WATLAS: high throughput and real-time tracking of many small birds in the Dutch Wadden Sea

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Abstract

Movement is a fundamental aspect of life and tracking wild animals under natural conditions has become central to animal behaviour, ecology, and conservation science. Data from tracked animals have provided novel scientific insights on extreme migratory journeys, mechanisms of navigation, space use, and early warning signals of environmental change. Studying movement is therefore important, particularly in systems that may be vulnerable to anthropogenic effects. Technological advancements, and chiefly the development of GPS tags, have enabled animal tracking at high spatiotemporal resolution, yet trade-offs between cost, sampling frequency, tag weight and data retrieval limit the use of GPS tags to relatively few individuals and large species. A new 'reverse-GPS' wildlife tracking system, ATLAS, employs an array of receiver stations that detect and localise small (~0.6 g without battery), low-cost (~25 euro) tags by calculating differences in the arrival time of tag signal at minimally three stations. In this study, we introduce the Wadden Sea ATLAS system (WATLAS), implemented in the Dutch Wadden Sea, the Netherland's only natural UNESCO World Heritage Site, yet affected by a suite of anthropogenic activities, such as commercial fishing, mining, shipping, as well as sea level rise. From July 2017 to July 2021, we tracked 821 red knots, 182 sanderlings, 33 bar-tailed godwits, and 6 common terns. With four examples, we illustrate how WATLAS opens-up possibilities for studying space-use, among-individual variation in movement, and intra-specific interactions, and inter-specific (community) space use in the wild. We additionally argue that WATLAS could provide a tool for impact assessment, and thus aid nature conservation and management of the globally important Wadden Sea ecosystem.

Keywords: animal tracking, ATLAS, biologging, biotelemetry, conservation, high-throughput movement ecology, reverse-GPS, shorebirds, space use, Wadden Sea UNESCO World Heritage Site, waders.

Introduction

Movement is a fundamental aspect of life and tracking wild animals under natural conditions has become central to animal behaviour, ecology, and conservation science (Nathan *et al.* 2008; Kays *et al.* 2015; Allen & Singh 2016; Tucker *et al.* 2018; Hays *et al.* 2019). Animal tracking has revealed extreme and large-scale migratory journeys (Gill *et al.* 2009; Lindström *et al.* 2021) and detailed patterns of habitat use (Dickie *et al.* 2020; Beardsworth *et al.* 2021b), as well as elucidated mechanisms of navigation (Guilford & Biro 2014; Harten *et al.* 2020; Toledo *et al.* 2020), predator-prey dynamics (Fortin *et al.* 2005), and social interactions (Strandburg-Peshkin *et al.* 2015). Insights from animal tracking studies are regularly incorporated in policy and conservation management (Choi *et al.* 2019; Hays *et al.* 2019). For example, identifying important areas for the protection of migration routes (Middleton *et al.* 2020; Pekarsky *et al.* 2021), detecting wildlife crime (Murgatroyd *et al.* 2019), and quantifying the human-wildlife conflict (Preisler, Ager & Wisdom 2013).

The introduction of the 'movement ecology' framework (Nathan *et al.* 2008), coupled with the rapid development of new tracking technologies and data-processing tools (Joo *et al.* 2020a; Williams *et al.* 2020) has led to an exponential increase in animal movement ecology research (Joo *et al.* 2020b). These developments, particularly the miniaturization of tags capable of generating high-throughput localization data for many individuals simultaneously, allow for novel opportunities to address contemporary questions on individual, group, population, and community level behaviours in the wild (Börger *et al.* 2020). For instance, studies on intra-specific variability (Verhoeven *et al.* 2019; Shaw 2020; Hertel *et al.* 2021), collective behaviour (Strandburg-Peshkin *et al.* 2017), and interactions among individuals and species with their physical, biotic, and anthropogenic environments (Bedriñana-Romano *et al.* 2021). Furthermore, the ongoing miniaturization of tags allows tracking ever smaller species, and thus may give a more complete pictures how different species use their habitat (Kays *et al.* 2015).

The most common tracking methods, which allow monitoring the movement of animals at high temporal and spatial resolution in the wild, are Global Navigation Satellite Systems (GNSS), such as the Global Positioning System (GPS). Due to trade-offs between sampling frequency, data retrieval, battery size and tag weight, however, the use of these tags and the biological insights gained are often limited to larger species (MacCurdy, Gabrielson & Cortopassi 2011; Kays *et al.* 2015). Moreover, because GPS-tags are expensive, sample sizes are often small, which limits possibilities for studying intra-specific variation, collective behaviour, and inter-specific interactions in the wild.

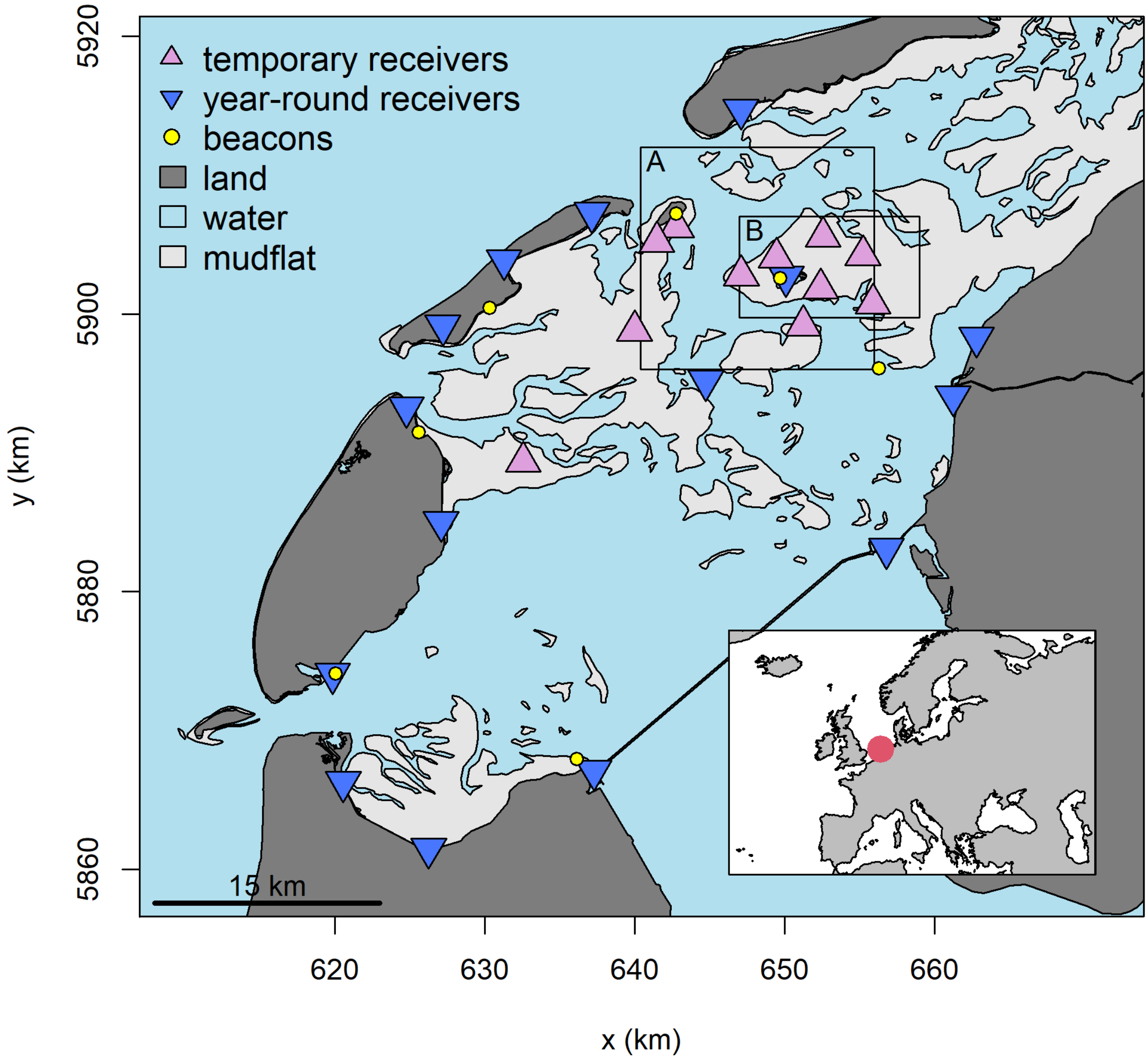
ATLAS (Advanced Tracking and Localization of Animals in real-life Systems) is a reverse-GPS system, developed and deployed by Weller-Weiser *et al.* (2016). ATLAS builds on the pioneering time-of-arrival wildlife tracking system of MacCurdy *et al.* (2009) and comprises an array of stationary receivers that continuously listen for transmissions from small tags. Locations are calculated based on differences in tag-signal arrival times at minimally three receiver stations. Tags are light-weight (0.6 g without battery and coating) and relatively inexpensive (25 €), which facilitates tracking small species and hundreds of individuals simultaneously. Location data is available without retrieval of the tag and in real time, which avoids the need to recapture tagged animals for data retrieval, and allows for locating tagged individuals for auxiliary behavioural observations (Ersoy *et al.* in press) or for confirming mortality (Beardsworth *et al.* 2021b). Whereas GPS systems allow global tracking, ATLAS requires a local array of receivers. Because signal detection requires a 'line of sight' between the receiver and tag (Xia *et al.* 1993), the regions in which the system can be utilized are limited. In open landscapes, with published detection ranges up to 40 km (Toledo *et al.* 2020), its spatial scale limited only by the number of receiver stations. ATLAS has already been established at sites of large scientific or conservation value, such as the Hula Valley in Israel (Weller-Weiser *et al.* 2016; Toledo *et al.* 2020), and the Wadden Sea, where reverse-GPS tracking was pioneered (MacCurdy *et al.* 2009; Bijleveld *et al.* 2016).

