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Chapter 6

Movement as an orchestration by the environment: from grouping nomads to solitary residents in one species

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ABSTRACT

Developmental and behavioural plasticity allow fine-tuning of movements to the environment. They can enhance individual variation in space use, but also underlie space-use patterns at the population level. Consequently, patterns of aggregation and site fidelity, usually considered species-specific, may reflect environmental context more directly than often assumed. We studied space use of red knots (*Calidris canutus*, a migratory shorebird) in two similar intertidal areas but with contrasting resource distributions, the Wadden Sea in The Netherlands and the Banc d'Arguin in Mauritania. Resource patches were much larger in the Wadden Sea, and red knots there showed strong aggregation and weak site fidelity, the opposite of red knots in Banc d'Arguin. We suggest that population space-use patterns reflect individual responses to the resource environment, implying direct consequences of environmental change on population space-use. This calls for studies on the individual development of movement that include the relevant environmental details.

INTRODUCTION

Animal space use is in continuous interaction with the environment, ultimately because all species characteristics that enable and limit movement evolve through natural selection in interaction with that environment (Nathan *et al.* 2008). More directly, individuals adjust to the environment via developmental plasticity in these characters (West-Eberhard 2003; Piersma & van Gils 2011). Even more directly, individuals adjust to their surroundings via individual decisions, which are informed by cues on environmental resources (e.g., Stephens & Krebs 1986). The latter two mechanisms may explain part of the individual variation *within* populations (Stamps & Groothuis 2010; Bolnick *et al.* 2011; Dall *et al.* 2012), also in space use (e.g., Spiegel *et al.* 2017). What has received less attention in movement ecology, is that the same mechanisms also cause differences *between* populations of the same species in different environments. Even if a trait shows little or no individual variation within a population, its expression may still be largely a consequence of plastic development and/or individual decisions, and hence a direct consequence of the environment (Piersma & van Gils 2011).

An ability to adjust space use to local circumstances would be a particularly helpful characteristic of migratory species, which in the course of an annual cycle encounter sequences of habitats (Greenberg & Marra 2005). Indeed, considerable variation in space-use patterns has been described within single migratory bird species, in terms of *aggregation* (e.g., Myers 1980; Ens 1983; Colwell 2000) as well as in terms of *site fidelity* (e.g., Tim Tinker *et al.* 2012; Patrick *et al.* 2014). Here, we define *aggregation* as spatial patterns in the locations of multiple individuals at one point in time (e.g., inter-individual distances, group size, sociality), and *site fidelity* as spatial patterns in the locations of single individuals over time (e.g., home range, return rate, exploration). Both are relevant when asking how movement patterns of foragers depend on the characteristics of the environment, and specifically the distribution and availability of resources. Matched observations with enough detail on both resources landscapes and population space-use, between individuals as well as over time, have only been too rare.

Aggregation and site fidelity: a concert, orchestrated by the resource landscape

Both the optimal degree of aggregation and site fidelity can be constrained by local resource density and depletion (Fretwell & Lucas 1970; Switzer 1993). Through competition, higher degrees of aggregation and site fidelity become increasingly incompatible as the local resource abundance decreases. To clarify this interaction, consider a landscape with a number of patches, each containing a number of resource units (Fig. 6.1). Ideal and free foragers move between resource-containing patches and consume one resource unit at each time step. Now consider different levels of aggregation and site fidelity by the foragers. In this context, we define aggregation as the number of individuals that simultaneously visit the same patch, and site fidelity as the number of time steps spent by an individual in the same patch. With the lowest degrees of aggregation and site fidelity (Fig. 6.1C, we could call these foragers “solitary nomads”), each visited patch needs to contain only one resource unit. In contrast, with full aggregation and full site fidelity (so-called

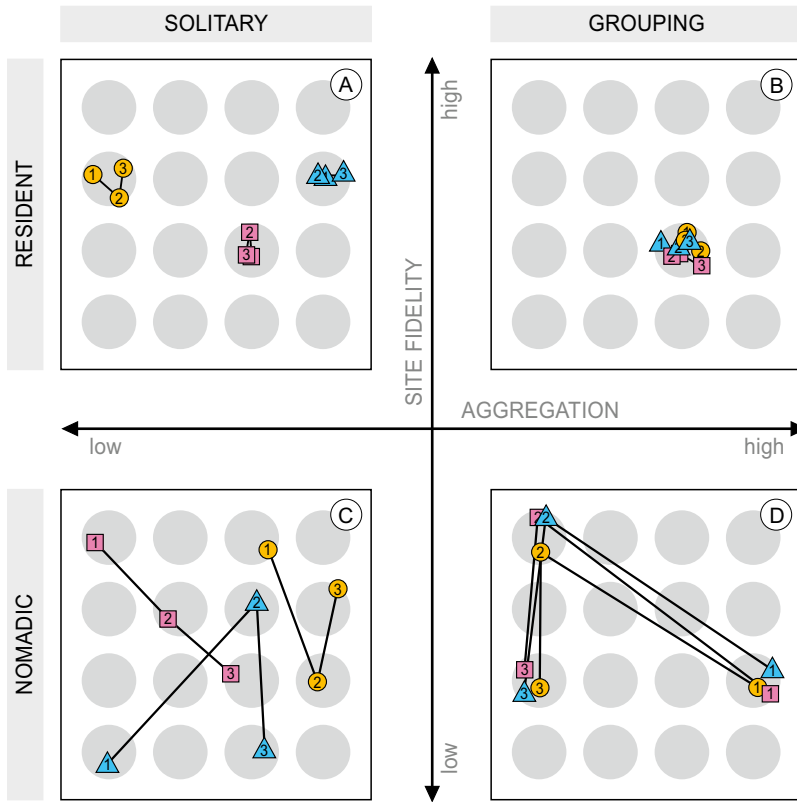


Figure 6.1 The two fundamental patterns in population space use, with degree of aggregation on the x-axis and degree of site fidelity on the y-axis. Simulations of the four extreme strategies are plotted in the panels, which we named “solitary residents” (A), “grouping residents” (B), “solitary nomads” (C) and “grouping nomads” (D). Of course, intermediate strategies also exist. Grey circles represent resource patches. Coloured symbols denote three different individuals, and the thin lines connect subsequent positions of the same individual in three time steps, which are denoted by the numbers in the symbols. Individual positions within patches are arbitrary.

