = 0.798$, $SE = 0.069$, $CI = [0.655, 0.94]$, $P = 0.001$, $n = 28$).

Satellite tracking

After the trial, we fitted a 4.5 g solar Platform Terminal Transmitter (PTTs, Microwave Telemetry, USA) to each of the Great Knots. These tags were the lightest satellite transmitters available at the time of the study. The transmitter comprised 3% of a Great Knot’s average lean mass (mean of 151 g, SD 20, measured in this study). Transmitters were deployed using a body harness (Chan et al. 2016) made of elastic nylon (Elastan, Vaessen Creative, The Netherlands), which degrades and breaks, thus releasing the tags after one to two years. In some cases the tag was shed earlier, which is evident from several individuals marked with leg-band of colour combinations being resighted after the tag ceased transmitting with the tag not seen on the bird. We then kept the birds for at least 24 hours to allow acclimation to the transmitter and harness before releasing them into the wild at the capture location.

PTTs were programmed to operate on a duty cycle of 8 hours of transmission and 25 hours off. On average, six locations (3 SD) were received from the Argos system (Collecte Localisation Satellites, CLS) per tag in each transmission period. Tags that stopped transmitting were considered to indicate a broken harness, a malfunctioning tag, or the death of the bird. This work was carried out under Regulation 17 permits SF 010074, SF010547 and 01-000057-2 issued by the West Australian Department of Biodiversity, Conservation and Attractions.

Data analyses

We filtered the Argos locations to retain all standard locations (i.e., the location classes 3, 2, and 1) and applied the Hybrid Douglas filter (Douglas et al. 2012) to remove any

implausible auxiliary locations (i.e., the location classes 0, A, B and Z, for details of how locations classes were assigned, see CLS 2016) by setting filtering parameters at 120 km/h for the maximum sustainable rate of movement and 10 km for minimum redundant distance. We further accounted for spatial error in the Argos telemetry by fitting the tracking data with a continuous-time random walk state-space model with the 'fit_ssm' function in the 'foiegras' R package (Jonsen et al. 2020). The state-space model incorporated the error ellipse information of the Kalman filter-based Argos locations, and the fitted locations from the model were used in the analysis of identifying migration stops and timing.

To identify stopover sites, we first identified locations with ground speed less than 5 km/h as 'stationary'. Stopovers were defined as a cluster of at least 3 stationary locations within 20 km of each other, with the first and last recorded locations at the stopover being at least 2 hours apart. Departure times were extrapolated over the intervening travel distance between the last location at a stop and the next location, arrival times were calculated in the same way. Breeding site was defined as the site within the breeding range where the individual stayed the longest. The spatial behaviour during migration was quantified by the number of stops with a length of stay of longer than one day and the proportion of 'new' stops during southward migration (i.e. not visited during northward migration). General linear models with normal errors were used to test for the relationships between these spatial behaviours (log-transformed) and the fraction of time spent searching in the tent ('exploration score' hereafter); sex was included as a fixed effect in the model.

At the Yalu Jiang Estuarine Wetland National Nature Reserve (39.8°N, 123.9°E, located on the Chinese side of the Yalu Jiang estuary on the China-North Korea border; Yalu Jiang NNR hereafter), the population of the bivalve *P. laevis*, a high-quality prey of Great Knots (Choi et al. 2017), has sharply declined in 2013 and continued declining in subsequent years; the very high density in 2011 (708.06 ind/m², accounting for 94% of the total biomass of macrozoobenthos at the site) have declined by >99% in 2016 (Zhang et al. 2018). To examine individual responses to the sharp decline in *P. laevis*, we selected the individuals which arrived there in mid-April and extracted the date when they moved to other sites in the Yellow Sea. We also quantified departure date from the Yellow Sea and arrival date at their breeding site. We tested the relationship between these phenological measurements and the exploration score by general linear models.