The Wadden Sea is recognized as a UNESCO World Heritage Site for providing a rich habitat for marine mammals (Aarts *et al.* 2019), fish (van der Veer *et al.* 2015), invertebrates (Beukema & Dekker 2020), birds (van Roomen *et al.* 2012), and especially migratory shorebirds (van de Kam *et al.* 2004). Shorebirds form an important component of the Wadden Sea ecosystem, which they use for breeding (Allen *et al.* 2019), refuelling during migratory journeys (Rakhimberdiev *et al.* 2018), and finding food and safety during their non-breeding periods (Piersma *et al.* 1993; van Gils *et al.* 2006b; Bijleveld *et al.* 2016; Bakker *et al.* 2021). Millions of shorebirds depend heavily on the worms, snails and shellfish that are found on and in the sediments of the mudflats (Zwarts, Blomert & Wanink 1992). Perhaps uniquely, over the past decade, the Wadden Sea has been subject to a large scale benthic macrofauna monitoring survey (Synoptic Intertidal BEnthic Survey (SIBES), Bijleveld *et al.* 2012; Compton *et al.* 2013), which maps food resources for shorebirds (Bijleveld *et al.* 2016; Oudman *et al.* 2018). Combining resource mapping with the simultaneous tracking of many birds offers novel opportunities for studies on space use, trophic interactions and collective behaviour in the wild (King *et al.* 2018). Many of the shorebird species are declining in numbers (van Roomen *et al.* 2012), and appear particularly susceptible to the effects of habitat destruction, disturbance, overexploitation of resources, and global climate change (Boere & Piersma 2012). Detailed studies of shorebird space use, in conjunction with knowledge of resource landscapes will offer novel ecological insights and, in combination with monitoring anthropogenic activities, will allow quantifying if and how animals are impacted, which may assist in evidence-based conservation efforts in this important region (Piersma & Lindström 2004). The Wadden Sea with its flat and open landscape, large numbers of birds, and conservation value, is an ideal candidate for an ATLAS system.

Here, we introduce the Wadden Sea ATLAS tracking system (WATLAS). In 2017, WATLAS started with 5 receivers and has since grown to have 26 receivers in 2021, making it the largest ATLAS system in the world. The 26 receiver stations are located in the western Dutch Wadden Sea and encompass 1,326 km^2 (Fig. 1) with a focus on the mudflats surrounding Griend, an important shorebird high-tide roosting site and nature reserve. WATLAS allows simultaneous tracking of several hundred animals at high temporal and spatial resolution comparable to GPS tracking (Beardsworth *et al.* 2021a). So far, WATLAS has been used to track 821 red knots *Calidris canutus* (~120 g), 182 sanderlings *Calidris alba* (~50 g), 33 bar-tailed godwits *Limosa lapponica* (~240 g), and 6 common terns *Sterna hirundo* (~130 g), but there is scope to track an even larger range of species. Due to the small and light-weight tags, birds from as little as 20 g (e.g., little stints *Calidris minuta*) can be tracked, which were previously too small to track remotely at high spatial accuracy. In this paper, we will first introduce WATLAS. Second, to investigate space use and environmental drivers of movement, we show how space use of red knots tracked in 2019 varies across the entire study area and on a small spatial scale across tidal cycles. Third, we give an example of among-individual variation in distance travelled for red knots tagged in 2020. Fourth, we show the fine-scale high-resolution movement data WATLAS provides, and how this allows estimating social interactions (proximity-based networks) in red knots. Fifth, as an example of community tracking, we show differences in home ranges between sanderlings, red knots, and common terns near Richel and Griend. We end by discussing how WATLAS offers possibilities for both fundamental and applied research into the natural and anthropogenic drivers of bird movement in the Wadden Sea.

The WATLAS system

The Wadden Sea ATLAS system (WATLAS) comprises an array of receivers that continuously listen for tag transmissions. When a transmission is detected, the receiver records the arrival time. These arrival time measurements are sent to a centralized server where location estimates can be computed when at least three receivers detect the signal. Receivers can detect a transmission from any tag in the system at any time, so the tags can transmit as frequently as a localization is needed. Beacons (tag-like transmitters in fixed known locations) enable clock-synchronisation across receiver stations.



RECEIVERS

The WATLAS system currently consists of 26 receiver stations located in the western Wadden Sea (Fig. 1). Fourteen receivers were installed on buildings and other stable structures where power was available, which allowed receivers to be operational year-round.

One year-round receiver was placed high on a dune and powered with twelve 100 W solar panels (EnjoySolar). Eleven receivers were placed temporarily on the mudflats. Because of the increased likelihood of weather damage in winter, the temporary receivers (Fig. 2) were only in place between July and November each year. One of these temporary receivers was placed on an anchored pontoon that housed a solar powered field station (Fig. 2C). The other ten temporary receivers were attached to scaffolds (Fig. 2A and B) and powered with four 100 W solar panels (EnjoySolar) and a 100 W wind turbine (Ampair), which were connected to three 100 Ah AGM batteries (Beaut). For visibility and safety, a solar powered LED-light was placed on top of the scaffold.

