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High-throughput tracking reveals differences in low-tide space use between day and night in wintering Red Knots

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Within intertidal ecosystems, the availability of foraging areas for shorebirds changes rapidly with the tidal cycle, imposing a strict regime of foraging opportunity. Several shorebird species have been reported to forage during both diurnal and nocturnal low-tide periods, making the most of available foraging times, but detailed descriptions of behaviour at night are rare. We may expect shorebirds to engage in distinct spatial behaviours between day and night due to differences in risk landscape, or because moving between foraging sites and searching for indicators of profitable foraging patches may require different strategies. Comparing the diurnal and nocturnal behaviour of the same individuals on intertidal mudflats is a challenge and requires high temporal and spatial resolution data collected over several weeks so that low-tide periods that fall mostly in the day or in the night can be compared. We used ATLAS—a high-throughput radiotracking system—to collect high-resolution tracking data from Red Knots *Calidris canutus*, between September and October (2018–2022) in the Dutch Wadden Sea. We found that the Red Knots stayed within patches longer at night and that patches were also slightly closer (~100 m) to the roost site at low tide, and covered a smaller area per tide. Red Knots were found to use 20% of their diurnal range at night, and 41% of their nocturnal range during the day. At night, Red Knots showed higher site fidelity across tides. We suggest that these differences in behaviour are probably due to a combination of navigational capacity, risk perception and/or prey conspicuousness.

Keywords: animal tracking, nychthemeral, shorebirds, tidal movement, waders.

According to the optimal foraging theory, animals must decide when, where and how to forage to maximize their efficiency, energetic net gain and fitness (Charnov 1976, Pyke *et al.* 1977). For many species, peaks in foraging effort correlate strongly with light levels, with animals tending to be either diurnally or nocturnally active (Hut *et al.* 2012). However, temporal flexibility in activity patterns is often necessary in response to environmental challenges, such as changes in ambient temperatures, niche competition or food availability (Reebs 2002, Levy *et al.* 2019). For shorebirds that primarily forage on benthic invertebrates, temporal plasticity in foraging behaviour is crucial. In semi-diurnal tidal zones, low tides can occur twice per 24-h period, giving specific and constrained periods when foraging areas are available. Rather than only foraging during one low-tide period per day, many shorebird species forage during both, pushing some foraging opportunities partially or completely into the night

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(McNeil & Rodríguez 1996, Lourenço *et al.* 2008, Cohen *et al.* 2011, Jourdan *et al.* 2021). Unique challenges during the night could influence when, where and how shorebirds choose to forage (Jourdan *et al.* 2022). However, due to the difficulty of observing individuals on intertidal zones at night, the nocturnal behaviour in these animals is poorly understood.

In recent years, wildlife tracking technology has improved markedly, allowing us to gather more detailed insights into the ecology of animals, even when and where they are difficult to physically follow (Nathan *et al.* 2008, 2022, Cagnacci *et al.* 2010). Fine-scale spatio-temporal movement data from global navigation satellite systems such as GPS (Cagnacci *et al.* 2010, Hebblewhite & Haydon 2010) or from radio-based automated tracking systems such as ATLAS (Weller-Weiser *et al.* 2016, Toledo *et al.* 2020, Beardsworth *et al.* 2022, Bijleveld *et al.* 2022) can give frequent and precise positioning estimates which can be used to assess multiple aspects of animal ecology (e.g. habitat selection (Bijleveld *et al.* 2016, Dickie *et al.* 2020, Beardsworth *et al.* 2021), dispersal (Klarevas-Irby *et al.* 2021) and social behaviour (Strandburg-Peshkin *et al.* 2015, Papageorgiou & Farine 2020)). High-throughput tracking systems can allow researchers to assess the adaptive value of particular strategies (Klarevas-Irby *et al.* 2021, Nathan *et al.* 2022), because how an animal interacts with the social and physical environments around it can ultimately determine fitness outcomes (Nathan *et al.* 2008).

Shorebirds may forage at night for a number of reasons. For example, foraging can be interrupted during the day by flooding during high tide periods, and therefore individuals may not have the opportunity to obtain enough food to meet their energy demands (Goss-Custard 1969, Dugan 1981). Alternatively, nocturnal foraging may be a preference, to allow them to take advantage of higher activity in prey (Evans 1988), a lack of diurnal predators (Thibault & McNeil 1994) or reduced disturbance from humans (Burger & Gochfeld 1991, Gaynor *et al.* 2018). Throughout the diel cycle, foraging efficiency should be maximized, but different challenges between day and night in terms of light levels, predation risk or prey activity may manifest in behavioural differences within a population.

Measuring and comparing diurnal and nocturnal movements when activity is primarily dictated by the tidal cycle can be challenging, and requires fine-scale monitoring of behaviour over several weeks to be able to monitor low-tide periods that both start within day or night (as movements may be autocorrelated) and fall primarily within the same day/night scenario. We used high-throughput tracking technology (ATLAS) to monitor the movements of over 100 Red Knots *Calidris canutus* in the Wadden Sea. Each bird was tracked across at least five diurnal low tides and five nocturnal low tides so that we could undertake detailed comparisons of behaviour between these contrasting contexts.

Specifically, we investigated differences in movement choices within low-tide periods that fell mostly (≥70%) within the day or night. Red Knots have previously been shown to forage at night, as well as during the day (van Gils & Piersma 1999, Sitters *et al.* 2001). They mostly forage by probing the sediment in search of hard-shelled prey such as Baltic Tellins *Macoma balthica* or Cockles *Cerastoderma edule* (Zwarts & Blomert 1992, Piersma *et al.* 1993, 1994, Bijleveld *et al.* 2015, 2016), which are generally sessile organisms and therefore form a highly predictable resource (Armonies & Hartke 1995). Red Knots can use visual foraging to eat faster moving prey such as Brown Shrimp *Crangon crangon*, but this is irregular and only constitutes a small part of their diet, so is unlikely to influence large-scale space use (Ersoy *et al.* 2022). While tactile probing is a suitable foraging tactic throughout the diel cycle, it is plausible that the birds may go to different places or alter how long they stay grounded before flying to a new location, depending on whether it is day or night. Indeed, factors such as navigational challenges, disturbance or risk perception may induce a change in spatial behaviour between day and night low-tide periods in the same individuals. To investigate differences in movement behaviour, we first identified areas of residence (hereafter residence patches) (Barraquand & Benhamou 2008, Bijleveld *et al.* 2016, Oudman *et al.* 2018, Gupte *et al.* 2022) and compared the duration of residence between day and night. Longer durations within residence patches at night have previously been shown in Red Knot (Oudman *et al.* 2016, Bulla *et al.* 2017), where the difference was suggested to be due to predation risk (Oudman *et al.* 2016). We therefore also expected our study population to spend longer in residence patches at night than during the day. To investigate potential differences in spatial behaviour, we

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assessed the distance of residence patches from a major high tide roost site, the total area used per low-tide period and site fidelity both between (which we call overlap) and within (which we call revisiting) day and night. Site fidelity has been suggested to reduce uncertainty in energy intake rate and can increase both movement and foraging efficiency within a predictable resource landscape by restricting movement to more profitable areas (Switzer 1993, Van Moorter *et al.* 2009, Merkle *et al.* 2014, Riotte-Lambert & Matthiopoulos 2020). Due to the low within-season mobility of many of their main prey items, such as *Macoma balthica* (Beukema 1993) or Cockles (Flach 1996, Coffen-Smout & Rees 1999), we may expect Red Knots to show high site fidelity during all low-tide periods. However, if there is a difference in navigational capacity, disturbance or risk perception, we may expect low overlap in space use between day tides and night tides.

METHODS

Tracking Red Knots

We monitored Red Knot movements using the Wadden Sea ATLAS system (Bijleveld *et al.* 2022). ATLAS is a reverse-GPS that uses an array of receiver stations and time-of-arrival principles to calculate the location of small ultra-high-frequency radio transmitters (Toledo 2020, Beardsworth *et al.* 2022). Receivers continuously scan for specific ATLAS tags (see below) and send information about detections to a centralized server. When three or more receivers detect a transmission, location estimates are computed through multilateration. The accuracy of the ATLAS system has been estimated to be 10 m on the Griend mudflat, where we have the densest array of receivers (Beardsworth *et al.* 2022). For this reason, analyses were restricted to individuals that stayed on the Griend mudflat for the majority of the low-tide period. Minor changes to the array across years can be seen in Supporting Information Fig. S1.