For all tracked individuals, we quantified their arrival dates at their breeding site. We tested the relationship between arrival dates and exploration scores by general linear models. We used the duration of stay at the breeding site as a proxy for hatching success based on the findings of Lisovski et al. (2016a) and Tomkovich (1996). They found that females take 8–12 d from arrival to egg-laying and the incubation period is 23 d, thus we assume that a stay of ≥34 d meant the birds successfully hatched a clutch. In Great Knots, females leave the brood at the time of hatching and males accompany the chicks for another 24–30 days (Tomkovich 1995). Clearly, the relationships between duration of stay at a breeding site and exploration score have to be examined separately

for each sex, but since only 3 males arrived at breeding sites, we could only test this relationship in females. To further understand the linkage between arrival date, breeding site location, and breeding success, we obtained the elevation of all breeding sites from the Global Multi-resolution Terrain Elevation Data 2010 using GoogleEarthEngine. We analysed percent snow cover at breeding sites at a scale of 500 m resolution from MOD09A1.006 Terra Surface Reflectance 8-Day Global 500m dataset (Vermote 2015), where we derived Normalized Difference Snow Index (NDSI; ranges from -1 to 1 , the land surface is snow free when $\text{NDSI} \leq 0$, Riggs & Hall 2016). To obtain the first snow free date at each breeding site, we extrapolated the NDSI values (every 8 days) to obtain the date when it reached 0, i.e. no snow was present. All statistical analyses were performed in R v 3.6.2 (R Core Team 2019) with significance level set at $P < 0.1$.

r esults

The satellite-tracked Great Knots stopped at 5.6 ± 1.5 sites during northward migration ($n = 21$ birds with the entire northward migration tracked) and at 5.3 ± 1.8 sites during southward migration ($n = 10$; Fig. 8.2). There was no relationship between the number of stopping sites used and exploration score ($P > 0.1$, Fig. 8.2A & B). However, the more explorative birds visited a higher proportion of 'new' sites (those that were not visited during northward migration) during southward migration ($F_{2,7} = 3.897$, $P = 0.07$; Fig. 8.2C). Among the seven Great Knots that reached Yalu Jiang NNR in 11–22 April 2015–2016, the more explorative individuals left Yalu Jiang NNR earlier than the less explorative ones ($F_{1,5} = 71.3$, $P < 0.001$) and 6 of the birds moved to other staging sites in the Yellow Sea; the least explorative bird did not move to any other staging site (Fig. 8.3). All individuals departed from the Yellow Sea on 19–20 May and reached their breeding sites on average on 25 May (range: 23–27) except the least explorative individual which departed the Yellow Sea on 25 May and reached its breeding site on 2 June (Fig. 8.3).

Among the 21 birds that were tracked till their breeding sites, females arrived on their breeding sites between 21 May and 8 June ($n = 18$), and males between 23 and 27 May ($n = 3$; Fig. 8.4). There was a trend of more explorative individuals reaching their breeding sites earlier than less explorative individuals ($F_{1,19} = 3.366$, $P = 0.082$, Fig. 8.4). The more explorative a female, the longer it stayed at their breeding site ($F_{1,13} = 4.897$, $P = 0.045$). Breeding sites were at altitudes of 117–1816 m (mean = 918 m) and become snow-free between 9 May – 20 June (mean = 1 June). There was no relationship between exploratory tendencies and the breeding site's elevation or phenology (snow-free date) (all $P > 0.1$). Most birds (18 out of 21) arrived 8.2 ± 5.2 days before the first snow-free date at the breeding site. For birds that appeared to successfully hatch a nest, arrival times were predicted by snow-free dates at the breeding sites ($F_{1,8} = 4.704$, $P = 0.062$).