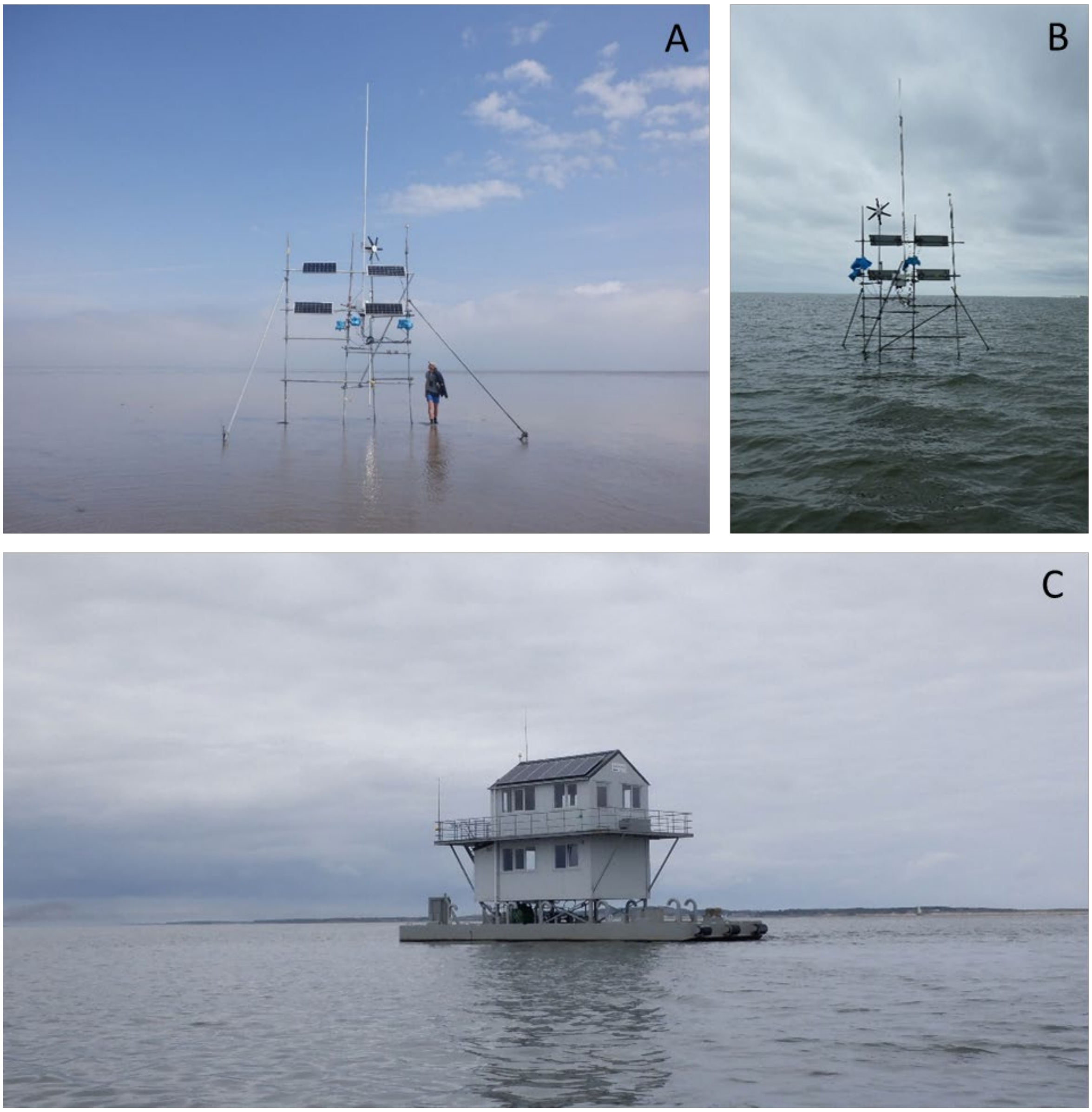


Fig. 2 *Examples of the temporary solar- and wind powered receiver stations placed on mudflats shown at A) low tide and B) high tide, and C) on the field station.*

Each receiver had a 1.5 m Ultra High Frequency (UHF) antenna (Diamond X-50N) mounted on a 6 m aluminium scaffold. To increase the range of tag detections, receiver antennas were placed as high as possible. Antenna height for temporary receivers in 2019 was on average 9.5 m (range: 8.4 – 11.7 m) above sea level, and on average 18.7 m (range: 10.9 to 44.4 m) for year-round receivers.

A coaxial cable connected the antenna to a water-proof cabinet (53 x 43 x 20 cm, Supplementary Fig. S1) via a custom built external Low Noise Amplifier (LNA). The LNA includes a helical bandpass filter to protect against static discharge from thunderclouds. These LNAs connect to a custom front-end unit that acts as a bandpass filter, radio frequency limiter, and power supply to the LNAs (Melamed & Toledo 2017). Next comes the Software Defined Radio (SDR) consisting of an USRP N200 with WBX40 daughter board (Ettus Research). This SDR precisely timestamps incoming signal detections using a GPS disciplined oscillator (GPSDO, Ettus Research). The GPSDO was connected to an external amplified ceramic patch antenna (Ettus Research), which allowed the clock rates of all receivers to be synchronized with the atomic clocks from GPS-satellites. Signal transmissions are processed by an onboard computer (Intel NUC i7) that runs Linux (Ubuntu 16 or 20). The number of unique tags the WATLAS systems can detect depends on the processing capability of this Intel NUC. With our onboard computers, we estimate that we can reliably track 300 unique tags that send a transmission every second simultaneously. All receiver stations were connected to internet using a 3G cellular modem (Huawei E3372 4G/LTE dongle) and an externally mounted antenna (GTT OS-UMTS-0103-C0) to send detection reports to a central server at NIOZ Royal Institute for Sea Research. This server runs software that estimates tag locations from time-stamped tag and beacon detections (Weller-Weiser *et al.* 2016). All data are stored in an online database running MySQL (v5.7, https://www.mysql.com/). Localizations are visualised on www.nioz.nl/watlas in real-time.

TAGS

Tags consist of an assembled Printed Circuit Board (PCB), a battery, an antenna, and a protective coating (Fig. 3). The PCBs are based on a CC1310 or CC1350 microcontroller with a built-in Radio-Frequency (RF) transceiver that can transmit a code unique to the tag at 433 MHz. The radio signal is emitted through a 17 cm long antenna made of gold plated multistranded steel wire with a plastic coating, which can handle mechanical stress in a marine environment. Tags were coated with a mixture of two-component epoxy (3M Scotch Weld DP270). To reduce tag weight, the epoxy was mixed with low density glass spheres at a ratio of 1:2. PCB's are fitted with a (Hall) sensor allowing the tag to be switched on and off with a magnet placed next to the tag. Tags operate at a voltage of 1.8 to 3.8 V and can be fitted with a range of batteries. For example, a pair of silver oxide batteries (0.26 g), single lithium coin-cell batteries ranging from CR1025 (0.7 g) to CR2477 (10.5 g), or a pair of AA batteries (24 g). At signal transmission costs of approximately 0.4 mJ, the capacity of the battery determines the number of transmissions that can be sent, and together with the frequency of transmissions, sets the tag's operational lifetime (longevity). In 2017 and 2018 we used tag transmission intervals of 1 or 3 s, and in later years 6 s. With WATLAS, we have used CR1620 (1.3 g) and CR2032 batteries (3.0 g), which resulted in final tag weights of respectively 2.4 and 4.4 g (Fig. 3). With a signal transmission interval of 6 s this corresponds to an estimated longevity of 3 and 8 months for the lighter and heavier tag, respectively.

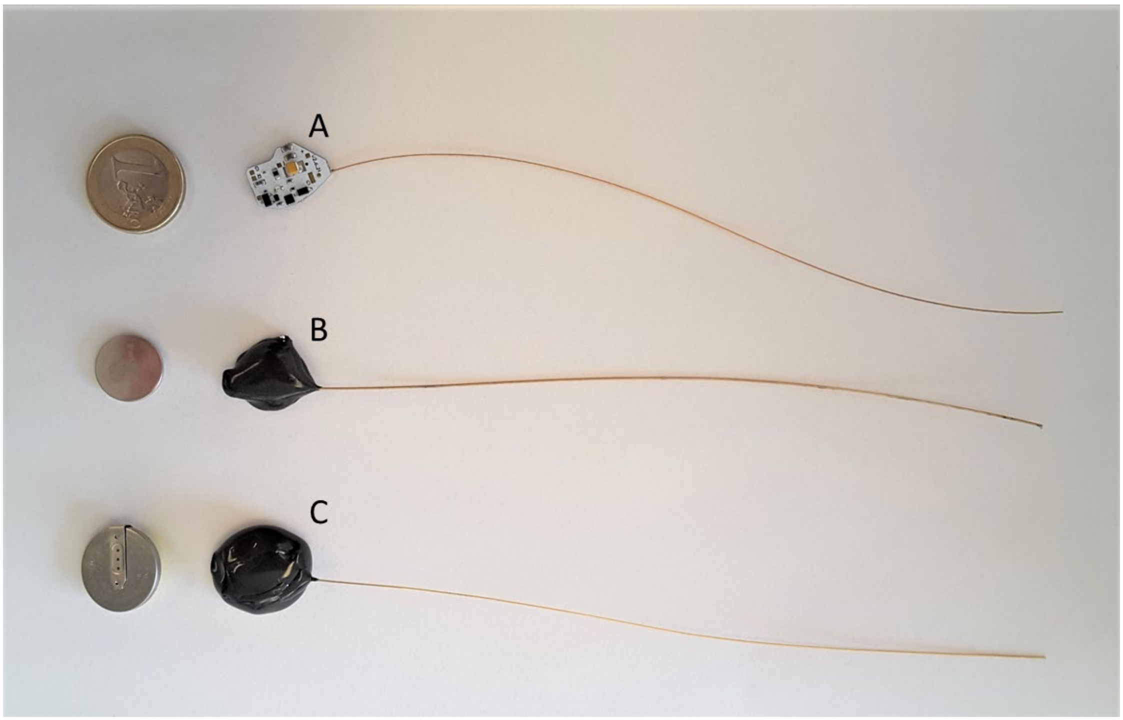


Fig. 3 *WATLAS tags and batteries. A) tag without battery and coating and a one-euro coin for scale. B) 2.4 g coated tag with CR1620 battery. C) a 4.4 g coated tag with CR2032 battery. The batteries of the tags are shown on the left.*

BEACONS

Beacons were built as standard WATLAS tags, but fitted with one lithium C cell and a helical bandpass filter to protect against static discharge from thunderclouds and connected to a vertical colinear antenna providing 7dB gain in the horizontal plane (Diamond X-50N) identical to the antennas on receivers. The transmission interval of beacons was set to 1 s. Seven beacons were mounted on 6 m aluminium scaffold poles (Supplementary Fig. S2). To ensure that each receiver detected at least one beacon consistently, beacons were placed across the study area (Fig. 1). During deployment, the locations of receivers and beacons were recorded with dGPS at 1.5 cm accuracy (Topcon HiPer SR).