“grouping residents” Fig. 6.1B), the patch needs to contain enough resources for each individual during all time steps. At intermediate resource abundances, either full aggregation (“grouping nomads”, Fig. 6.1A) or full site fidelity (“solitary residents”, Fig. 6.1D) are possible, but not both at the same time. Because the consequences of aggregation and site fidelity act in concert, understanding either one of them may require an understanding of both. Here, we make a start in studying them simultaneously.

Space use by one species in two contrasting environments

We exploited an opportunity to determine whether levels of site fidelity and aggregation were adjusted to local resource landscapes in a molluscivore specialist and migratory shorebird, the red knot (*Calidris canutus*) in superficially similar intertidal habitats that

contrasted in the distribution of food resources. The forager's morphological traits were similar in the two areas (Piersma 2007), which allowed to study the specific effect of the distribution of resources on forager movement behaviour. Using a novel automated tracking system with a high resolution both in space and time (MacCurdy *et al.* 2012; Piersma *et al.* 2014), detailed tracks of individual red knots were collected in the two main wintering areas of red knots along the East-Atlantic Flyway: the Wadden Sea in The Netherlands (53°15'N, 5°15'E), and the Banc d'Arguin in Mauritania (19°53'N, 16°17'W) (Piersma 2007).

Individual foraging itineraries were described as a sequence of patch visits during a single low tide period (Bijleveld *et al.* 2016). In both study areas, using exactly the same technology, we described (1) the degree of aggregation, i.e. whether red knots were distributed across the whole used area in each tide, or aggregated in part of it, and (2) the degree of site fidelity, i.e. whether individual tagged red knots visited the whole area used by the population, or showed individual site fidelity. To explain the differences observed, we compared differences in the resource landscape. These were based on standardized, spatially explicit resource sampling efforts (Bijleveld *et al.* 2012b), interpreted in the light of an experimentally tested diet-choice model (van Gils *et al.* 2005b; Chapters 2 to 4). This allowed the spatial mapping of potential intake rates, much more explicit and precise than indirect indices of food such as via satellite-based chlorophyll indices (e.g., Sims *et al.* 2008; Avgar *et al.* 2013; Hopcraft *et al.* 2014). We determined local food densities and the spatial scale of heterogeneity in the distribution of potential food intake rates in the two non-breeding areas. Comparing these to the scale of movement by red knots, we discuss whether these parameters explain the observed differences in the degree of aggregation and site fidelity of red knots between the two areas.

METHODS

Setting the scale

During low tide, red knots move over intertidal mudflats in search of buried mollusc prey, which they find by repeated probing of the sediment with their ca. 3.5 cm long bill (Piersma *et al.* 1995; van Gils *et al.* 2016). As the tide retreats, red knots fly to foraging locations, roughly 100 m to 10,000 m away from the roost, and visit one or several different locations before returning to the roost when the water returns (Bijleveld *et al.* 2016; Chapter 5). After landing, red knots search for prey on foot, and may walk 100 m or more between flights. Hence, red knots search for resources on two spatial scales. They move between foraging locations by flight, and move on foot within these locations.

Tracking red knots

In the Wadden Sea 47 red knots were tracked between 12 and 26 August 2011. At Banc d'Arguin, 46 red knots were tracked between 9 January and 13 February 2013. In the Wadden Sea we tracked the subspecies *C. c. islandica*, who spends the winter in intertidal systems in north-western Europe, including the Wadden Sea. At Banc d'Arguin, tracked

red knots were of the subspecies *C. c. canutus*, who winter in West-Africa, with a majority at Banc d'Arguin, and with some staging in the Dutch Wadden Sea in late summer when returning from the breeding grounds in Taimyr, north-central Siberia (Piersma & Davidson 1992; Nebel *et al.* 2000). The two subspecies are genetically barely distinct (Buehler & Baker 2005; Buehler *et al.* 2006), and occur in mixed flocks in the Wadden Sea (Nebel *et al.* 2000) where they cannot be distinguished visually (Nebel *et al.* 2000; van Gils *et al.* 2006). In the Wadden Sea in August, daily temperatures were roughly the same as at the Banc d'Arguin in January, and given the similarity in the tidal movements, so would be daily energy expenditures (Wiersma & Piersma 1994).

The 6.5 g radio tags (ranging from 5.5 to 7.5 g; <5% of body mass) were glued on the rump with Superglue (Warnock & Warnock 1993). Every sec the tags emitted an individual-specific radio signal, to be received by an array of receiver stations in the study area. When received by at least three receiver stations, the tag's location was calculated from arrival times at the different stations (Piersma *et al.* 2014).

The raw position data was summarized into a series of residence patch visits during each low tide period (2h before to 2h after low tide). This was done in four steps. First, the raw position data was median-filtered using a 5-point sliding window. Then, using a the method described by Barraquand & Benhamou (2008), the duration of stay within 125 m of each position was calculated, allowing excursions outside the radius for less than 30 sec. The resulting sequence of "residence times" was segmented by the penalized contrasts method (Lavielle 2005) into locations with an arrival and departure time. Finally, adjacent residence patches closer than 125 m were combined into one residence patch. Patch visits shorter than 10 min were not used in the analysis, because birds were then probably travelling rather than foraging (Bijleveld *et al.* 2016). The subsequent patch visits of a single bird during a single low tide period were defined as one foraging itinerary. This resulted in 144 foraging itineraries of 13 different birds in the Wadden Sea, and 1323 itineraries of 38 birds in the Banc d'Arguin. For further details we refer to Bijleveld *et al.* (2016) for the Wadden Sea study and Chapter 5 for the Banc d'Arguin study.