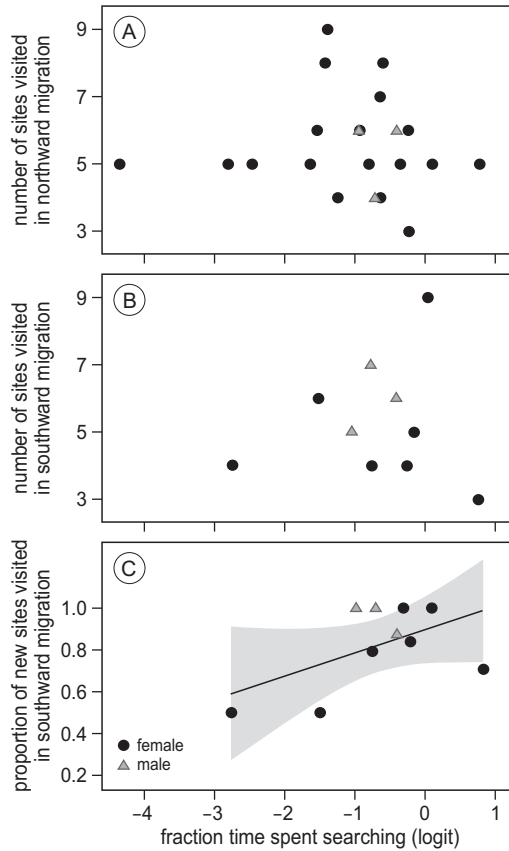


Figure 8.2. The number of stops during (A) northward and (B) southward migration, and the (C) proportion of new sites visited during southward migration (i.e. not visited during northward migration) of Great Knots tracked from a Northwest Australia non-breeding site to eastern Russia breeding sites in 2015–2018.

Discussion

We show that the exploratory tendencies of Great Knots measured in the laboratory is related to the speed of response to a collapse of prey stock at a migratory staging site in 2015 and 2016. Our results of the more explorative birds leaving the site earlier is consistent with the findings of van Overveld & Matthysen (2010) on a small-scale spatial response of Great Tits to a manipulation of reduced food availability. To our knowledge, our study is the first to show this phenomenon on a large spatial scale where a major migratory staging site was experiencing sudden dramatic reduction in food availability.

The quick response to prey collapse of more explorative individuals may be facilitated by the larger amount of environmental information they have acquired by visiting

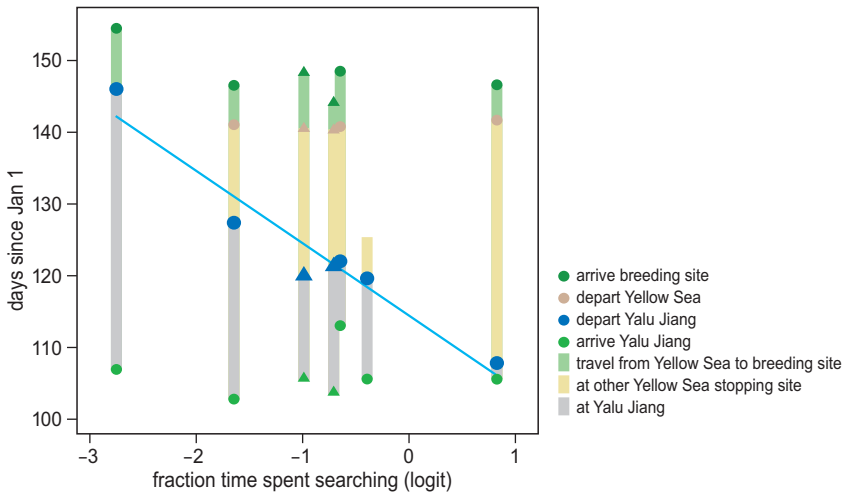


Figure 8.3. The timing of events during northward migration for seven satellite tracked Great Knots that reached Yalu Jiang Estuarine Wetland National Nature Reserve in early to mid-April 2015–2016, plotted against exploration score, i.e. fraction of time spent searching in the tent (see text). Blue line shows the significant negative relationship between departure date from Yalu Jiang and the fraction of time spent searching.

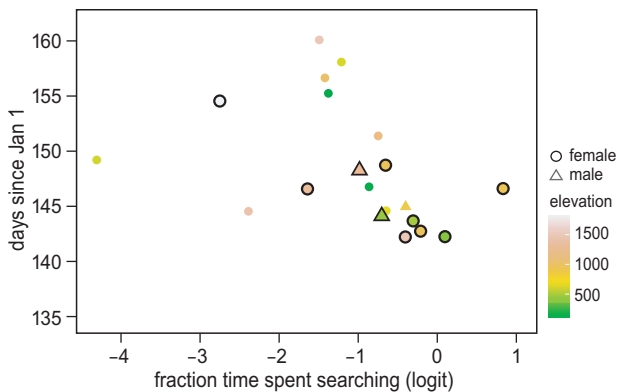


Figure 8.4. Arrival dates at breeding sites and exploration scores of 21 satellite-tracked Great Knots. Symbols with thick borders indicate individuals that apparently hatched eggs (i.e., they stayed at breeding sites for ≥ 34 d, see text).