We caught adult Red Knots on high-tide roosts on the islets of Griend (53.25°N, 5.25°E) and Richel (53.25°N, 5.01°E) using mist-nets during new moon periods between July and October in 2018 (n = 125), 2019 (n = 157), 2020 (n = 164), 2021 (n = 61) and 2022 (n = 142) (Fig. 1). Birds will use the Richel high-tide roost site during spring tides, but birds captured on Richel or Griend are expected to use the Griend mudflat for foraging (van Gils *et al.* 2000). All birds were ringed, colour ringed and morphometric measurements were taken. Using cyanoacrylate glue, an ATLAS tag (4.4 g) was glued to the rump of each bird, which was then released at the catch location. Tags were on average 3.2% (sd = 0.2) of the birds' body-weight. On release, birds were observed until they flew away to ensure that the tag did not affect their normal behaviour. For a separate project, the birds were found again up to several weeks later and observed foraging within a flock, behaving as would be expected (Ersoy *et al.* 2022). Transmission intervals were set to 1/3 Hz in 2018 and were lowered to 1/6 Hz in 2019–2022 to preserve battery life. Tags are expected to last 4.5 (1/3 Hz) to 8 (1/6 Hz) months but are moulted off the bird before migration (April/May) (Bijleveld *et al.* 2022).

Selecting data

Low-tide periods are defined as water levels below 50 NAP (Normaal Amsterdams Peil), the mean water level for Amsterdam that serves as a national measurement for sea level in the Netherlands. Due to longer periods of daylight in summer, few low-tide periods fall completely within the night before September. Other conditions also vary across time, such as resource availability and weather patterns. Therefore, to assess behaviour during day tides and night tides with comparable conditions, we only used data from 1 September to 31 October for analysis in each year. We calculated the sun's position in degrees below the horizon using the *solarpos* function from the *maptools v1.1-6* R package (Bivand & Lewin-Koh 2022) to determine day and night. Night was defined as the angle of the sun being below the horizon by at least 6 degrees, and day was above this level. Each low-tide period was given a unique tide ID, then categorized into day (low tide begins in daylight and ≥70% of tide was during daylight), night (tide begins during the night and ≥70% of tide was during night) or twilight (<70% of the tide was within the day or night) tides. Twilight tides were removed from the analysis.

As 2018 data were sampled at 1/3 Hz, whereas all other years were sampled at 1/6 Hz, we subsampled the 2018 data to 1/6 Hz. We did not include location estimates recorded within the 24 h

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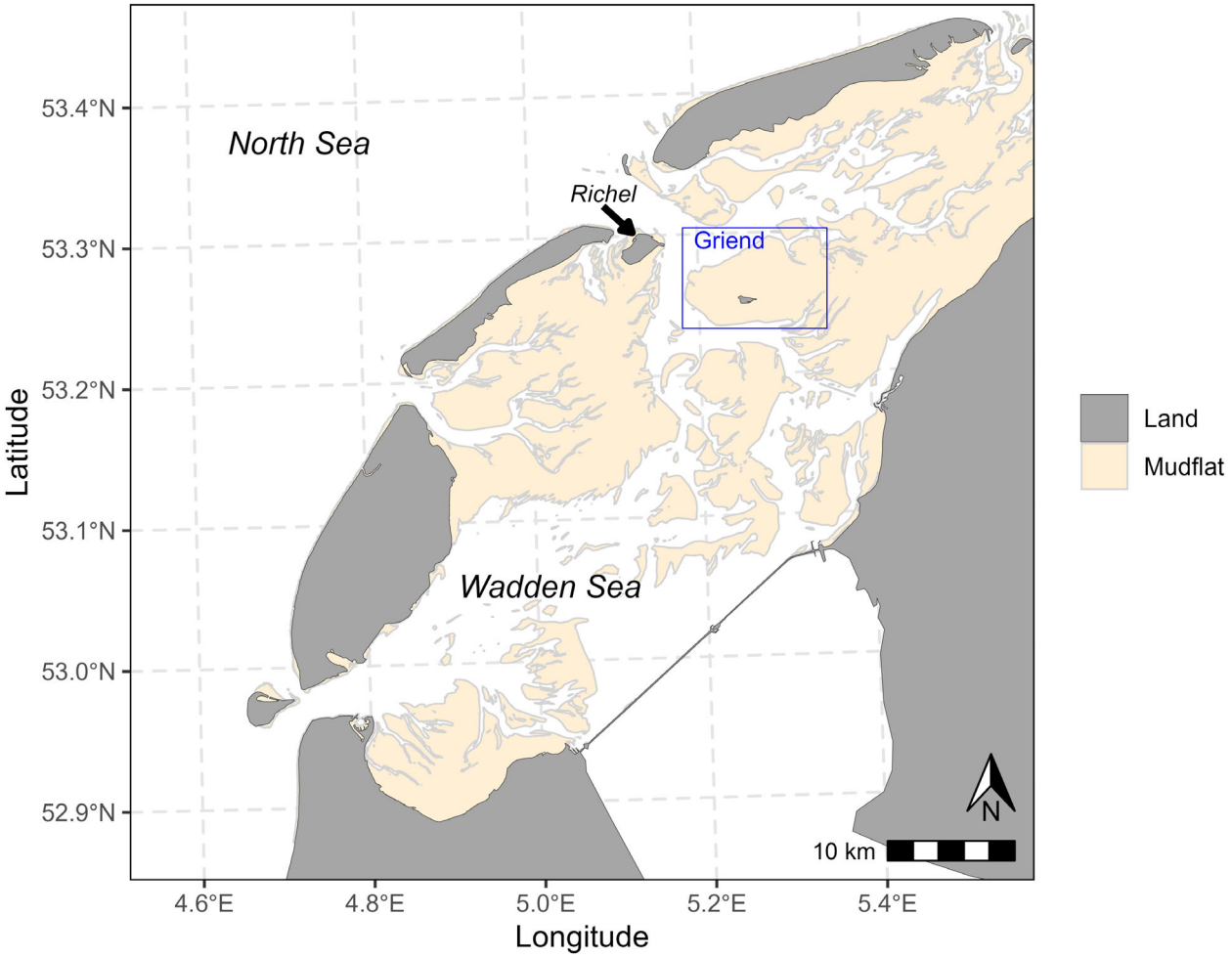


Figure 1. Birds for this study were caught at either Griend (blue box) or Richel (black arrow). Mudflats are shown at 144 NAP from Rijkswaterstaat bathymetry data (2015).

immediately following the release of the birds, to minimize any effects due to the stress of capture and personality testing (which was conducted for another study; Ersoy *et al.* 2022) from biasing analyses. Individual location estimates were preprocessed following an established protocol (Beardsworth *et al.* 2022, Gupte *et al.* 2022). We first removed large-scale errors identified through the uncertainty estimates given by the ATLAS system for both the x (VARX) and y (VARY) axis by removing estimates with values over 5000 m^2 and where movement speed between locations was above 30 m/s. To account for finer scale errors, we smoothed the data using a 5-point moving median of the x and y coordinates. We only analysed data from birds that were tracked for at least five day tides and five night tides, as well as being tracked for at least 240 min within each of these low-tide periods. The duration tracked per tide was calculated by summing the duration within non-roosting residence patches (see below for definition of residence patches). While this data selection method reduced the number of birds included in our sample (2018 = 36; 2019 = 23; 2020 = 7; 2021 = 24; 2022 = 18), we felt that this was necessary to produce a comparable dataset of night and day tides (n bird-tides: 2018 day = 386, night = 262; 2019 day = 365, night = 195; 2020 day = 49, night = 65; 2021 day = 410, night = 186; 2022 day = 239, night = 124). The number of day tides that birds were tracked for ranged from 5 to 27 (median = 13), and the number of night tides that birds were tracked for ranged between 5 and 16 (median = 7). The difference between the

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number of day tides and the number of night tides for which a single bird was tracked ranged from −7 to 17 (median = 5).

Residence patches

Following methods described by Barraquand and Benhamou (2008) and developed further for Red Knot specifically (Bijleveld *et al.* 2016, Oudman *et al.* 2018, Gupte *et al.* 2022), we calculated residence patches within tides where a bird had at least 100 localizations between consecutive high tide times, to ensure that each bird had an adequate amount of data with which to analyse. Residence patches were defined as ≥3 localizations (Fig. S2) within a 75-m spatial buffer (Fig. S3) of the previous localization, lasting at least 2 min (Fig. S4). As per Gupte *et al.* (2022), each subsequent localization that fell within the buffers of prior localizations was categorized as the same residence patch. When the speed between consecutive localizations was >3 m/s (Fig. S5), or when birds were not localized for longer than 180 min (either because they had left the area or because there was poor reception of the transmitter, Fig. S6), localizations within the previous buffer zone were classed as a new residence patch. This ensures that values such as 'duration in a residence patch' are not overestimated. For all the above threshold values, we tested both higher and lower values for each threshold (Figs S2–S6), after which three experienced observers visually inspected plots (e.g. Fig. 2) to refine and determine the final values to be used for representing residence patches of Red Knot within this system. We only analysed residence patches that started and/or ended in non-roosting areas of the mudflat, that is where the water level (West-Terschelling gauge) was above >50 NAP.