Measuring aggregation and site fidelity

The degree of aggregation can be calculated from location data by comparing the average distance between the locations of different individuals regardless of time, with the average distances between the locations of different individuals at the same point in time. Similarly, the degree of site fidelity can be calculated by comparing the average distances between all locations regardless of individual with the average distances between all locations of a single individual (an inverse measure of site fidelity, see Fig 6.1; Guilford *et al.* 2011; van Bemmelen *et al.* 2017). Figure 6.2 shows the result of these measures for simulated data of the four contrasting strategies (depicted in Fig. 6.1).

To compute an absolute measure of the mean distance between two red knot itineraries, the distance between them was calculated each 5 min from 2 h before to 2 h after low tide, as the shortest distance between the patch location in the first itinerary to the nearest patch location in the second itinerary within one hour (time relative to the low

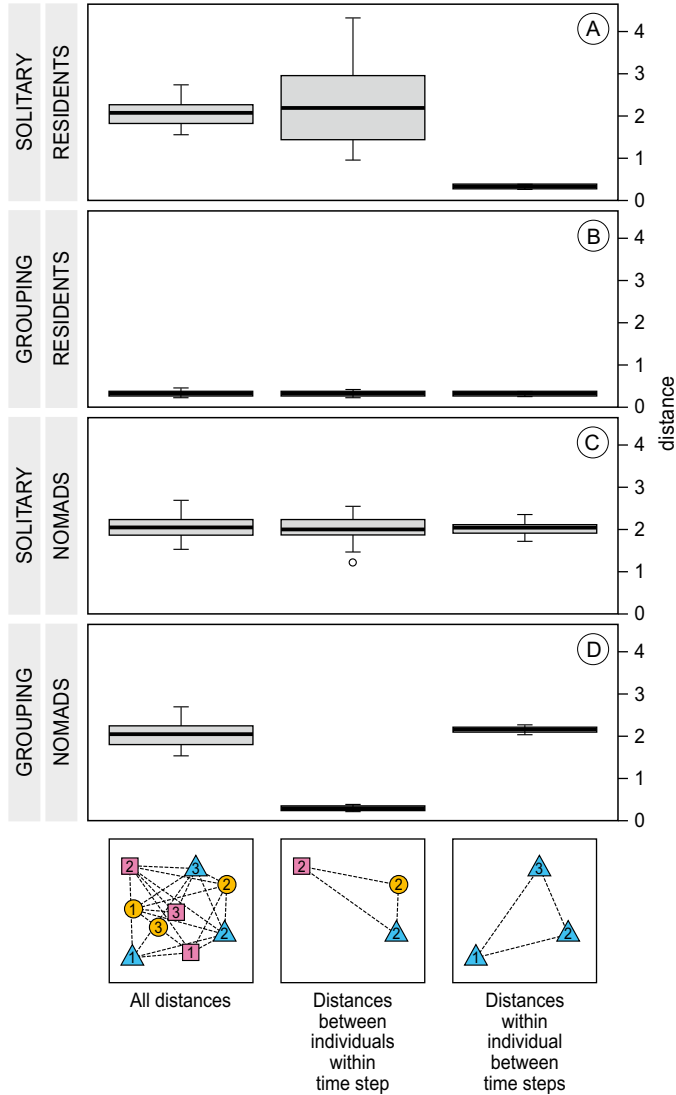


Figure 6.2 Mean distances between individuals in simulations of four different space use strategies. For each of the four extreme strategies shown in Fig. 6.1, data was simulated for 16 individuals during 16 time steps. Fig. 6.1 shows the first 3 time steps of 3 simulated individuals. The distance between neighbouring patches is taken as the unit of distance. Left boxes show the distances between all combinations of locations, averaged per individual. Middle boxes show the distances between all locations and the other locations in the same time step, averaged per individual. Right boxes show the distances between all locations and the other locations of the same individual, averaged per individual.

tide). These nearest-neighbour distances were averaged to obtain a single mean distance between the two itineraries, i.e. the mean nearest-neighbour distance. Because of a difference in behaviour between day and night (Chapter 5; Bulla *et al.* in review), daytime locations were only compared with other daytime locations, and night time locations were only compared with other locations at night. Locations recorded in the hour before sunrise and after sunset were not used at all. Mean distances between itineraries within birds in different low tide periods were calculated by averaging, for each itinerary, the distances to all other itineraries by the same bird. Likewise, mean distances between itineraries of different birds in the same low tide period were calculated by averaging for each itinerary the distances to all itineraries by other birds in the same tide.

Due to the complex structure of the data, significance of the observed differences between nearest-neighbour distances of all itineraries and nearest-neighbour distances between individuals within tides (to show aggregation), as well as the differences between nearest-neighbour distances of all itineraries and nearest-neighbour distances within individuals between tides (to show site fidelity) was tested by a repeated (10,000 times) randomization procedure. For each randomization, all tag-IDs and tide-IDs from the original itineraries were randomly re-assigned, the distances between all pairwise combinations of itineraries calculated and then averaged per itinerary, to arrive at a randomized estimate for the average distance between itineraries. To calculate a randomized estimate for its difference with between-individual distances within tides, tide-IDs were randomized per individual, all pairwise distances between itineraries within the same tide calculated, and then averaged per itinerary. To arrive at a randomized estimate for mean distances within individuals between tides, tag-IDs were randomized per tide, all pairwise distances between itineraries within the same tag calculated, and then averaged per itinerary. Significance was assessed by calculating the proportion of simulations that resulted in a more extreme difference than the actual observed difference (two-tailed p-value). To assess significance of differences between the Wadden Sea and Banc d'Arguin, mean-nearest neighbour distances were averaged per tag to arrive at independent observations, and tested by linear regression.