WATLAS COSTS

The most substantial costs are setting up an initial array of receivers. The costs of WATLAS components fluctuate, and more economical configurations are being developed. However, at the time of writing the receiver cabinet with the radio frequency electronics costs about 4,500 €. For receiver stations that require independent power supply, the equipment for generating wind and solar power costs an additional 5,000 €. Tag cost is dominated by costs of assembling the electronics, and this largely depends on the numbers of tags produced in a batch: 100 € each at 20 pcs and 22 € each at 200 pcs. The labour costs of tag assembly can easily cost an equal amount. Operational costs can be quite substantial as well, such as those for mobile data transfer. For example, between August and November 2018 receivers transferred an average of 14 GB of data per month (7 to 18 GB per receiver per month). Per receiver, the monthly costs for an unlimited data plan were 35 €.

TRACKING SHOREBIRDS WITH WATLAS

We present examples from red knots tracked between 2018-2020 (N = 668), sanderling tracked in 2018 (N = 94) and common terns in 2021 (N = 3). Red knots were caught on Richel (53.28° N, 5.01° E) and Griend (53.25° N, 5.25° E) (Fig. 1) with mist nets during new moon periods each year between July and October. In 2018, 2019 and 2020 we respectively tracked 193, 226 and 249 red knots. Most sanderling (N = 82) were caught on Griend by means of canon netting on 26 July 2018, but some by mist-netting on 12 August 2018 (N = 2) and 10 September (N =10). Within a pilot experiment, three incubating common terns were caught with spring traps (TW45, Moudry) on Griend on 3 June 2021. All birds were banded with unique combinations of colour-rings and released after gluing a WATLAS tag to their rump with cyanoacrylate glue (Fig. 4). Red knots were fitted with 4.4 g tags (Fig. 3C) that were on average 3.2 % (SD = 0.2) of body mass. Sanderling and common terns were fitted with 2.4 g tags (Fig. 3B) that were on average 4.4 % (SD = 0.4) of body mass for sanderling and 2.0 % (SD = 0.2) for common terns. All birds were released from Richel and Griend.

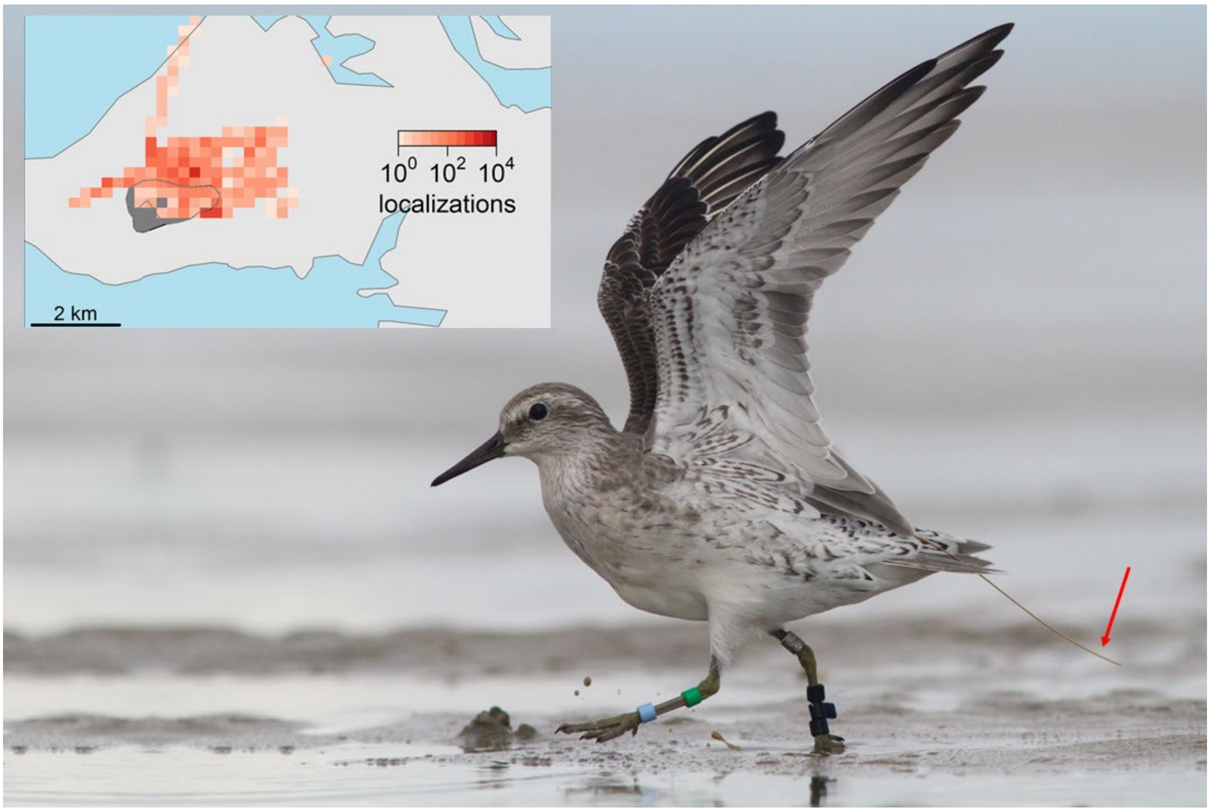


Fig. 4 *A colour-ringed red knot in winter plumage, bearing a WATLAS tag glued to its rump; the tag antenna can be seen extending beyond the tail to the right of the image as indicated with the red arrow. WATLAS tags allow free movement of the wings and fall off as the feathers underneath the tag regrow. The inset shows this bird's localizations around Griend, collected between 15 September and 21 September 2017. See rectangle B in Fig. 1 for placement of the inset within the study area. © map data from Rijkswaterstaat, and photo taken on 16 September 2017 by Benjamin Gnep.*

PRE-PROCESSING WATLAS DATA TO IMPROVE POSITION ESTIMATES

The accuracy of WATLAS localizations is comparable to conventional GNSS systems (Beardsworth *et al.* 2021a) and to the Hula Valley ATLAS system (Weller-Weiser *et al.* 2016). However, in common with other positioning systems, WATLAS data can contain some inaccurate localization estimates. Filtering and smoothing such data, to reduce errors in positioning estimates, is common practice in movement ecology (Gupte *et al.* in press). Here, we used a simple filter-smoothing process on the raw data using the error estimates, namely variance in the Easting and Northing (VARX and VARY). We removed localizations that had high VARX and VARY (>2,000) and smoothed the data by computing a 5-point median smooth across the localizations (Bijleveld *et al.* 2016; Gupte *et al.* in press), which can reduce the localization error to several metres (Beardsworth *et al.* 2021a).