Spatial and statistical analyses

We first asked whether birds spent more time within residence patches depending on whether it was day or night. For this, we used a general linear mixed model (GLMM) through the *lme4* v.1.1-31 (Bates *et al.* 2015) and *lmerTest* v3.1-3, (Kuznetsova *et al.* 2017) R v4.2.2 (R Core Team 2021) packages. Degrees of freedom were calculated using Satterthwaite's method (Giesbrecht & Burns 1985, Fai & Cornelius 1996). Duration in residence patch (in minutes) was $\log_{10}$ transformed and was used as the response variable in the GLMM, with a day/night categorical variable used as a fixed effect. Since birds are more likely to be forced to move inland by flood tide, we included an interaction between day/night and tidal direction (ebb/flood) tides. We also included bird ID, year and tide ID as random intercepts.

Secondly, we examined whether residence patches differed in distance from the estimated high-tide waterline at 100 NAP (above which Red Knots are unlikely to forage) on Griend between day and night. Using the *sf* package (v1.0-9, Pebesma 2018) in R, we calculated the distance (using the function *st_distance*) between residence patch start locations and an *sf* polygon representation of waterline on Griend at 100 NAP. We used the furthest start location distance from this polygon per individual, per tide as the dependent variable in a GLMM. To identify whether birds moved further away from the islet depending on whether it was a day or night tide, we included day/night as a fixed effect, as well as the low-tide water level, since we may expect birds to go further onto the mudflats if the water level is lower. Within the models, we centred the low-tide water level variable so that model estimates were compared to mean low-tide level (note that in plots we show the actual low-tide level). We also included year and bird ID as random intercepts.

Next, we examined whether the amount of space the birds used (area used per low-tide period) differed between day and night, and how much of this space was used in both day and night (overlap). For calculating both the area used per low-tide period and overlap, we first created spatial polygons of the residence patches using a 10-m buffer (matching the error of our ATLAS system, Beardsworth *et al.* 2022) around localizations. To compare the area used between day and night, we first merged all residence patch polygons per bird and per tide into one *sf* multi-polygon and calculated the area (km^2) of the multi-polygon. We accounted for differences in tracking time between individuals by dividing the area by the minutes tracked per tide, then multiplied this by 360 (low-tide periods are ~360 min) so that each value represented area (km^2) used per low-tide period. These values were used as the dependent variable in a GLMM to assess differences in area used per low-tide period between

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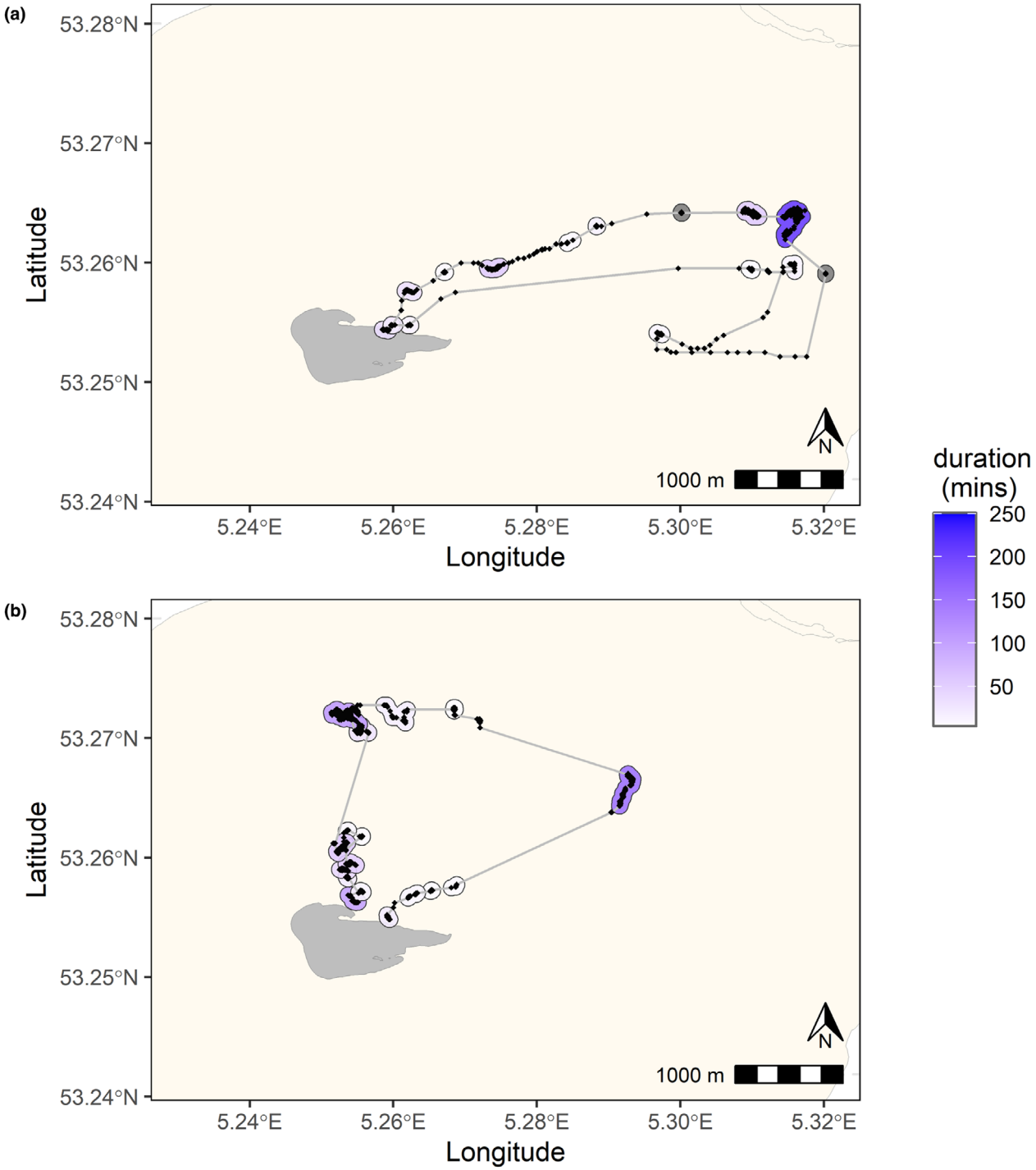


Figure 2. Example trajectories for a Red Knot (ID: 2117) on (a) tide 535 (3 October 2020—day) and (b) tide 536 (4 October 2020—night) which demonstrates the classification of residence patches around location estimates.

day and night. We used day/night as a fixed effect and used bird ID and year as random intercepts.

To calculate site fidelity between contexts, we measured the overlap of space use between day and night. First, we merged all day polygons into

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one, and all night polygons into one for each bird. We then used the *sf* function *st_intersection* to compare the percentage of overlap of day and night polygons for each bird. To give context to the percentage overlap, we also calculated the total area used per bird over all day tides and all night tides. However, the total area used in day or night for each bird should be interpreted with caution since there are sample size differences between birds in the number of day and night tides they were tracked for, and how long they were tracked.

Finally, we examined whether site fidelity differed within contexts of night and day by assessing the revisit probability in both circumstances separately. To do this, we first created a raster across the Griend mudflat consisting of 75 × 75-m cells and gave a value of 1 if one or more residence patch polygons overlapped a raster cell by over 50%, and 0 if there was <50% overlap. We created one raster per bird, per tide. We then summed raster values for each individual across all day tides and night tides that they were present. We defined site fidelity as at least one revisit (cell value = 2), although we also investigated higher thresholds for site fidelity which gave the same outcome (see Fig. S7). We ran a binomial GLMM with the number of revisited cells versus the number of cells visited as the response variable. Day or night was used as a fixed effect with an offset for the number of tides tracked ($\log_{10}$ transformed). Bird ID and year were included as random intercepts.