Resource sampling

The mollusc food of red knots was sampled at 880 locations in the Wadden Sea between 15 and 19 July 2011, and at 265 locations at Banc d'Arguin between 4 and 17 January 2013. Both sampling schemes consisted of a 250 m grid with a spatial accuracy of approximately 10 m, with an additional 20% locations placed randomly on the grid lines (Bijleveld *et al.* 2012b; Bijleveld *et al.* 2016). Samples were taken by pushing a core into the sediment to at least 20 cm depth, and sieving the top 4 cm over a 1 mm mesh (either one core with a surface of $1/56 \text{ m}^2$ or two cores of $1/112 \text{ m}^2$). All molluscs were collected and stored in 4% formaldehyde, except for bivalves longer than 8 mm in the Wadden Sea, which were frozen.

All individual molluscs were identified to the species level, and length was measured to the nearest 0.1 mm. Dry mass of the shell (DM_{shell}) and ash-free dry mass of the flesh ($AFDM_{\text{flesh}}$) was measured in a subset of the samples as described in Piersma *et al.*

(1993). Individuals below 8 mm (Wadden Sea) and 5 mm (Banc d'Arguin) in length were pooled before weighing when in the same sample. In *Limecola balthica* (until recently *Macoma balthica*), *Ensis directus* and *Mya arenaria*, flesh and shell were weighed together, and the ash-free dry mass of the shell was estimated with calibration lines from Zwarts (1991). The gastropod *Peringia ulvae* was also weighed as a whole, assuming that 12.5% of organic matter resided in the shell (Dekker 1979). For bivalve species weighed whole, DM_{shell} and $AFDM_{\text{flesh}}$ of the unweighted individuals were estimated by non-linear local regression of the log-transformed masses and lengths of the weighed individuals (Bijleveld *et al.* 2015a).

To determine which potential prey species contributed to the diet of red knots, we analyzed the composition of the droppings and calculated the relative contribution of different prey species to the diet (Dekinga & Piersma 1993; Onrust *et al.* 2013). Droppings were collected in the field at locations where radio-tagged red knots were observed foraging (2 – 10 droppings at 32 locations in the Wadden Sea and 45 locations in Banc d'Arguin). The droppings were aggregated per location and sieved over a 300 μm mesh. All bivalve hinges and last coils of gastropods were identified to the species level and measured. Each measurement was converted to an estimated $AFDM_{\text{flesh}}$ mass, using species-specific calibration measurements of whole individuals (Dekinga & Piersma 1993; Onrust *et al.* 2013).

Calculating potential resource intake rates

Potential intake rates (mg $AFDM_{\text{flesh}}$ per second) of the relevant mollusc species were estimated at each sampling station as a function of the observed densities by using an experimentally tested optimal diet choice model for red knots that takes into account search time, size-dependent handling time, size- and species-dependent digestive quality, and the toxicity of the main available prey species at Banc d'Arguin, *Loripes lucinalis* (Chapters 2 and 3). Digestive capacity varies among individual red knots, with diet and with season (van Gils *et al.* 2005a) and scales to the square of gizzard mass (van Gils *et al.* 2003a; van Gils *et al.* 2005b). Gizzard masses were measured by ultrasonography (Dietz *et al.* 1999; Dekinga *et al.* 2001) immediately after the catch, and were lower in the Wadden Sea (mean \pm SD, 7.0 ± 2.0 g) than at Banc d'Arguin (8.5 ± 1.8 g). This resulted in predicted maximum processing rates of $2.5 \text{ mg } DM_{\text{shell}} \text{ s}^{-1}$ in the Wadden Sea and $3.7 \text{ mg } DM_{\text{shell}} \text{ s}^{-1}$ at Banc d'Arguin (note that only those mollusc species were taken into account that were estimated to comprise at least 1% of the red knots diet, in terms of $AFDM_{\text{flesh}}$). Search efficiency was estimated at $6.4 \text{ cm}^2/\text{s}$ in the Wadden Sea (Piersma *et al.* 1995) and, due to obstruction by seagrass roots, at $2.0 \text{ cm}^2/\text{s}$ at Banc d'Arguin (de Fouw *et al.* 2016). Handling times (s) were assumed to be a function of shell size, previously estimated for *Cerastoderma edule* as $3.3 \times \text{length} [\text{cm}]^2$ (Piersma *et al.* 1995). The relevant molluscs at Banc d'Arguin (*Loripes lucinalis*, *Dosinia isocardia*, *Diplodonta circularis* and *Abra tenuis*) were assumed to have handling times similar to *Limecola balthica* ($2.1 \times \text{length}^2$ when buried at an average depth of 2 cm) (Piersma *et al.* 1995), as they are all relatively flat and round burying bivalves with a smooth surface. The toxin constraint on the intake of *Loripes lucinalis* was set at $0.1 \text{ mg } AFDM_{\text{flesh}} \text{ s}^{-1}$ (Chapter 2).

The distribution of resources

To determine range of autocorrelation in the resource landscape, spatial autocorrelation in the predicted AFDM_{flesh} intake rates was calculated at discrete distances of 50 with the function “correlog” in R-package “ncf” (R Core Team 2015), using *Moran’s I* index as the measure of autocorrelation (Kraan *et al.* 2009a; Kraan *et al.* 2009b; Bijleveld *et al.* 2016). The autocorrelation range was estimated by the distance at which the spatial autocorrelation went below 0.1, which can be interpreted as a measure of resource patch size (Kraan *et al.* 2009a).

RESULTS

Aggregation and site fidelity of tagged red knots

In the Wadden Sea, during each low tide red knots aggregated in some part of the total foraging range; mean distances between itineraries *in the same tide* were significantly smaller than the mean distances between *all* combinations of itineraries (on average 1900 m and 2500 m, $p < 0.001$, Fig. 6.3A). Red knots did not show site fidelity in the Wadden Sea, as mean distances between itineraries *of the same bird* were not significantly smaller than the mean distances between *all* combinations of itineraries (both 2500 m on average, $p = 0.09$, Fig. 6.3A). These differences agree with the differences in the simulated data of “grouping nomads” (Fig. 6.2D).