EXAMPLES OF WATLAS

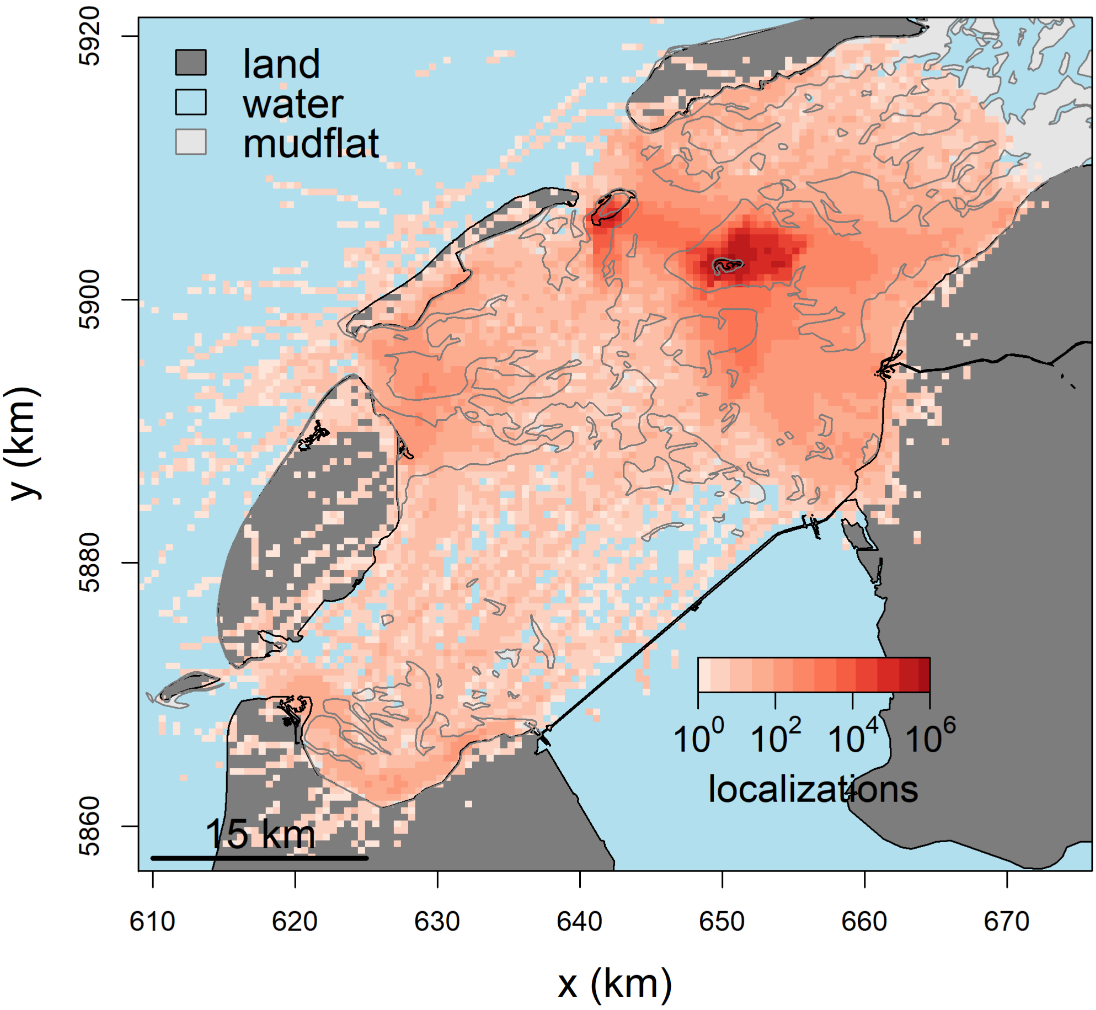
We will demonstrate examples for how WATLAS opens-up possibilities for studying space-use and environmental drivers of movement, among-individual variation in distance travelled, intra-specific (social) interactions, and community tracking with interspecific space use in the wild. All analyses were done in R v4.0.2.

EXAMPLE 1. ESTIMATING SPACE-USE

To show how WATLAS can be used to investigate space use and e.g. identify hotspots, we created heatmaps of the localisations of 221 red knots tracked between 1 August 2019 and 1 November 2019 (92 days). We created heatmaps at two spatial scales: The large spatial scale of the entire study area in grid cells of 500 x 500 m, as well as the smaller spatial scale around Richel and Griend with grid cells of 250 x 250 m. To additionally illustrate how WATLAS data can be used to investigate environmental drivers of space use, we created heatmaps on the smaller spatial scale separately for the different phases of the tidal cycle. The tidal-phases were selected based on the water level (NAP; Amsterdam Ordnance Datum) at the tide gauge at West-Terschelling (53.37° N, 5. 22° E): high tide (> 100 cm NAP), first ebb tide (outgoing tide between 50 and 100 cm NAP), second ebb tide (outgoing tide between -50 and 50 cm NAP), low tide (< -50 cm NAP), first flood tide (incoming tide between -50 and 50 cm NAP), second flood tide (incoming tide between 50 and 100 cm NAP). These tags were programmed to transmit every 6 s, thus each location represents at least 6 s of space use.

The large-scale heatmap confirmed that Richel and Griend, where the knots were caught, are hotspots. Nonetheless, red knots spread-out across the entire study area (Fig. 5). It should be noted, however, that because the density of receivers is higher at Richel and Griend, the relative number of localizations could be exaggerated compared to the rest of the study area. As can be seen from the localizations over relatively deep gullies, several birds moved between islands and the mainland (Supplementary Fig. S3). Likewise, localizations across the North Sea suggest that birds crossed in the direction of the United Kingdom. In some cases, these birds were detected up to 34 km from the closest receiver.

On a smaller spatial scale, the heatmaps for different phases of the tidal cycle around Richel and Griend showed how the tidal dynamic affects space use of red knots on a population level (Fig. 6). With the outgoing tide, the birds moved out on the now-exposed mudflats in search of invertebrate prey. Interestingly, space-use differed between ebb and flood tides even though the water level was the same. This can, for instance, be seen by comparing Fig. 6C with 6E, and Fig. 6B with 6F. The fewest localizations were observed during the low tide period, probably because birds spread out and even moved outside the tracking area. With the incoming tide the birds returned and aggregated on Richel and Griend.



328 ***Fig. 5*** *Large-scale space use of 221 red knots tracked between 1 August and 1 November*
329 *2019 (92 days) within the entire study area. The colour scale represents the number of*
330 *localizations in 500 x 500 m grid cells. Note that the colour scale is logarithmic. Water is*
331 *coloured blue, land dark grey, and mudflats light grey with a solid line indicating their*
332 *boundery. Because the tags send a signal at 1/6 Hz, each localization represents a minimum*
333 *of 6 s of space use for red knots. The coordinate system refers to UTM 31N. © map data from*
334 *Rijkswaterstaat.*
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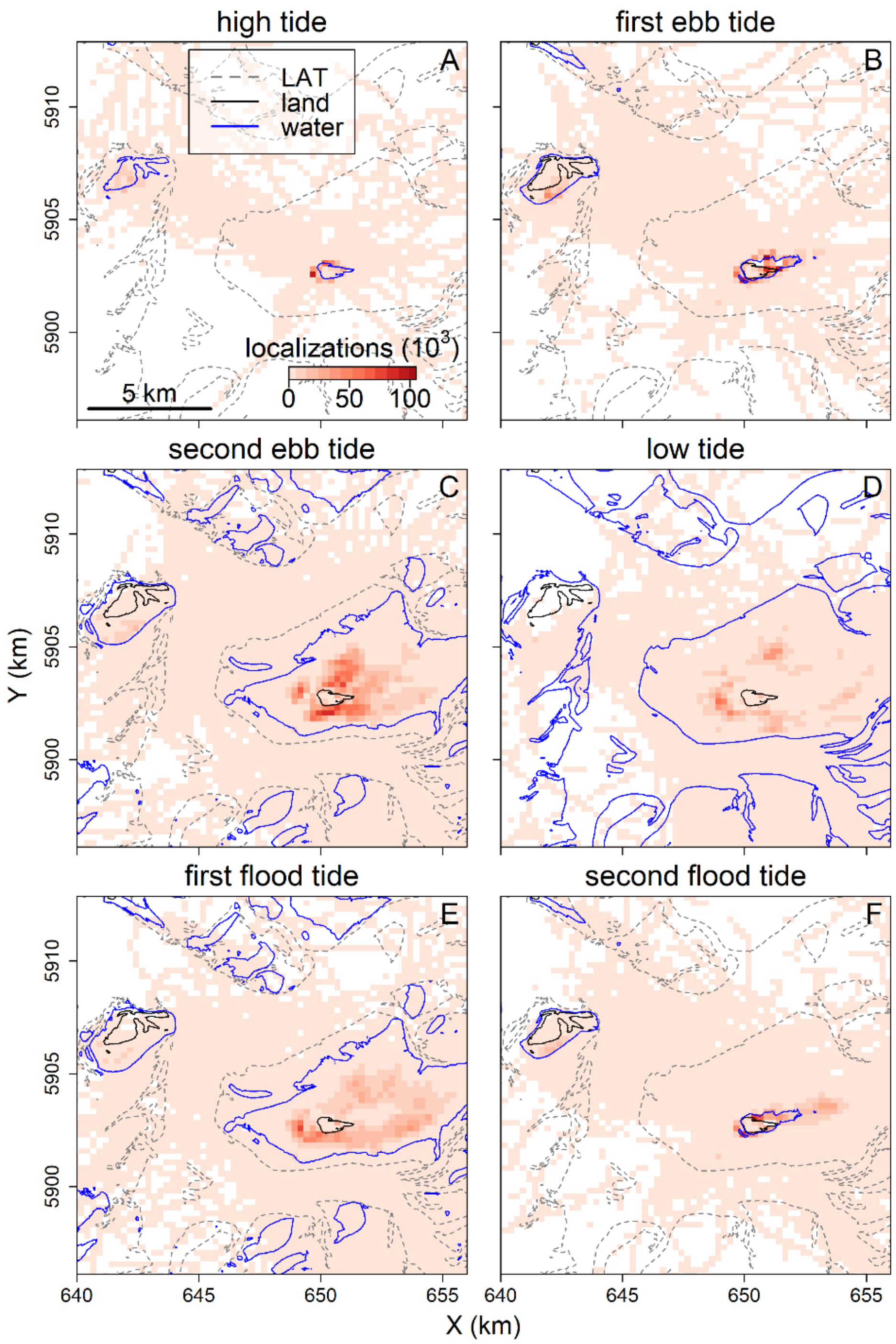