RESULTS

We found that duration within a patch was longer at night during ebb tide (β (night:ebb tide): 0.18 ± 0.01, df = 50976.43, t = 18.94, P < 0.001; Table 1, Fig. 3a). At night, Red Knots also stayed slightly closer to Griend (~100 m) than during the day (β ± se = −108.02 ± 45.91, df = 2185.96, t = 2.35, P = 0.019, Fig. 3b, Table 1) and during higher low-tide heights (β ± se = −7.31 ± 0.71, df = 2187.38, t = 10.31, P < 0.001) (Table 1). Birds used a smaller area per tide at night (mean predicted area ± sd: 0.33 km^2 per tide ±0.04) than during the day (mean predicted area ± sd: 0.40 km^2 per tide ±0.04; β ± se: −0.07 ± 0.01, df = 2222.36, t = 13.03, P < 0.001, Fig. 3c).

The mean total space a bird used over all nocturnal tides tracked was smaller (mean ± sd = 2.05 km^2 ± 0.76), than the mean space use over all diurnal tides (4.48 km^2 ± 1.78), but the mean number of tides tracked per bird was also fewer for nocturnal tides (7.81 ± 2.51) than diurnal tides (13.54 ± 5.12). Birds overlapped in some of their space use between day and night, using a mean of 19.96% (sd = 8.96) of their diurnal area at night, and a mean of 40.96% (sd = 11.91) of their nocturnal area in the day (Fig. 3d). Although

Table 1. Model outputs from general linear mixed models (1–3) and a binomial mixed model (4). Degrees of freedom for t statistic are calculated for Models 1–3 using the Satterthwaite method.

Question Model predictors	β estimate ± se	df	Test statistic	P value
1. Do Red Knots spend longer in residence patches at night?			t	
Intercept	1.106 ± 0.015	4.373	71.66	<0.001
Time (night)	0.075 ± 0.007	48580.886	11.00	<0.001
Tidal direction (ebb)	0.188 ± 0.005	58242.161	41.07	<0.001
Time (night) × Tidal direction (ebb)	0.179 ± 0.009	50976.434	18.94	<0.001
2. Do Red Knots stay closer to the roost (Griend islet) at night?			t	
Intercept	2456.159 ± 92.201	1.865	26.639	0.002
Time (night)	−108.023 ± 45.912	2185.958	−2.353	0.019
Low-tide level (centred)	−7.308 ± 0.709	2187.378	−10.311	<0.001
3. Do Red Knots use smaller areas at night?			t	
Intercept	0.395 ± 0.011	4.566	36.27	<0.001
Time (night)	−0.065 ± 0.005	2222.362	−13.03	<0.001
4. Is revisiting probability higher at night?			z	
Intercept	−3.868 ± 0.052	–	−73.71	<0.001
Time (night)	0.394 ± 0.016		24.94	<0.001

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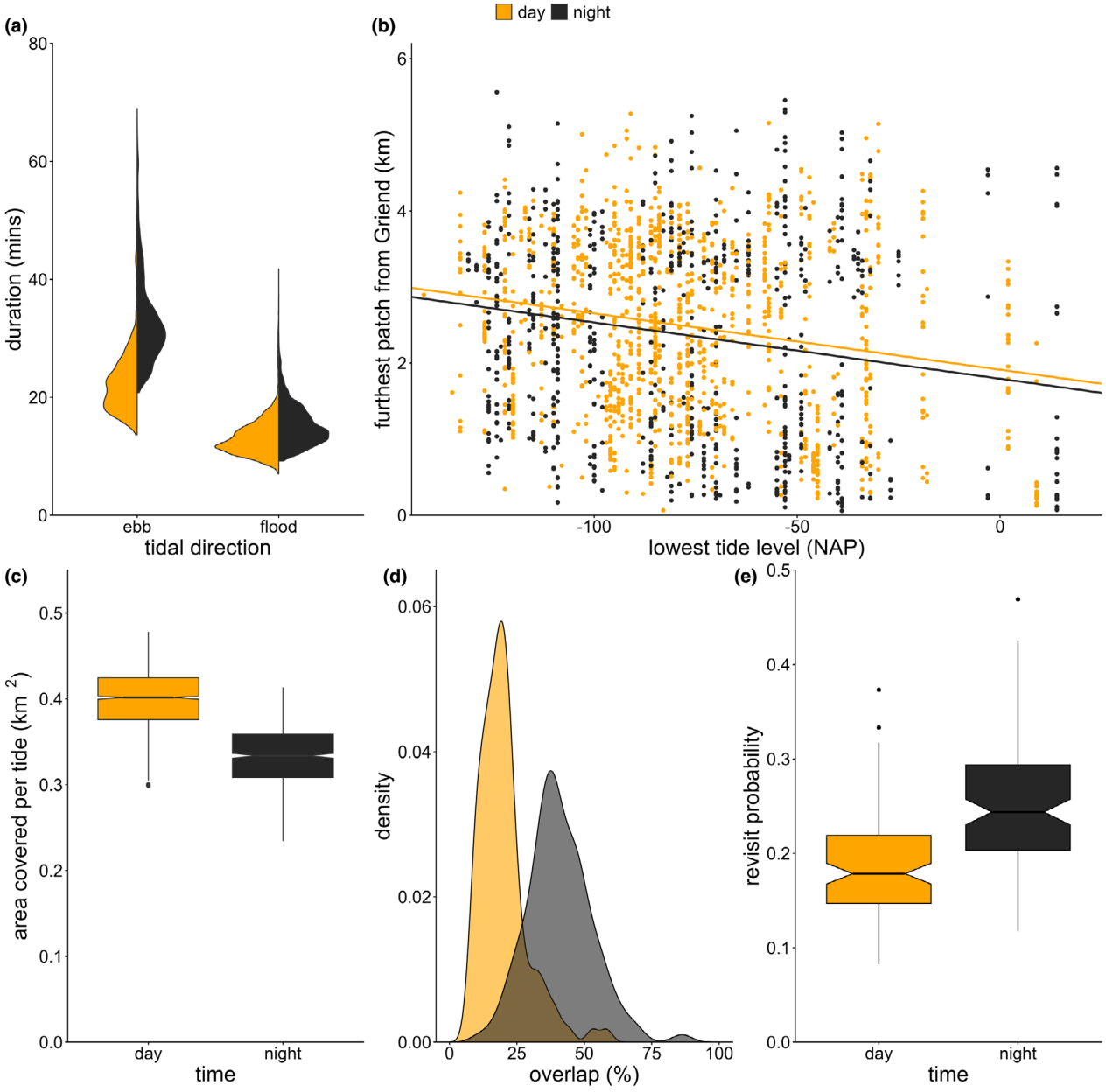


Figure 3. Data presented for Red Knots *Calidris canutus* on the Griend mudflat (53.25°N, 5.25°E) in September and October 2018–2022. (a) Model predictions for the time spent (duration in minutes) within a residence patch during diurnal tides (yellow) and nocturnal tides (dark grey) split between ebb and flood tides. (b) Raw data (dots) and model predictions (lines) to show the maximum distance of residence patches (on the same mudflat) from the nearest roost (Griend) at different low-tide levels. (c) Model predictions for the area covered (km^2) during day tides (yellow) and night tides (dark grey). Notches in the boxplots display confidence intervals around the median (median ± 1.58*IQR/sqrt(*n*)). Dots show outliers. (d) Area used in day (yellow) that overlaps with areas used at night and vice versa (dark grey). (e) Probability of revisiting an area at least once (higher revisiting thresholds are shown in Fig. S7). Notches in the boxplots display confidence intervals around the median. Dots show outliers.

the larger overlap on their nocturnal area may be a consequence of covering a smaller area at night. Red Knots showed higher revisit probability during nocturnal tides than diurnal tides (night: $\beta \pm se = 0.39 \pm 0.02$, $z = 24.94$, $P < 0.001$, Figs 3e & 4).