In contrast, red knots at Banc d’Arguin showed strong site fidelity, as mean distances between all combinations of itineraries *of the same bird* were much smaller than mean distances between *all* combinations of itineraries (on average 600 m and 1600 m, $p < 0.01$, Fig. 6.3B). Red knots at Banc d’Arguin also did aggregate, but the area used per tide was only slightly smaller than the area used by the study population. Distances between itineraries of birds in the same tide were on average 100 m smaller than distances between *all* combinations of itineraries (1500 m and 1600 m, $p = 0.01$, Fig. 6.3B). These differences agree best with the simulated data of “solitary residents” (Fig. 6.2A).

Note that all absolute distances averaged per bird in the Wadden Sea were larger than at the Banc d’Arguin (2500 and 1600 m, $F_{1,49} = 27.3$, $p < 0.001$), suggesting that overall the tagged red knots used a larger area within the range covered by the receiver stations in the Wadden Sea than at Banc d’Arguin. Average distances between tagged birds within the same tide were also larger in the Wadden Sea than at the Banc d’Arguin (1800 and 1500 m, $F_{1,49} = 4.5$, $p = 0.04$).

Resource densities and resource patch sizes

Maximum resource densities, in terms of available ash-free dry flesh mass per square meter, were much larger in the Wadden Sea (26.2 g AFDM/m²) than in Mauritania (7.7 g AFDM/m²). Nevertheless, due to the various constraints that red knots face on intake rate, particularly their digestive and toxin constraints (van Gils *et al.* 2005b; Chapter 2), the mean potential resource intake rates (mean \pm SD, 0.07 ± 0.10 mg AFDM/s in the Wadden Sea and 0.09 ± 0.08 mg AFDM/s in the Banc d’Arguin, $p > 0.1$), as well as the maximum

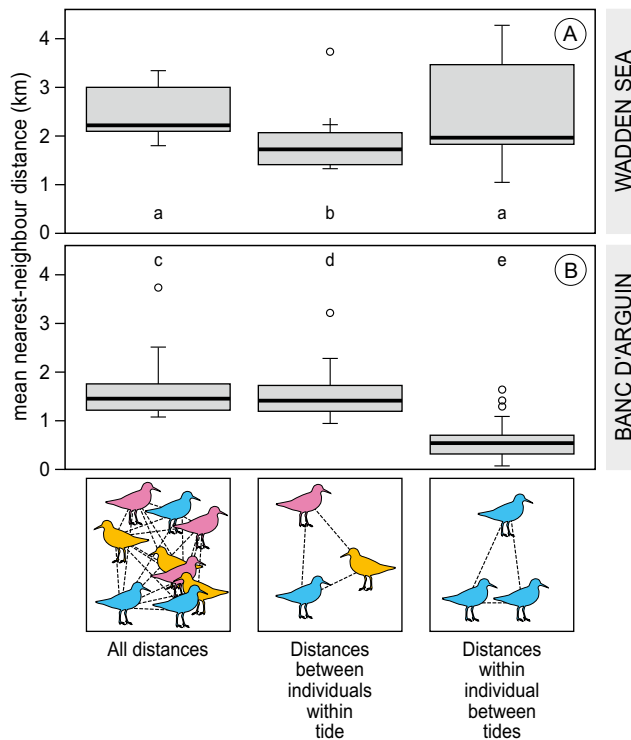


Figure 6.3 Aggregation and site fidelity of red knots in the Wadden Sea and at Banc d'Arguin. Shown are the mean distances between all itineraries (left), the mean distances between itineraries of the same bird in different low tide periods (middle, a measure of site fidelity), and mean nearest-neighbour distances between itineraries of different birds during the same low tide (right, a measure of aggregation). Data is averaged per bird. Boxes a, b, c, d and e differ significantly from each other.

potential resource intake rates (0.28 mg AFDM/s in the Wadden Sea, and 0.40 mg AFDM/s in Banc d'Arguin) were similar in the two areas (Fig. 6.4). However, the intercept as well as the range of spatial autocorrelation intercept in the potential resource intake rate was strikingly different between the Wadden Sea (intercept = 0.97, range = 1700 m) and Banc d'Arguin (intercept = 0.18, range < 50 m, Fig. 6.5, Table 6.1). Hence, the size of resource patches strongly differed. In the Dutch Wadden Sea, estimated patch size was on average larger (1700 m) than the Banc d'Arguin (50 m, the minimum resolution allowed by the measurements, Figs 6.4 and 6.5, Table 6.1).

Dropping analyses showed that during the studied red knots in the Wadden Sea had a virtually monospecific diet, which for more than 99% of the estimated consumed ash-free dry flesh mass consisted of *Cerastoderma edule* (Table 6.1). In Banc d'Arguin, four different species each contributed more than 10% to the diet (Table 6.1). In addition, on average 15% of the dropping dry mass in Banc d'Arguin consisted of plant material (ranging between 0 and 85%), presumably rhizomes of seagrass *Zostera noltii* (van Gils *et al.* 2016).

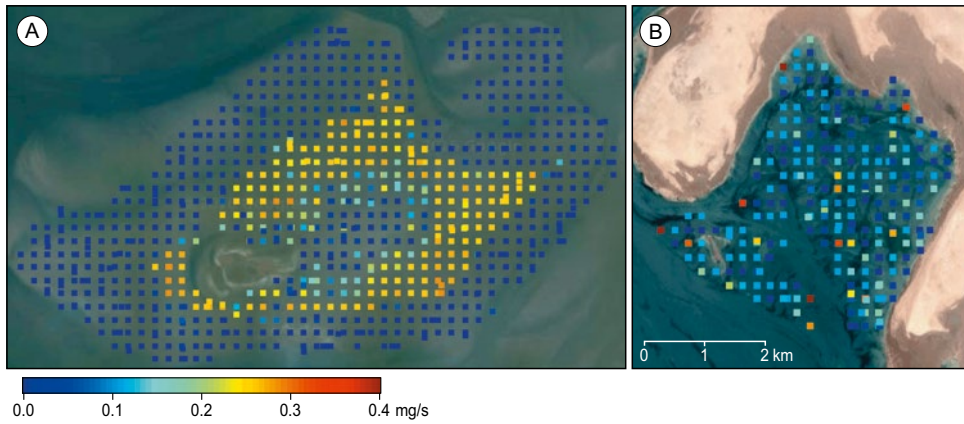


Figure 6.4 Intake rate by red knots in the Wadden Sea (A) and at Banc d'Arguin (B) predicted on the basis of estimates of food abundance using grid-sampling. The two maps are to scale, and each square represents one sampling location. The potential intake rate of ash-free dry flesh mass ($AFDM_{\text{flesh}}$) was calculated by an experimentally tested diet choice model. Calculations were based on mollusc species making up at least 1% of the red knot's diet (Table 6.1). Differences in mean digestive capacity between the tagged Wadden Sea and Banc d'Arguin red knots were taken into account.