Fig. 6 *Small-scale space use during different phases of the tidal cycle for 221 red knots near Richel and Griend between 1 August and 1 November 2019 (92 days). Panels show different phases of the tidal cycle from high tide (panel A), through ebb tide (panels B and C), to low tide (panel D) and flood tide (panels E and F). The colour scale represents the number of localizations in 250 x 250 m grid cells. The boundary of mudflats are indicated with a grey dashed line (i.e. the Lowest Astronomical Tide, LAT). The blue line indicates the lowest water level within the different tidal phases. Land is indicated with a solid black line. Because the tags send a signal at 1/6 Hz, each localization represents a minimum of 6 s of space use for red knots. See rectangle A in Fig. 1 for placement of this map within the study area. The coordinate system refers to UTM 31N. © map data from Rijkswaterstaat.*

EXAMPLE 2. AMONG-INDIVIDUAL VARIATION IN MOVEMENT

To illustrate the large-scale application of WATLAS tracking and to explore among-individual variation in space use, we selected data from seven red knots (out of 44) on 17 October 2020. These tags were programmed to transmit every 6 s. Additionally, we calculated cumulative distance between successive localizations to reveal variation in daily distances travelled for all individuals tracked that day.

Red knots were successfully localized in large parts of the study area, though gaps in the tracks also occurred (Fig. 7). The tracking data revealed substantial differences among individuals in the distance travelled over a 24-hour period, which ranged between 42 and 328 km day^{-1} for all 44 birds (mean±SD: 131±49 km d^{-1}, histogram in Fig. 7). There were also differences in the number of localizations between birds (mean = 2,111 $bird^{-1}$; range = 144 - 3,680), which significantly explained distance travelled per day (slope = 26.3 m per localization, $p<0.01$). Nonetheless, when dividing the distance travelled by the number of localizations per bird, there were still large among-individual differences (mean = 83.1 m per localization; range = 27.3 - 316.5), which shows that the among-individual variation in distance travelled is not merely caused by differences in the number of successful localizations.

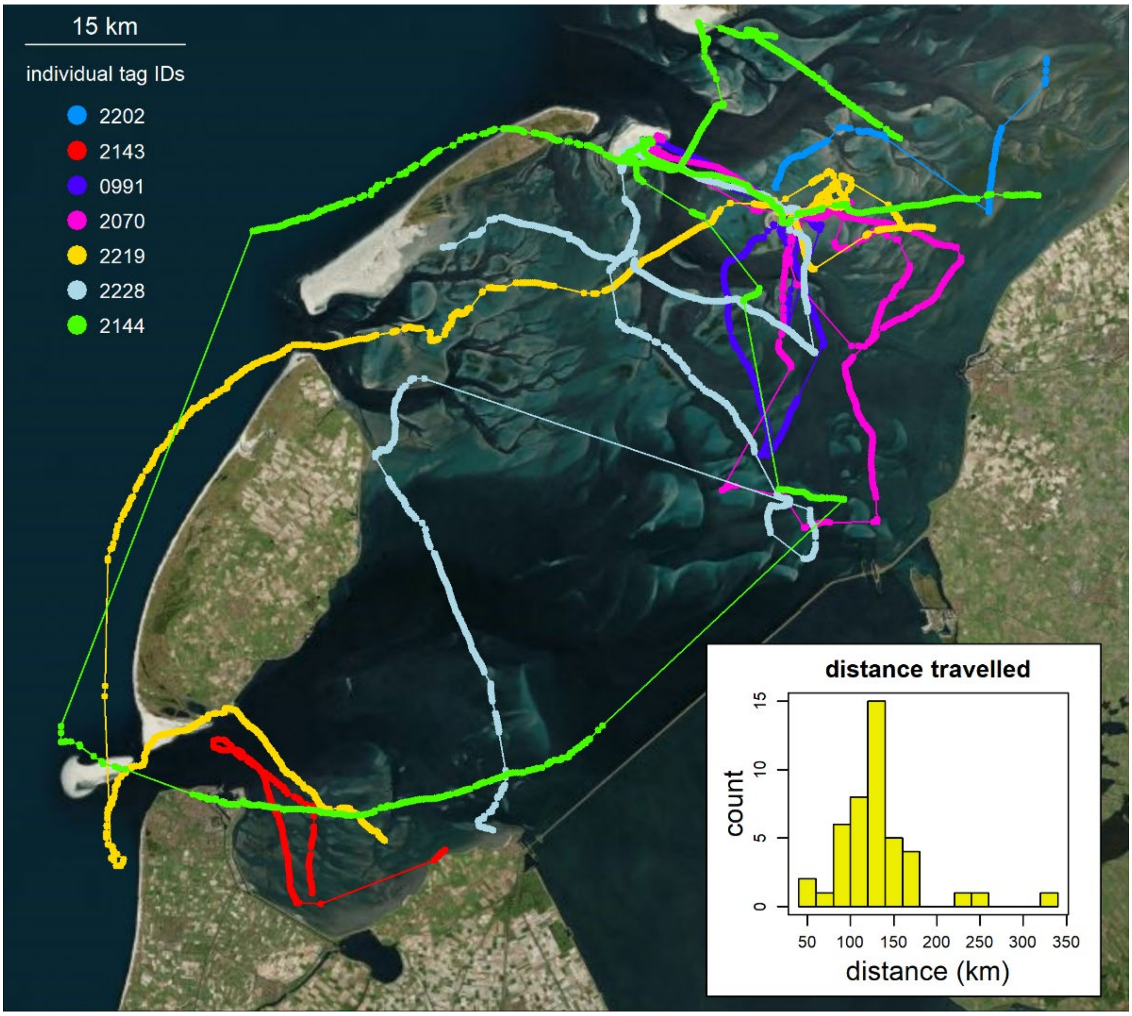

***Fig.** 7 Tracks for a subset of seven individual red knots that differ in the spatial scale of space use across the entire study area. Data collected over 24 hours on 17 October 2020 are shown. The inset shows the histogram of cumulative distance travelled for all 44 birds tracked on this day. © map data from OpenStreetMap.*

EXAMPLE 3. FINE SCALE MOVEMENT AND INTRA-SPECIFIC INTERACTIONS

To illustrate the application of high-resolution WATLAS data for investigating social interactions, we selected seven red knots tracked near Griend (Fig. 1) between two high tides at 00:50 and 13:16 CEST on 31 August 2018. These data, recorded at 1/3Hz, were aggregated into 30 s timesteps, and the mean coordinates were calculated. Within these time steps, social proximity was defined as being within 50 m of each other (Farine & Whitehead 2015). The social network was created in R with the library 'spatsoc' (Robitaille, Webber & Vander Wal 2019).

The fine-scale movement patterns of the red knots show (Fig. 8) that birds roosted on Griend during high tide and, as the water recedes with the ebb tide, moved out onto the exposed mudflat to forage. While foraging, the birds walked across the mudflat, which resulted in areas with dense localizations. Birds flew between different areas to forage as can be seen by the areas of dense localizations connected by lines with sparser localizations (flight). An animation of the fine-scale movement with the incoming tide can be found in the supplement (Supplementary Animation A1). Tracking the fine-scale movements of many tagged animals allows for the investigation of inter-individual interactions. For instance, the proximity-based social network of our subset of seven red knots revealed that some individuals were often in close proximity (e.g. birds with tag IDs 409 and 412; Fig. 8), whereas some individuals were rarely close to the other individuals. The individual with tag ID 458 was mostly static, hence rarely close to any other tagged individual within this period. The comparison between the tracks and proximity network further shows the merit of collecting fine-scale high-resolution tracking data. Visually, for example, the individual with tag ID 409 seems to have much higher overlap with the individual with tag ID 418 than with the individual with tag ID 412. Nonetheless, the spatiotemporal proximity network shows that individuals with tag IDs 409 and 412 have the highest overlap.