sites. We tested the relationship between information acquisition and exploratory tendency by assuming that visiting more sites during migration would represent the gathering of more environmental information. However, we did not find a relationship between exploratory tendency and number of stops during northward and southward migration. We did find that explorative individuals visited relatively more ‘new’ sites during southward migration. This indicates that during southward migration, more

explorative individuals tend to forgo the benefits of familiarity which comes with using the same sites as during northward migration, and instead visit sites that they have less information about. The number of sites visited in a single migration might not be indicative of the tendency to gather information, as it could be affected by environmental conditions encountered en route. For example, an unfavourable situation could prompt an individual to move to another site, which might increase the number of sites visited. Information on sites will be accumulated not just during a single migration, but will accumulate over several years. Therefore, only by tracking individuals over multiple years can we properly test the relationship between the number of stops made (as a proxy for amount of environmental information) and exploratory tendency.

Being explorative seemed to be advantageous during the years we conducted our study, as we found that more explorative females stayed relatively longer which suggested they successfully hatched a nest. Our small sample size of three males does not allow testing whether explorative males would attain higher breeding success. We also found that more explorative individuals arrived earlier at breeding sites. There are known benefits of earlier arrival that lead to higher breeding success, such as a higher chance to acquire a higher quality mate and a better territory as shown in previous studies of other bird species (e.g. Lozano et al. 1996, Smith & Moore 2005). Moreover, birds need to arrive in-time to catch the seasonal food peaks at their breeding sites; arriving too late and missing the food peak could negatively impact the growth of chicks and fledging success. We did find that the Great Knots that bred successfully matched their arrival time with the phenology (snow-free date) of their breeding sites. For long-distance migratory shorebirds like the Great Knot, one factor that constrain how early they can arrive at the breeding site is how fast they can fuel up at the stops during their migration. Our results indicate two potential mechanisms of more exploratory individuals to achieve a faster fuelling rate: one being moving more quickly from a site of poor quality, and the other being having more information on alternative stopping sites and their habitat quality.

If exploratory behaviour is heritable in Great Knots like it is in great tits where heritability has been measured (Dingemanse et al. 2002), a higher breeding success of explorative birds could lead to more explorative individuals within the population, which might be better suited to deal with the habitat deterioration at the intertidal areas in the Yellow Sea where they stop for fuelling during migration (Murray et al. 2015, Melville et al. 2016a). Moreover, exploratory tendencies are related to dispersal characteristics in some species (Dingemanse et al. 2003, Cote et al. 2010); therefore a selection for exploration would also lead to more dispersive individuals that are more likely to discover and occupy new breeding and non-breeding habitats, and rely less on the Yellow Sea during migration. As more explorative individuals are able to arrive at the breeding sites earlier, a general increase in the exploratory tendency in the population would also prepare Great Knots to keep up with possible advancements in breeding ground phenology caused by global climate warming which is currently affecting many species (Parmesan & Yohe 2003, Visser & Both 2005).

However, the direction of selection on exploratory tendency also depends on survival costs. For the tracked Great Knots in this study, survival could not be estimated from tag lifespan since the tag was often shed when the harness degraded. Previous studies revealed that the relationship between explorative behaviour and survival depends on the environment and life stage. It has been shown that explorative individuals have survival costs during the juvenile phase in European rabbits *Oryctolagus cuniculus* (Rödel et al. 2015), while other studies showed balancing selection or disruptive selection on exploratory behaviour, dependent on the environmental regime (Dingemanse et al. 2004, Adriaenssens & Johnsson 2013, Bergeron et al. 2013, Le Galliard et al. 2013). For long-distance migratory shorebirds like the Great Knots, their 'long-jump' migration strategy of stopping at only a few sites for fuelling and flying non-stop between them (Piersma 1987) has probably evolved in environments where there are stable and predictable seasonal resources far apart in space, and to reduce risks associated with stopping, e.g. exposure to hunters, predators and pathogens (Gill et al. 2009, Conklin et al. 2017). Nowadays, habitat degradation in the staging sites and global climate change have made resources less stable. Moreover, explorative individuals might be subject to greater risks of exposure to hunters, predators and pathogens when making more and unfamiliar stops during migration. In this study, we have showed that the variation in exploratory tendency provides a way for Great Knots and other long-distance migratory birds to maintain adaptive capacity to sudden environmental changes. Investigations on the costs associated with being explorative would be a next step towards predictions of the responses of these bird populations to negative environmental changes.

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