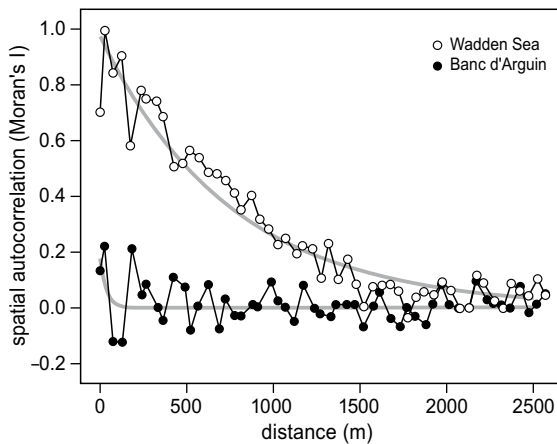


Figure 6.5 Correlogram of estimated maximum $AFDM_{\text{flesh}}$ intake rates in the Wadden Sea and at Banc d'Arguin. Spatial autocorrelation was estimated by calculating Moran's I values, based on the estimated potential $AFDM_{\text{flesh}}$ intake rates at the sampling stations shown in Fig. 6.4. Grey lines show exponential regression of the Moran's I values.

DISCUSSION

In the Wadden Sea red knots showed aggregation, but no site fidelity, whereas at Banc d'Arguin red knots showed strong site fidelity, but barely any aggregation. We will discuss how these differences can be explained as a consequence of differences in the benefits and costs of aggregation and site fidelity. Because predicted individual energy intake rates and expenditure levels were similar, we will focus on the spatial grain of the resource distributions. We also discuss the potential influences of individual diet specializations and predation risk in explaining the observed differences between the areas.

Aggregation and site fidelity: in need of a joint theory

Until now, aggregation and site fidelity have structurally been studied with different methods. The commonly used framework that relates the resource landscape to forager aggregation is the ideal-free model and its descendants (Fretwell & Lucas 1970; Sutherland 1983; Tregenza 1995). This simplistic model has been successful as a null

Table 6.1 Diet proportion, availability and spatial autocorrelation of molluscs in the Wadden Sea and at Banc d'Arguin.

Species ^a	Proportion in diet ^b	Numerical density (1/m ²)	AFDM _{flesh} (mg/m ²)	Autocor. intercept	Autocor. range ^c (m)
Wadden Sea					
<i>Cerastoderma edule</i>	0.99	762	760	0.51	900
<i>Limecola balthica</i> ^d	<0.01	31	268	0.04	0
<i>Peringia ulvae</i>	<0.01	427	134	0.52	1600
<i>Ensis directus</i>	<0.01	35	70	0.26	600
<i>Mya arenaria</i>	<0.01	40	38	0.44	1100
<i>Abra tenuis</i>	<0.01	36	34	0.52	700
AFDM _{flesh} intake rate (mg/s) ^e				0.97	1700
Banc d'Arguin					
<i>Loripes lucinalis</i>	0.51	251	1337	0.63	400
<i>Diplodonta circularis</i>	0.19	8	101	0.03	0
<i>Dosinia isocardia</i>	0.16	25	77	0.00	0
<i>Abra tenuis</i>	0.14	32	31	0.65	0
<i>Senilia senilia</i>	<0.01	6	29	0.15	200
AFDM _{flesh} intake rate (mg/s) ^e				0.18	50

^a Only mollusc species with more than 10 mg AFDM_{flesh} per m² that are in the upper 4 cm of the sediment and ingestible by red knots.

^b AFDM_{flesh} proportion of all listed mollusc prey in the diet, based on dropping data (hinge measurements).

^c Range is defined as the distance at which the spatial autocorrelation drops below 0.1. The autocorrelation function is estimated by exponential regression of the Moran's *I* index at discrete distances. Species specific autocorrelation functions are based on the summed AFDM_{flesh} density at each location.

^d Until recently *Macoma balthica*

^e Autocorrelation function of the predicted intake rate (see Fig. 6.5), taking in account only those prey species that had an estimated average proportion of more than 0.01 in the diet.

hypothesis to deduce which mechanisms underlie patterns of aggregation (Fretwell 1972; Sutherland & Parker 1985; Switzer 1993; van Gils *et al.* 2006). However, this approach has been less useful in explaining site fidelity patterns, because it does not predict individual movement, but only the resulting population distribution at a given moment in time. The study of the relation between the resource distributions and site fidelity has been approached mainly by modelling individual movements (Switzer 1993; Börger *et al.* 2008; Bartumeus *et al.* 2016; Spiegel *et al.* 2017; Bastille-Rousseau *et al.* 2017) and the empirical analysis of individual tracks (Weimerskirch 2007; Barraquand & Benhamou 2008; Fryxell *et al.* 2008; van Moorter *et al.* 2016; Bastille-Rousseau *et al.* 2017). However, models of individual movement generally do not consider the interactions between conspecifics that form the basis of the ideal-free model approach, and as a consequence they do not predict the degree of aggregation. The consequence is that their interplay basically goes unaccounted in theoretical predictions of space use.