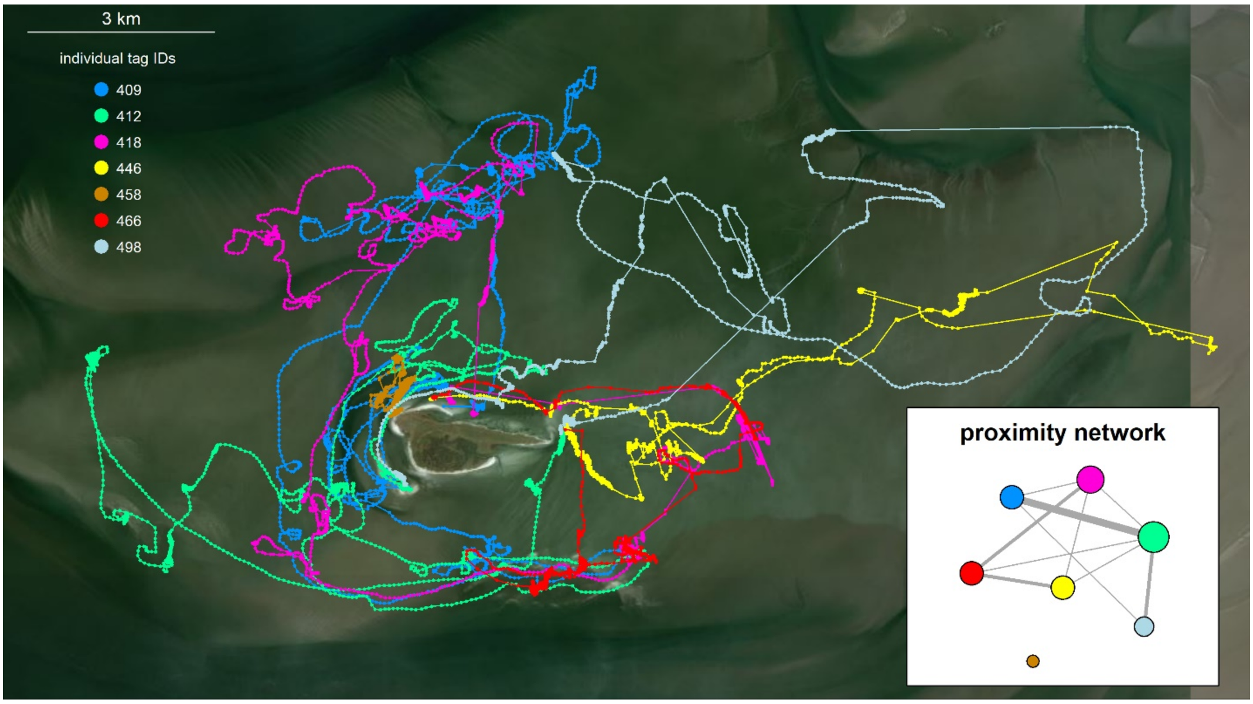

Fig. 8 *Detailed movements from a subset of seven tracked individual red knots around Griend. Data between two high tides at 00:50 and 13:16* CEST *on 31 August 2018 are shown. The inset shows the proximity network for these seven birds based on a spatial proximity of 50 m (see methods). In total, 79 individuals were localized in this timeframe for which an animation of their movement relative to the tide can be found in the Supplementary Information. See rectangle B in Fig. 1 for placement of this map within the study area. © map data from OpenStreetMap.*

EXAMPLE 4. COMMUNITY TRACKING

Tracking individuals from different species within one region, allows investigations of inter-specific space use. To show how space use, comprised of individual movements, scales up to community-level space use, we analyse differences in the home ranges of sanderlings, red knots, and common terns. The terns were included because they use a very different (foraging) niche than shorebirds, and thus are expected to differ in space use. Kernel densities were calculated with the R-library 'amt' (Signer, Fieberg & Avgar 2019) for 74 sanderling tracked between high tides 9:25 and 21:45 CEST on 26 July 2018, 66 red knots tracked between high tides 9:46 and 22:06 CEST on 25 August 2018, and 3 common terns tracked during the whole day on 6 June 2021.

The home-range analyses show that although sanderlings and red knots both roost on Richel and Griend, they differ in their low-tide distribution (Fig. 9). The home range of sanderlings appeared larger than that of red knots and included the intertidal flats to the west of Griend. The differences in space use between sanderlings and red knots might be related to differences in the behaviour and spatial distribution of their prey. For instance, red knots forage on patchily distributed and relatively sessile shellfish, whereas sanderlings forage on shrimp that are mobile and follow the tide. As expected from their piscivorous diet, common terns foraged in the relatively deep gullies instead of on intertidal flats like the shorebirds, and showed the largest home range between the three species.

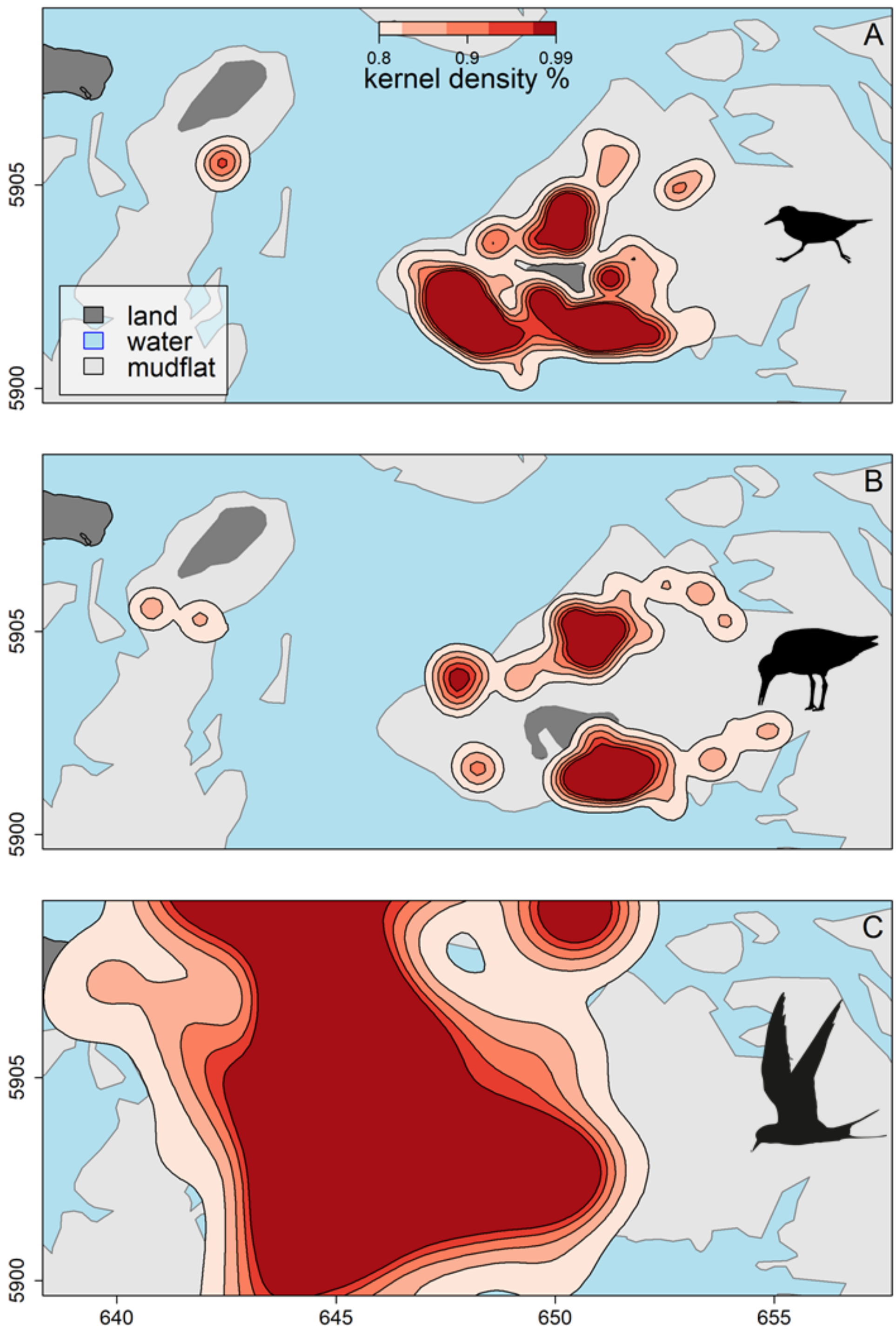

Fig. 9 Space use by sanderlings, red knots and common terns*. The colour scale shows home range estimates with kernel densities for A) sanderling during a low tide period on 26 July 2018, B) red knots during a low tide period on 25 August 2018, and C) common terns during the day on 6 June 2021. Water is coloured blue, land dark grey, and mudflats light grey. See rectangle A in Fig. 1 for placement of this map within the study area. The coordinate system refers to UTM 31N. © map data from Rijkswaterstaat.*