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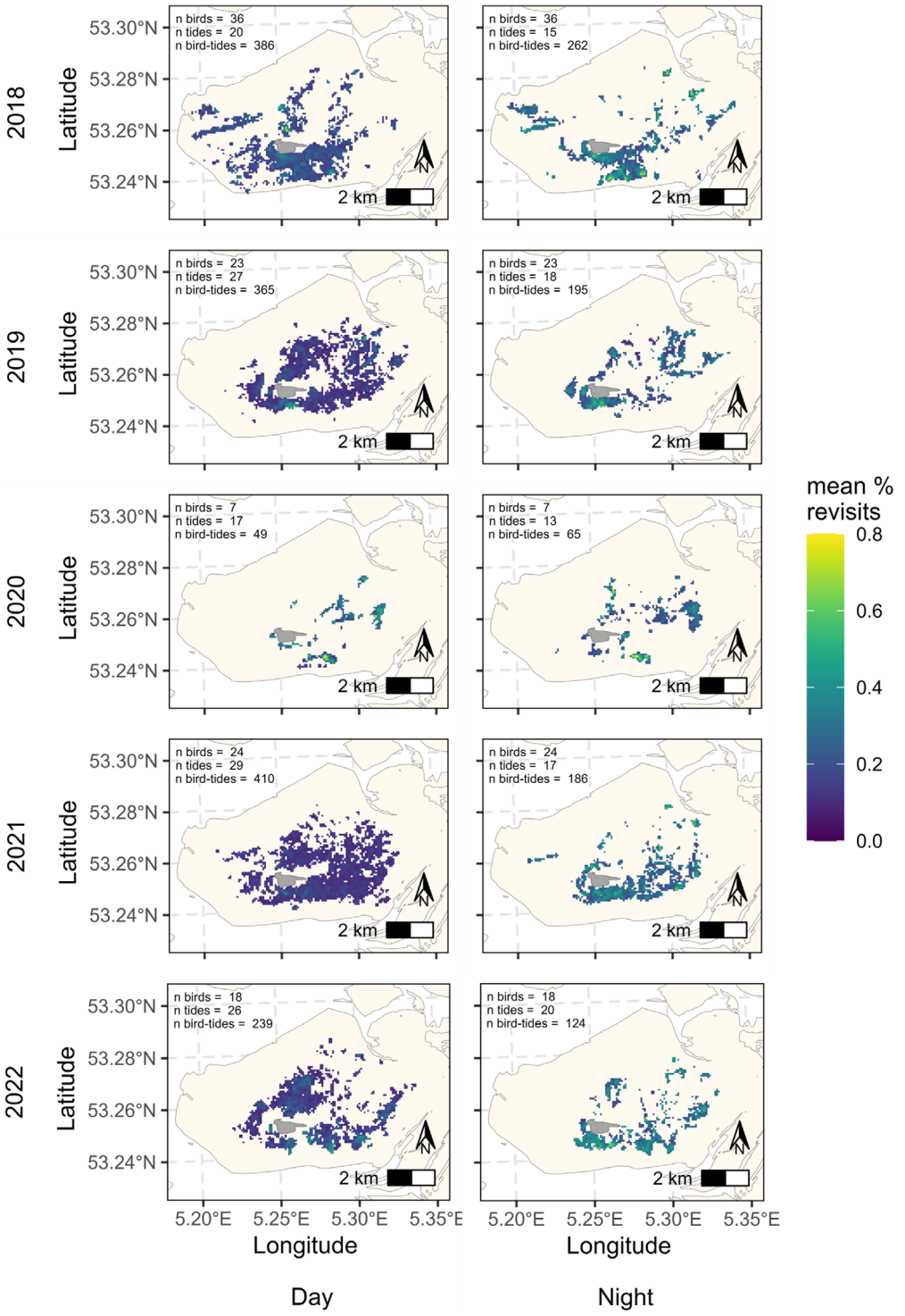


Figure 4. Locations of revisited areas for all Red Knots (that have the minimum tracking data required to be included in this study) on the Griend mudflat between 2018 and 2022. The maps show raster cells (75 × 75 m) that are coloured by the mean revisiting proportion across all tides for each bird. Values for areas that a bird only visited once, or did not visit, were not used to calculate the mean.

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DISCUSSION

By monitoring Red Knot movements at high spatial and temporal resolutions for 2 months, we found differences in movement behaviours between day and night across 5 years. We found that Red Knots stayed longer within a residence patch at night before switching. In the night, these residence patches were slightly closer (~100 m) to the local islet and main roost site, and also covered a smaller area per tide than daytime residency patches. Red Knots differed in diurnal and nocturnal space use with less than 50% overlap in area. Specifically, an average of 20% of the diurnal area was also used during the night, and 41% of the nocturnal area was used within the day. Birds were also found to be more site faithful across tides at night than in the day.

Longer durations of patch use, combined with higher site fidelity and smaller space use at night, suggest that birds were more selective of where to spend their time in the night than during the day. Site fidelity is a widespread phenomenon in the wild, and increased spatial familiarity can increase individual fitness (Switzer 1993), not only through knowledge of resources (Dyer 1996, Fagan *et al.* 2013), but also of spatial risk patterns (Tillmann 2009). Evidence from Pheasants *Phasianus colchicus* demonstrates that individuals that are less familiar with an area are more likely to be predated (Heathcote *et al.* 2023) and therefore animals must determine how they use space carefully. Yet, these patterns of risk are temporally, as well as spatially, dynamic (Palmer *et al.* 2022) and a change in cue salience, as with lower luminosity, could change the perception of risk. Low-light conditions cause behavioural changes in anti-predator responses in many species. For instance, large mammalian herbivores have been shown to alter spatial distributions depending on nocturnal light levels and lunar phase (Palmer *et al.* 2017). At night, Peahens *Pavo cristatus* emit differing vocalizations in response to the same simulated predator (Yorzinski & Platt 2012) and Semipalmated Sandpipers *Calidris pusilla* show higher rates of 'false alarms' (Beauchamp 2010).

The change in spatial distribution and reduced space use of the tracked Red Knots could also be due to increased navigational challenges. A longer period within a patch equally means a longer period between flights and is comparable to another study that shows that in lower light conditions, Eurasian Curlew *Numenius arquata* are less likely to initiate flight (Jolkkonen *et al.* 2023). Jolkkonen *et al.* (2023) suggest their results could indicate that it may be more difficult to find safe places to land and therefore increase costly time on the wing. Indeed, night-time flight has been shown to increase the risk of fatal collisions in other species (Desholm & Kahlert 2005). Jolkkonen *et al.* (2023) also found that Eurasian Curlews were less likely to initiate flight at lower water levels, when foraging opportunities are greatest, which is consistent with optimal foraging theory (Charnov 1976, Pyke *et al.* 1977, Pyke 1984). We found an interaction between day/night and tidal direction, which indicated that duration within a patch was longer at night during ebb tide, and that flood tide had a more similar patch duration between day and night than ebb tide. We suggest that this is because flood tide forces the birds to move and switch patches when the water levels get too high. In contrast, ebb tide allows birds more freedom to choose when to leave the patch and, similar to the study from Jolkkonen *et al.* (2023), that the willingness to stay in a valuable foraging patch and/or the unwillingness to fly is greater. During the day, birds may also be more willing to fly to keep up with the receding tide line and may more easily use cues such as conspecifics or other surface cues to indicate patch profitability. This argument could also help to explain why, at night, birds stayed nearer to the islet of Griend, the closest roost site on the mudflat. Jourdan *et al.* (2022) similarly found that Black-tailed Godwits *Limosa limosa* foraged closer to the coast and used smaller areas at night, attributing this to the human disturbance and the use of different foraging grounds. However, it should be noted that the model-estimated distance from the Griend roost site was only ~100 m shorter at night than in the day, whereas the birds typically foraged several kilometres away from the roost in both day and night. We therefore suggest that rather than staying close to the roost site for an element of safety, this difference is probably linked to birds being more selective over space use, that is, being more site faithful to specific areas and spending more time in those residence patches during the night, while exploring more readily during the day.

As tactile foragers, Red Knots do not require visual surface cues to hunt for their prey and therefore do not necessarily detect prey more easily in very recently exposed areas, as has been

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shown in other species (Smith 1975). Tactile foraging shorebirds have been shown to use area-restricted search, using slow tortuous movement in prey-rich areas, which may lead to staying in a patch for longer than with other foraging tactics such as visual search (Dias *et al.* 2009). Another study of Red Knots in the Dutch Wadden Sea found that more exploratory birds will also hunt and eat soft-shelled prey, such as Brown Shrimp (e.g. *Crangon crangon*), using visual tactics (Ersoy *et al.* 2022). While the study did not investigate these behaviours at night, Red Knots have smaller eyes compared to shorebirds like plovers, which primarily use visual foraging and often feed at night (Martin & Piersma 2008). It is therefore unlikely that visual searching in Red Knot is as effective in low-light conditions, and this could contribute to their site selection, since shrimp are more spatially variable than bivalves (Penning *et al.* 2026). If birds are using a higher proportion of tactile foraging at night, this could help to explain increased duration in residence patches. Our result showing that a large proportion of the space use was unique to either day or night supports the suggestion that there may also be differences in prey choice or foraging tactics between day and night. Furthermore, if birds feed on a higher proportion of bivalves at night, it may be expected that they take more frequent digestive breaks (van Gils *et al.* 2005) which could increase time spent in a residence patch. Conversely, Ersoy *et al.* (2022) reported a large variation in how much soft-shelled prey individual Knots eat, with some eating very few; therefore, there may not be enough of a dietary change to lead this difference in behaviour from diet alone.