Benefits and costs of aggregation

Aggregation allows shared vigilance for predators and decreases per capita predation risk (Lima & Dill 1990), as well as the communication of social information (Giraldeau & Caraco 2000). Red knots use social information to assess foraging opportunities; they observe and respond to the foraging success of others (Bijleveld *et al.* 2015b). However, foraging success of conspecifics provides information on foraging opportunities only within the spatial autocorrelation range of resources, i.e. within a resource patch. Hence, the benefits of aggregation increase with increasing spatial heterogeneity in the resource distribution.

The main cost of forager aggregation is competition for resources (Pulliam & Caraco 1984). When resource abundance is below the level at which the functional response rate reaches a plateau (e.g., Duijns *et al.* 2015), then aggregation will decrease the *per capita* resource intake rate (Vahl *et al.* 2005; Bijleveld *et al.* 2012a). As resource density increases, the cost of aggregation lowers. In some particular cases, e.g., when culling enhances prey growth rates, aggregation may even increase resource availability (Fryxell 1995; Giraldeau & Caraco 2000). Hence, the optimal degree of aggregation depends both on absolute resource density and on the scale of spatial heterogeneity. When both local resource abundance and autocorrelation range become higher, aggregation is expected to increase. Indeed, this can explain why red knots aggregated more strongly in the Wadden Sea, where maximum resource abundance was much higher and resource patch size much larger than at Banc d'Arguin.

Benefits and costs of site fidelity

As site fidelity allows animals to return to good patches and stay away from bad patches, high fidelity is beneficial for individual foragers especially when the difference in quality between different foraging locations is high, i.e. when spatial heterogeneity is high (Switzer 1993; van Moorter *et al.* 2016). Qualitative differences between patches in heterogeneous landscapes may be enhanced from the viewpoint of the forager if local experience increases the energy intake only there, e.g., because of spatial differences in

prey species composition (Estes *et al.* 2003; Araújo *et al.* 2011), or through phenotypic effects of previous experiences (Piersma & van Gils 2011; Bijleveld *et al.* 2016). High site fidelity has costs when foraging has consequences for resource availability through depletion (Sutherland & Anderson 1993) or predator avoidance behaviour by the prey (Lima & Dill 1990).

In the Wadden Sea, the average distance between used foraging locations ranged from 2 to 3 km (left box in Fig. 6.3A). The spatial range of resource intake autocorrelation was 1700 m (similar to previous years; Kraan *et al.* 2009a), but Fig. 6.4A shows that the resource landscape in the year of study actually consisted of one large resource patch stretching over more than 4 km. Hence, even though the terrain as a whole shows large heterogeneity, the used area was relatively homogeneous. At Banc d'Arguin, the average distance between used foraging locations ranged from 1 to 2 km (left box in Fig. 6.3B). This is a much larger distance than the measured autocorrelation range of resources there, estimated at 50 m or less (Figs 6.4B and 6.5). This means that there is a large potential difference in maximum resource intake rate between locations. This provides an explanation for the high site fidelity, and it may also help to explain the low degree of aggregation. Resource density is low at Banc d'Arguin, and because foraging patches are small and site fidelity is high, there may simply not be enough resources to have high site fidelity and maintain a high degree of aggregation (Fig. 6.1).

Because resource patches were smaller than the inter-sample distance, the resource sampling scheme at Banc d'Arguin is likely to have missed many foraging patches (Figs 6.4B and 6.5). Indeed, red knots found locations where potential resource intake rate was high, in between our sampling locations where it was not (Appendix 6.1, Fig. A6.1).

Predation risk

Predation risk is a main determinant of habitat quality for red knots in Banc d'Arguin (van den Hout *et al.* 2014; Chapter 5) as well as the Wadden Sea (Piersma *et al.* 1993). However, the large differences in space use between the Banc d'Arguin and the Wadden Sea are unlikely to be explained by differences in predation risk (Piersma 2012). Being depredated mainly by falcons, which attack by surprise from behind concealing habitat structures such as ridges of dunes, predation pressure will be relatively low when foraging on the offshore intertidal mudflats (van den Hout *et al.* 2016). Indeed, predation is thought to mainly take place in the two hours before high tide (Bijlsma 1990), a period that was not included in the analyses. Moreover, even when spaced out, shorebirds maintain the potential to coalesce into tight flocks when necessary (Myers 1980; van den Hout *et al.* 2009).

Conclusions and future directions

This study shows that in superficially very similar habitats and at similar energy expenditure levels, contrasts in the spatial grain of food resource distributions can lead a single species (and probably single individuals in different seasons, see below) to show highly diverse patterns of aggregation and site fidelity, behavioural adjustments which seem to be adaptive. We encourage theoreticians working on individual movement decisions to

emphasize the interaction between aggregation and site fidelity, thereby bridging the current gap between the advanced mathematical models of individual movement and the classic ideal-free model literature that has provided so many ecological predictions.

Secondly, although our results stress the overriding importance of the environment in explaining differences in space use, the results do not show to what extent individual foragers can adjust their space use to the environment. This begs for research on how individual animals develop and adjust their behavioural strategies to resource landscapes. Did the different observed strategies evolve to be individually innate, or are they the result of plastic development or behavioural flexibility in response to the environment (West-Eberhard 1989; Danchin *et al.* 2004; Piersma & van Gils 2011)? The high phenotypic similarity between the two populations under study (Piersma & Davidson 1992; Piersma *et al.* 1993), and especially the observation that *canutus* red knots seem to blend in with *islandica* red knots when visiting the Wadden Sea during migration (Piersma *et al.* 1993; Nebel *et al.* 2000), imply that these birds continuously adjust their space use behaviour to their environment. Such observations call for a more inclusive theory of animal space use, and emphasize the need for measurements, with enough relevant detail, of the resource landscapes experienced by tracked individuals. Right now, it is not the tracking technology that limits progress (Kays *et al.* 2015), but the grain size at which we can measure relevant aspects of the environment.