Staying longer in residence patches during the night could also indicate lower intake rates, requiring more time in an area to obtain the same amount of food as in the day. This may be due to a switch in the proportion of other behaviours; for example, Red Knots may spend more time resting at night, increasing time within a patch. Alternatively, the efficiency of foraging tactics may decrease at night so that birds must spend longer foraging in any particular place. Other shorebirds have been shown to use surface cues—remnant of deposit feeding—to locate Baltic Tellins more effectively (Hulscher 1982), and intake rate reduced when these cues were removed, despite using a tactile foraging technique throughout. It is therefore also possible that Red Knots could be using a similar combination of visual and tactile foraging tactics during the day that could be impeded by reduced light levels. A reduced intake rate may therefore mean that birds must increase the amount of time spent within a location to maintain their total intake. Indeed, in the Tejo estuary in Portugal, prey intake was higher during the day than at night for five out of six assessed shorebird species, with the exception being the Grey Plover *Pluvialis squatarola*, whose large eyes make it an effective predator under low-light conditions (Lourenço *et al.* 2008). Across the mudflats, prey is patchily distributed, varying in both community composition and species density (Bijleveld *et al.* 2025). In our study, low overlap and differences in areas with high revisitation rates (Fig. 4) between day and night sites within years suggest that prey choice could differ. In other species, such as the Northern Shoveler *Spatula clypeata*, nocturnal and diurnal foraging patches have been shown to differ in prey density, with nocturnal sites having much higher densities of their preferred prey (Moreau *et al.* 2024). Previous work has demonstrated that Red Knots select areas of intermediate cockle densities to trade-off quantity and quality due to negative density dependence among prey (Bijleveld *et al.* 2016). It may be the case that Red Knots are able to be more selective in the day, leading to differences in site use between day and night. Notably, areas with high revisitation seem to change each year, so while prey seems to be predictable within years, there are probably spatial differences in resources across years.

It is also possible that differences in the activity levels of predators or prey could also directly elicit changes in spatial behaviour between day and night (Robert & McNeil 1989). Few studies have addressed the extent the prey of Red Knot change their behaviour between day and night (although see Esser *et al.* 2008). With regard to predators, the most common predators in our study area is the Peregrine Falcon *Falco peregrinus* which is not active at night, while Short-eared Owls *Asio flammeus* are present and can be active during both day and night (Page & Whitacre 1975, Rosa *et al.* 2006). Predator disturbance could be more likely in the day, and could lead to more frequently interrupted residence patches of shorter durations during daytime. Furthermore, disturbances in one area could lead more generally to wider space use by the population. Indeed, at

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night, the northern mudflats around Griend seem to be used rarely and while this could be due to differences in prey abundance or catchability, it could also be a consequence of a riskier environment—although understanding risk perception of Red Knots in this environment requires further research to provide conclusions. Disturbance from humans during the day is also a possibility, but highly restricted access to the Griend mudflat and islet means that this is unlikely to be a major cause of movement between patches.

Our study offers novel insights into how shorebirds cope with the challenge of differential prey availability throughout the tidal cycle, concurrently with marked changes in environmental conditions throughout the diel cycle. We show that Red Knots modify where they forage and how long for, depending on where the low-tide period falls within the diel cycle. The causes of these behavioural variations require more study, but we propose that limited light, or differences in prey or predator activity (which may also be a consequence of light intensity), could contribute to differences in behaviour. Future studies could investigate spatial behaviour within the night only, accounting for differences in illumination (via moonlight across the lunar cycle or artificial light).

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AUTHOR CONTRIBUTIONS

Christine E. Beardsworth: Conceptualization; methodology; data curation; formal analysis; investigation; writing – original draft; writing – review and editing; visualization. **Selin Ersoy:** Data curation; writing – review and editing; investigation; formal analysis. **Ran Nathan:** Funding acquisition; writing – review and editing; resources. **Sivan Toledo:** Resources; funding acquisition; writing – review and editing. **Allert I. Bijleveld:** Funding acquisition; writing – review and editing; methodology; data curation; conceptualization; supervision; resources; project administration.

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ETHICAL NOTE

Permission to catch, handle and tag Red Knots was granted to the NIOZ under protocol number NIOAVD8020020171505.

CONFLICT OF INTEREST

There are no known conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request. Code can be found at https://doi.org/10.5281/zenodo.13869873.

REFERENCES

Armonies, W. & Hartke, D. 1995. Floating of mud snails *Hydrobia ulvae* in tidal waters of the Wadden Sea, and its implications in distribution patterns. *Helgol. Meeresunters.* **49**: 529–538.

Barraquand, F. & Benhamou, S. 2008. Animal movements in heterogenous landscapes: identifying profitable places and homogenous movement bouts. *Ecology* **89**: 3336–3348.

Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**: 1–48.

Beardsworth, C.E., Gobbens, E., van Maarseveen, F., Denissen, B., Dekinga, A., Nathan, R., Toledo, S. & Bijleveld, A.I. 2022. Validating ATLAS: a regional-scale high-throughput tracking system. *Methods Ecol. Evol.* **13**: 1990–2004.

Beardsworth, C.E., Whiteside, M.A., Laker, P.R., Nathan, R., Orchan, Y., Toledo, S., van Horik, J.O. & Madden, J.R. 2021. Is habitat selection in the wild shaped by individual-level cognitive biases in orientation strategy? *Ecol. Lett.* **24**: 751–760.

Beauchamp, G. 2010. Determinants of false alarms in staging flocks of semipalmated sandpipers. *Behav. Ecol.* **21**: 584–587.

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Beukema, J.J. 1993. Successive changes in distribution patterns as an adaptive strategy in the bivalve *Macoma balthica* (L.) in the Wadden sea. *Helgol. Meeresunters.* **47**: 287–304.

Bijleveld, A.I., de la Barra, P., Danielson-Owczynsky, H., Brunner, L., Dekinga, A., Holthuijsen, S., ten Horn, J., de Jong, A., Kliene Schaars, L., Kooij, A., Koolhaas, A., Kressin, H., van Leersum, F., Miguel, S., de Monte, L.G.G., Mosk, D., Niamir, A., Oude Luttikhuis, D., Peck, M.A., Piersma, T., Roohi, R., Serre-Fredj, L., Tacoma, M., van Weerlee, E., de Wit, B. & Bom, R. 2025. SIBES: long-term and large-scale monitoring of intertidal macrozoobenthos and sediment in the Dutch Wadden Sea. *Sci. Data* **12**: 239.

Bijleveld, A.I., MacCurdy, R.B., Chan, Y.-C., Penning, E., Gabrielson, R.M., Cluderay, J., Spaulding, E.L., Dekinga, A., Holthuijsen, S., ten Horn, J., Brugge, M., van Gils, J.A., Winkler, D.W. & Piersma, T. 2016. Understanding spatial distributions: negative density-dependence in prey causes predators to trade-off prey quantity with quality. *Proc. R. Soc. B* **283**: 20151557.

Bijleveld, A.I., Twietmeyer, S., Piechocki, J., van Gils, J.A. & Piersma, T. 2015. Natural selection by pulsed predation: survival of the thickest. *Ecology* **96**: 1943–1956.

Bijleveld, A.I., van Maarseveen, F., Denissen, B., Dekinga, A., Penning, E., Ersoy, S., Gupte, P.R., de Monte, L., ten Horn, J., Bom, R.A., Toledo, S., Nathan, R. & Beardsworth, C.E. 2022. WATLAS: high-throughput and real-time tracking of many small birds in the Dutch Wadden Sea. *Anim. Biotelem.* **10**: 36.

Bivand, R. & Lewin-Koh, N. 2022. maptools: tools for handling spatial objects. Available at: https://r-forge.r-project.org/projects/maptools/

Bulla, M., Oudman, T., Bijleveld, A.I., Piersma, T. & Kyriacou, C.P. 2017. Marine biorhythms: bridging chronobiology and ecology. *Philos. Trans. R. Soc. B* **372**: 20160253.

Burger, J. & Gochfeld, M. 1991. Human activity influence and diurnal and nocturnal foraging of sanderlings (*Calidris alba*). *Condor* **93**: 259–265.

Cagnacci, F., Boitani, L., Powell, R.A. & Boyce, M.S. 2010. Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos. Trans. R. Soc. B* **365**: 2157–2162.

Charnov, E.L. 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**: 129–136.

Coffen-Smout, S.S. & Rees, E.I.S. 1999. Burrowing behaviour and dispersion of cockles *Cerastoderma edule L.* following simulated fishing disturbance. *Fish. Res.* **40**: 65–72.

Cohen, J.B., Gerber, B.D., Karpanty, S.M., Fraser, J.D. & Truitt, B.R. 2011. Day and night foraging of red knots (*Calidris canutus*) during spring stopover in Virginia, USA. *Waterbirds* **34**: 352–356.

Desholm, M. & Kahlert, J. 2005. Avian collision risk at an offshore wind farm. *Biol. Lett.* **1**: 296–298.

Dias, M.P., Granadeiro, J.P. & Palmeirim, J.M. 2009. Searching behaviour of foraging waders: does feeding success influence their walking? *Anim. Behav.* **77**: 1203–1209.

Dickie, M., McNay, S.R., Sutherland, G.D., Cody, M. & Avgar, T. 2020. Corridors or risk? Movement along, and use of, linear features varies predictably among large mammal predator and prey species. *J. Anim. Ecol.* **89**: 623–634.

Dugan, P.J. 1981. The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. In Jones, N.V. & Wolff, W.J. (eds) *Feeding and survival strategies of estuarine organisms*: 251–260. Boston, MA: Springer US.

Dyer, F.C. 1996. Spatial memory and navigation by honeybees on the scale of the foraging range. *J. Exp. Biol.* **199**: 147–154.

Ersoy, S., Beardsworth, C.E., Dekinga, A., van der Meer, M.T.J., Piersma, T., Groothuis, T.G.G. & Bijleveld, A.I. 2022. Exploration speed in captivity predicts foraging tactics and diet in free-living red knots. *J. Anim. Ecol.* **91**: 356–366.

Esser, W., Vöge, S. & Exo, K.M. 2008. Day-night activity of intertidal invertebrates and methods to estimate prey accessibility for shorebirds. *Senckenberg. Marit.* **38**: 115–122.

Evans, P.R. 1988. Predation of intertidal Fauna by shorebirds in relation to time of the day, tide and year. In Chelazzi, G. & Vannini, M. (eds) *Behavioral adaptation to intertidal life*: 65–78. Boston, MA: Springer US.

Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G., LaDage, L., Schlägel, U.E., Tang, W., Papastamatiou, Y.P., Forester, J. & Mueller, T. 2013. Spatial memory and animal movement. *Ecol. Lett.* **16**: 1316–1329.

Fai, A.H.-T. & Cornelius, P.L. 1996. Approximate F-tests of multiple degree of freedom hypotheses in generalized least squares analyses of unbalanced split-plot experiments. *J. Stat. Comput. Simul.* **54**: 363–378.

Flach, E.C. 1996. The influence of the cockle, *Cerastoderma edule*, on the macrozoobenthic Community of Tidal Flats in the Wadden Sea. *Mar. Ecol.* **17**: 87–98.

Gaynor, K.M., Hojnowski, C.E., Carter, N.H. & Brashares, J.S. 2018. The influence of human disturbance on wildlife nocturnality. *Science* **360**: 1232–1235.

Giesbrecht, F.G. & Burns, J.C. 1985. Two-stage analysis based on a mixed model: large-sample asymptotic theory and small-sample simulation results. *Biometrics* **41**: 477–486.

van Gils, J. & Piersma, T. 1999. Day- and night-time movements of radio-marked red knots staging in the western Wadden Sea in July-august 1995. *Wader Study Group Bull.* **89**: 36–44.

van Gils, J.A., Dekinga, A., Spaans, B., Vahl, W.K. & Piersma, T. 2005. Digestive bottleneck affects foraging decisions in red knots Calidris canutus. II. Patch choice and length of working day. *J. Anim. Ecol.* **74**: 120–130.

van Gils, J.A., Piersma, T., Dekinga, A. & Spaans, B. 2000. Distributional ecology of individually radio-marked knots Calidris canutus in the western Dutch Wadden Sea in august-October 1999. *Limosa* **73**: 29–34.

Goss-Custard, J.D. 1969. The winter feeding ecology of the redshank *Tringa totanus*. *Ibis* **111**: 338–356.

Gupte, P.R., Beardsworth, C.E., Spiegel, O., Lourie, E., Toledo, S., Nathan, R. & Bijleveld, A.I. 2022. A guide to pre-processing high-throughput animal tracking data. *J. Anim. Ecol.* **91**: 287–307.

Heathcote, R.J.P., Whiteside, M.A., Beardsworth, C.E., Van Horik, J.O., Laker, P.R., Toledo, S., Orchan, Y., Nathan, R. & Madden, J.R. 2023. Spatial memory predicts home range size and predation risk in pheasants. *Nat. Ecol. Evol.* **7**: 461–471.

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Hebblewhite, M. & Haydon, D.T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Phil. Trans. R. Soc. B: Biol. Sci.* **365**: 2303–2312.

Hulscher, J.B. 1982. The oystercatcher *Haematopus ostralegus* as a predator of the bivalve *Macoma balthica* in the Dutch Wadden Sea. *Ardea* **55**: 89–152.

Hut, R., kronfeld-schor, N., van der Vinne, V. & de la Iglesia, H. 2012. In search of a temporal niche: environmental factors. *Prog. Brain Res.* **199**: 281–304.

Jolkkonen, J., Gaston, K.J. & Troscianko, J. 2023. Artificial lighting affects the landscape of fear in a widely distributed shorebird. *Commun. Biol.* **6**: 1–6.

Jourdan, C., Fort, J., Pinaud, D., Delaporte, P., Gernigon, J., Lachaussée, N., Lemesle, J.-C., Pignon-Mussaud, C., Pineau, P., Robin, F., Rousseau, P. & Bocher, P. 2021. Nycthemeral movements of wintering shorebirds reveal important differences in habitat uses of feeding areas and roosts. *Estuar. Coasts* **44**: 1454–1468.

Jourdan, C., Fort, J., Pinaud, D., Delaporte, P., Hérault, T., Jankovic, M., Jomat, L., Lachaussée, N., Pineau, P., Robin, F., Rousseau, P. & Bocher, P. 2022. Daytime, tidal amplitude and protected areas influence movements and habitat use on mudflats of wintering black-tailed godwits. *Estuar. Coast. Shelf Sci.* **268**: 107782.

Klarevas-Irby, J.A., Wikelski, M. & Farine, D.R. 2021. Efficient movement strategies mitigate the energetic cost of dispersal. *Ecol. Lett.* **24**: 1432–1442.

Kuznetsova, A., Brockhoff, P.B. & Christensen, R.H.B. 2017. lmerTest package: tests in linear mixed effects models. *J. Stat. Softw.* **82**: 1–26.

Levy, O., Dayan, T., Porter, W.P. & Kronfeld-Schor, N. 2019. Time and ecological resilience: can diurnal animals compensate for climate change by shifting to nocturnal activity? *Ecol. Monogr.* **89**: e01334.

Lourenço, P.M., Silva, A., Santos, C.D., Miranda, A.C., Granadeiro, J.P. & Palmeirim, J.M. 2008. The energetic importance of night foraging for waders wintering in a temperate estuary. *Acta Oecol.* **34**: 122–129.

Martin, G.R. & Piersma, T. 2008. Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. *Proc. R. Soc. B Biol. Sci.* **276**: 437–445.

McNeil, R. & Rodríguez, J.R. 1996. Nocturnal foraging in shorebirds. *Int. Wader Stud.* **8**: 114–121.

Merkle, J.A., Fortin, D. & Morales, J.M. 2014. A memory-based foraging tactic reveals an adaptive mechanism for restricted space use. *Ecol. Lett.* **17**: 924–931.

Moreau, A., Rousseau, C., Bocher, P., Dupuy, C. & Farau, S. 2024. Home range sizes and nychthemeral habitat uses by the northern shoveler (*Spatula clypeata*) on prenuptial stopovers in Vendée marshes, western France. *Ornis Fenn.* **101**: 62–75.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.E. 2008. A movement ecology paradigm for unifying organismal movement research. *PNAS* **105**: 19052–19059.