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APPENDIX 6.1. Additional sampling at foraging locations at Banc d'Arguin

The estimated range of resource patches in the Banc d'Arguin, 50 m, was smaller than the inter-sampling distance of 250 m. Given the low autocorrelation intercept (*Moran's I* = 0.18), resource patches may have been smaller than the sampling accuracy, approximately 10 m. Therefore, it is expected that many resource patches were actually missed by the sampling grid. To verify this, we additionally performed an alternative sampling scheme, based on the idea that red knots are the champions when it comes to finding resource patches. Sampling locations were determined in the field. Two observers with telescopes searched for tagged red knots in the field, careful not to disturb foraging flocks of red knots. When a tagged red knot was observed, usually from a distance of 150–250 m, the knot and its precise location was carefully observed. After flying away, one of the observers was guided to the exact foraging location by the other observer. The location was stored in a GPS, and eight wooden picks were placed at foraging traces (holes left by a red knot bill, droppings, or footprints). A sample was taken at each of the picks within the following week, according to the same protocol as described in the main text, but on foot during low tide rather than by boat during high tide.

Given that red knots need an average energy intake of $0.2 \text{ mg AFDM}_{\text{flesh}} \text{ s}^{-1}$ to maintain a stable body mass in Banc d'Arguin (van Gils *et al.* 2009), only 7% of the locations in the sampling grid in the Banc d'Arguin harboured enough mollusc biomass (Fig. 6.4B). Contrarily, at 70% (34 out of 44) of the locations where tagged birds were observed foraging, at least one sample surpassed this threshold (Fig. A6.1). This way of sampling uncovered many more resource patches than the grid (compare Fig. A6.1 to Fig. 6.4B)

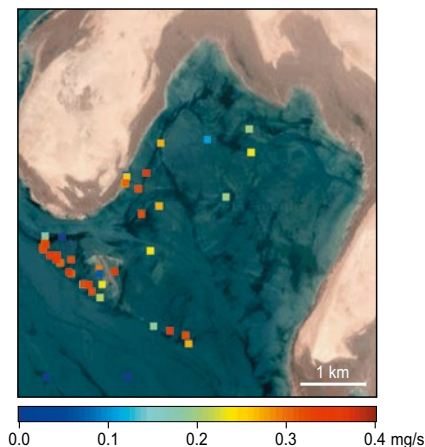


Figure A6.1 Potential intake rates by red knots at additional sampling locations at Banc d'Arguin. See Appendix 6.1 for explanation of this additional sampling scheme. Each square refers to one location, and the colour refers to the potential intake rate ($\text{mg AFDM}_{\text{flesh}} \text{ s}^{-1}$) at those locations. Samples with higher intake rates are plotted on top of samples with lower intake rates. Spatial scale and colour scale are equivalent to Fig. 6.4.

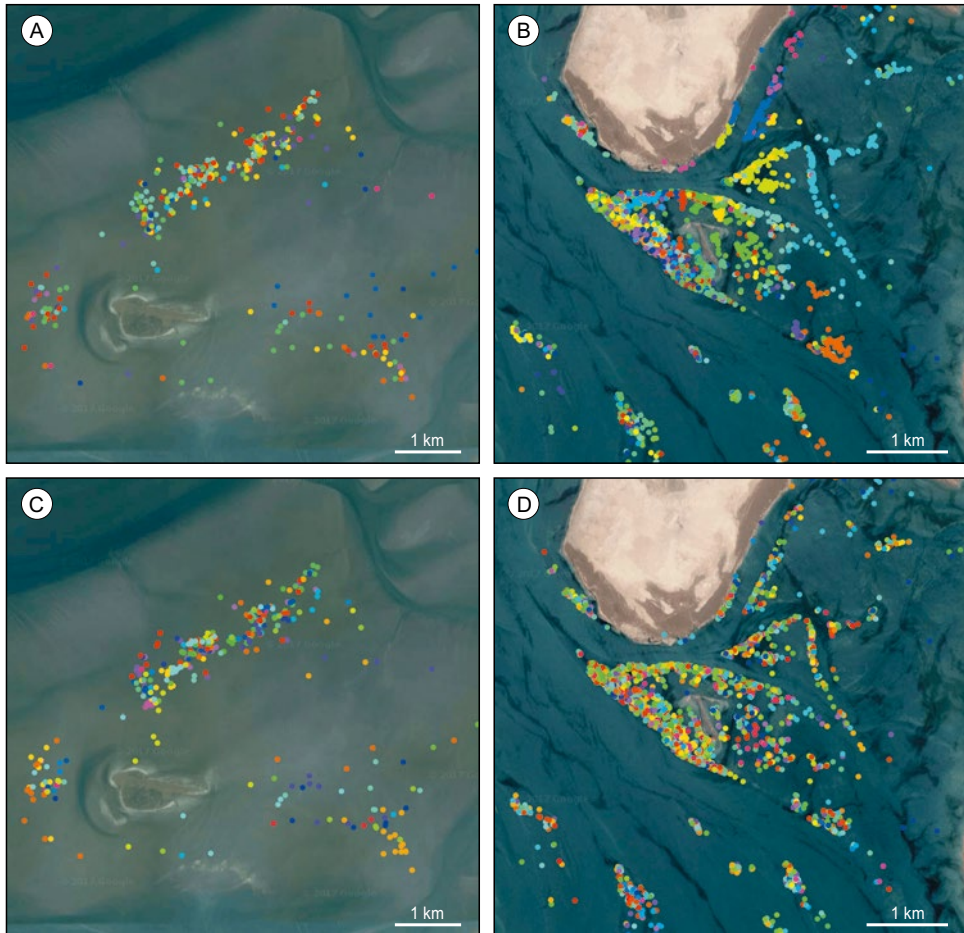


Figure A6.2 Map of residence patches of tracked red knots in the Dutch Wadden Sea (A and C) and at Banc d'Arguin (B and D). Each dot denotes one residence patch. In panels A and B, each colour denotes a different individual. Panels B and D show the same residence patches, but now each color refers to a single low tide period. Note that the spatial scale differs between the panels.