Nathan, R., Monk, C.T., Arlinghaus, R., Adam, T., Alós, J., Assaf, M., Baktoft, H., Beardsworth, C.E., Bertram, M.G., Bijleveld, A.I., Brodin, T., Brooks, J.L., Campos-Candela, A., Cooke, S.J., Gjelland, K.Ø., Gupte, P.R., Harel, R., Hellström, G., Jeltsch, F., Killen, S.S., Klefoth, T., Langrock, R., Lennox, R.J., Lourie, E., Madden, J.R., Orchan, Y., Pauwels, I.S., Říha, M., Roeleke, M., Schlägel, U.E., Shohami, D., Signer, J., Toledo, S., Vilk, O., Westrelin, S., Whiteside, M.A. & Jarić, I. 2022. Big-data approaches lead to an increased understanding of the ecology of animal movement. *Science* **375**: eabg1780.

Oudman, T., Bijleveld, A.I., Kavelaars, M.M., Dekinga, A., Cluderay, J., Piersma, T. & van Gils, J.A. 2016. Diet preferences as the cause of individual differences rather than the consequence. *J. Anim. Ecol.* **85**: 1378–1388.

Oudman, T., Piersma, T., Ahmedou Salem, M.V., Fies, M.E., Dekinga, A., Holthuijsen, S., ten Horn, J., van Gils, J.A. & Bijleveld, A.I. 2018. Resource landscapes explain contrasting patterns of aggregation and site fidelity by red knots at two wintering sites. *Mov. Ecol.* **6**: 24.

Page, G. & Whitacre, D.F. 1975. Raptor predation on wintering shorebirds. *Condor* **77**: 73–83.

Palmer, M.S., Fieberg, J., Swanson, A., Kosmala, M. & Packer, C. 2017. A 'dynamic' landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecol. Lett.* **20**: 1364–1373.

Palmer, M.S., Gaynor, K.M., Becker, J.A., Abraham, J.O., Mumma, M.A. & Pringle, R.M. 2022. Dynamic landscapes of fear: understanding spatiotemporal risk. *Trends Ecol. Evol.* **37**: 911–925.

Papageorgiou, D. & Farine, D.R. 2020. Shared decision-making allows subordinates to lead when dominants monopolize resources. *Sci. Adv.* **6**: eaba5881.

Pebesma, E. 2018. Simple features for R: standardized support for spatial vector data. *R. I. Dent. J.* **10**: 439–446.

Penning, E., Ersoy, S., Govers, L.L., Dekinga, A., Holthuijsen, S.J., Piersma, T. & Bijleveld, A.I. 2026. Avian prey exhibit repeatable abundances on intertidal mudflats. *Estuar. Coast. Shelf Sci.* **336**: 109900.

Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P. & Wiersma, P. 1993. Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the Western Wadden Sea in relation to food, friends and foes. *Neth. J. Sea Res.* **31**: 331–357.

Piersma, T., Verkuil, Y. & Tulp, I. 1994. Resources for long-distance migration of knots *Calidris canutus islandica* and *C. c. canutus*: how broad is the temporal exploitation window of benthic prey in the Western and eastern Wadden Sea? *Oikos* **71**: 393.

Pyke, G.H. 1984. Optimal foraging theory: a critical review. *Annu. Rev. Ecol. Evol. Syst.* **15**: 523–575.

Pyke, G.H., Pulliam, H.R. & Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. *Q. Rev. Biol.* **52**: 137–154.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: https://www.R-project.org/.

Reebs, S.G. 2002. Plasticity of diel and circadian activity rhythms in fishes. *Rev. Fish Biol. Fish.* **12**: 349–371.

Riotte-Lambert, L. & Matthiopoulos, J. 2020. Environmental predictability as a cause and consequence of animal movement. *Trends Ecol. Evol.* **35**: 163–174.

Robert, M. & McNeil, R. 1989. Comparative day and night feeding strategies of shorebird species in a tropical environment. *Ibis* **131**: 69–79.

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Rosa, S., Encarnação, A.L., Granadeiro, J.P. & Palmeirim, J.M. 2006. High water roost selection by waders: maximizing feeding opportunities or avoiding predation? *Ibis* **148**: 88–97.

Sitters, H.P., González, P.M., Piersma, T., Baker, A.J. & Price, D.J. 2001. Day and night feeding habitat of red knots in Patagonia: profitability versus safety? (Alimentación Diurna y Nocturna por Parte de Calidris canutus en Patagonia: ganancia vs. seguridad?). *J. Field Ornithol.* **72**: 86–95.

Smith, P.C. 1975. A study of the winter feeding ecology and behaviour of the bar-tailed Godwit (*Limosa lapponica*). Doctoral thesis, Durham University.

Strandburg-Peshkin, A., Farine, D.R., Couzin, I.D. & Crofoot, M.C. 2015. Shared decision-making drives collective movement in wild baboons. *Science* **348**: 1358–1361.

Switzer, P.V. 1993. Site fidelity in predictable and unpredictable habitats. *Evol. Ecol.* **7**: 533–555.

Thibault, M. & McNeil, R. 1994. Day/night variation in habitat use by Wilson's plovers in northeastern Venezuela. *Wilson Bull.* **106**: 299–310.

Tillmann, J. 2009. Fear of the dark: night-time roosting and anti-predation behaviour in the grey partridge (*Perdix perdix L.*). *Behaviour* **146**: 999–1023.

Toledo, S. 2020. *Location Estimation from the Ground Up*. Philadelphia, PA: Society for Industrial and Applied Mathematics.

Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y. & Nathan, R. 2020. Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system. *Science* **369**: 188–193.

Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S. & Gaillard, J.-M. 2009. Memory keeps you at home: a mechanistic model for home range emergence. *Oikos* **118**: 641–652.

Weller-Weiser, A., Orchan, Y., Nathan, R., Charter, M., Weiss, A.J. & Toledo, S. 2016. Characterizing the accuracy of a self-synchronized reverse-GPS wildlife localization system. In *2016 15th ACM/IEEE International Conference on Information Processing in Sensor Networks (IPSN)*: 1–12. Vienna, Austria: IEEE.

Yorzinski, J.L. & Platt, M.L. 2012. The difference between night and day: antipredator behavior in birds. *J. Ethol.* **30**: 211–218.

Zwarts, L. & Blomert, A.-M. 1992. Why knot Calidris canutus take medium-sized *Macoma balthica* when six prey species are available. *Mar. Ecol. Prog. Ser.* **83**: 113–128.

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SUPPORTING INFORMATION

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

Figure S1. (A) Locations of receivers (red triangles) in the Dutch Wadden Sea during September 2018–2022. Griend mudflat is denoted by blue box. (B) Photograph of receiver on flooded mudflat in 2020.

Figure S2. Example trajectory of Red Knot and residence patch over low-tide period showing differences in residence patch outputs with changes in the minimum fixes within a residence patch. Residence patches have been assigned using the following parameters: minimum fixes = 1 (A) or 3 (B) or 7 (C); spatial independence limit = 75 m; minimum duration = 120 min; max speed = 3 m/s; time independence limit = 180 min.

Figure S3. Example trajectory of Red Knot and residence patch over low tide period showing differences in residence patch outputs with changes in the spatial independence limit. Residence patches have been assigned using the following parameters: minimum fixes = 3; spatial independence limit = 35 m (A) or 75 m (B) or 150 m (C); minimum duration = 120 min; max speed = 3 m/s; time independence limit = 180 min.

Figure S4. Example trajectory of Red Knot and residence patch over low-tide period showing differences in residence patch outputs with changes in the minimum duration of a residence patch. Residence patches have been assigned using the following parameters: minimum fixes = 3; spatial independence limit = 75 m; minimum duration = 30 min (A) or 120 min (B) or 240 min (C); max speed = 3 m/s; time independence limit = 180 min.

Figure S5. Example trajectory of Red Knot and residence patch over low tide period showing differences in residence patch outputs with changes in the time independence limit. Residence patches have been assigned using the following parameters: minimum fixes = 3; spatial independence limit = 75 m; max speed = 3 m/s; time independence limit = 90 min (A) or 180 min (B) or 360 min (C); minimum duration = 120 min.

Figure S6. Example trajectory of Red Knot and residence patch over low-tide period showing differences in residence patch outputs with changes in the maximum speed. Residence patches have been assigned using the following parameters: minimum fixes = 3; spatial independence limit = 75 m; max speed = 1 m/s (A) or 3 m/s (B) or

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6 m/s (C); time independence limit = 180 min; minimum duration = 120 min.

Figure S7. Assessment of revisit probability was limited to one revisit in the manuscript, but these boxplots demonstrate that nocturnal revisit probability is generally higher in all years where revisits across tides are only counted when there are at least one, two, three or four revisits to the same 75 × 75-m raster cells.

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