Discussion

With an array of 26 receiver stations located in the western Dutch Wadden Sea, WATLAS covers 1,326 km^2 and is currently the largest reverse-GPS tracking system worldwide. With examples from red knots, sanderlings, and common terns, we illustrated various applications of the high spatial and temporal resolution movement data obtained by WATLAS. Moreover, we provided examples of how high-throughput movement data can be utilized to study important aspects of animal movement ecology and space use, such as among-individual variation in behaviour, intra-specific interactions (social networks) as well as inter-specific interactions (community assembly). For regional-scale studies on small animals, reverse-GPS systems like WATLAS are a promising alternative to conventional GPS tracking.

TECHNICAL CONSIDERATIONS

For successful localization, reverse-GPS tracking like WATLAS, requires at least three receivers to detect the tag's signal, and signal detection requires a 'line of sight'. A study on the accuracy of WATLAS localizations, showed that tags ~1.2m from ground were mostly detected by receivers within 5 km of the tag (Beardsworth *et al.* 2021a). Near Richel and Griend, where the distances between receivers were smallest, localizations were most numerous. Near the edges of the array and on the large-scale of the entire study area, where the distance between receivers was largest (Fig. 1), tags were less often localized causing gaps in the tracks (Fig. 7). To avoid missing localizations, the density of receivers can be increased, and the array should surround the main area of interest (Beardsworth *et al.* 2021a).

Tags attached to animals in flight generally have larger detection ranges than animals on the ground, due to their usually greater height. For instance, in another ATLAS system (Toledo *et al.* 2020), Egyptian Fruit Bats *Rousettus aegyptiacus* were detected during flight up to 40 km away from the receivers. In our study system, we recorded similar detection ranges of birds in flight, and we were able to localise them across the entire study area up to 34 km from the nearest receiver.

The most substantial costs for reverse-GPS are setting up an initial array of receivers. But because the costs of a tags are low, reverse-GPS tracking systems allow tracking large and representative samples of animal populations (MacCurdy *et al.* 2019). The number of unique tags WATLAS systems can detect simultaneously is limited by the processing capability of the computer within the receiver, as well as interference of overlapping transmissions between tags. The percentage of missed tag transmissions increases exponentially as a function of the number of transmitters within range (see Fig. 3.5 in MacCurdy *et al.* 2015). Note that both limitations are not an intrinsic limitation of ATLAS, but a limitation of the current implementation. More powerful processors in the receivers will, for instance, allow more and simultaneous tag detections.

Another advantage of ATLAS systems is the weight of the trackers. The tag without battery and coating weighs as little as 0.6 g, which allows tracking small and light-weight individuals that were previously too small to track remotely at high spatial accuracy. Other tracking systems that allow tracking of smaller free-living individuals, include MOTUS (Taylor *et al.* 2017), and light-level geolocation data loggers (Bridge *et al.* 2013). These devices can provide high temporal resolution data or be used to track birds over large areas. Compared to WATLAS, however, the spatial accuracy of localizations with MOTUS and geolocation loggers is large (kms) and retrieving data from geolocation loggers requires recapturing the tracked animals. Recapturing can be problematic and prevents real-time observations and analyses of tracked animals. Another promising tracking system is ICARUS (Wikelski *et al.* 2007), but this is under development and tags are estimated to be larger than those of ATLAS.

Reverse-GPS systems have dramatically reduced tag energy consumption compared to GPS systems, which allows high temporal resolution localizations to be collected with small batteries (MacCurdy *et al.* 2019). Compared to GPS equivalents, tags can be expected to last for longer with a given number of localizations (MacCurdy *et al.* 2015). Because of the eight months maximum lifetime of WATLAS-tags used in this study, the tags are glued to the backs of birds and will fall off during body moult. From an ethical perspective this is preferred over e.g. full body harnesses (Chan *et al.* 2016), because animals need to cope with the added weight and potential aerodynamic discomfort only temporarily (Bowlin *et al.* 2010). One potential downside of gluing tags to the birds is that trackers will end up in the environment. Given the ever-increasing number of tracking devices deployed, this is an ethical issue that ecologists and conservationists must deal with.

OPPORTUNITIES FOR ANIMAL MOVEMENT ECOLOGY AND CONSERVATION

Simultaneously tracking many small birds in the Wadden Sea at high spatial and temporal resolution, allows for novel studies on e.g. among-individual variation, collective behaviour, and inter-specific interactions in the wild. Moreover, because individuals from different species and different trophic levels can be tracked simultaneously, exciting opportunities exist for studying movement ecology at the community level (Schlägel *et al.* 2020). Within the Dutch Wadden Sea, of particular interest is the ability to combine shorebird tracking with knowledge on their food resources. In this study, we illustrated differences in home range between sanderlings and red knots. Because sanderling prefer shrimp and red knot prefer shellfish (Piersma *et al.* 1993), the differences in space-use are likely related to differences in the distribution of their preferred prey. The uniquely large-scale mapping of resources on the intertidal mudflats with SIBES (Bijleveld *et al.* 2012; Compton *et al.* 2013) will offer exciting opportunities for understanding consumer-resource interactions and space-use in intertidal ecosystems.

Despite strong legal protection and management measures being in place, many activities occur in the Dutch Wadden Sea that can have detrimental effects on its inhabitants (Kabat *et al.* 2012), such as commercial fishing, kite surfing, tourism, military exercises, and mining. In combination with large-scale phenomena, such as sea level rise and global warming (van de Pol *et al.* 2010), these anthropogenic activities can cause disturbances and habitat destruction, and thus contribute to population declines (van Gils *et al.* 2006a; Kraan *et al.* 2009). The causes underlying the declines of shorebird population numbers in the Wadden Sea are often debated, partly because of our limited understanding of environmental processes such as habitat use, which leads to tension and possibly conflict between stakeholders and management (Wolff 2005; Boere & Piersma 2012; Kabat *et al.* 2012; Floor, van Koppen & Lindeboom 2013). The development of WATLAS has opened-up possibilities for quantifying space use of many small shorebirds directly, automatically, and at high spatiotemporal accuracy. WATLAS could thus aid in studies of impact assessment, such as assessing the effect of mining and subsiding mudflats on shorebird space use. More generally, WATLAS could facilitate evidence-based conservation, and aid the management of this UNESCO world heritage site.

CONCLUSION

In this study, we introduced WATLAS as a high-utility tracking system in the Dutch Wadden Sea, capable of tracking hundreds of small individuals simultaneously at high spatiotemporal resolution. After the initial investment for an array of receivers, the costs per tag are low, which facilitates regional, long-term studies on movement ecology and space use of many individuals and multiple species and facilitates collaboration between researchers across research institutes. Because tags are light-weight as well as cheap, WATLAS can facilitate studies on, for instance, collective behaviour, social information use, and movement ecology of entire communities of free-living animals. WATLAS can also support evidence-based nature conservation and management, for example with assessing the impact of anthropogenic activities on space use of shorebirds. More generally, with WATLAS, animals can function as sentinels informing us about the state of the Wadden Sea ecosystem (Piersma & Lindström 2004), and thus aid nature conservation and management of this globally important ecosystem.

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References

Aarts, G., Brasseur, S., Poos, J.J., Schop, J., Kirkwood, R., van Kooten, T., Mul, E., Reijnders, P., Rijnsdorp, A.D. & Tulp, I. (2019) Top-down pressure on a coastal ecosystem by harbor seals. *Ecosphere,* **10,** e02538.

Allen, A.M., Ens, B.J., Van de Pol, M., Van der Jeugd, H., Frauendorf, M., Oosterbeek, K. & Jongejans, E. (2019) Seasonal survival and migratory connectivity of the Eurasian Oystercatcher revealed by citizen science. *The Auk,* **136**.

Allen, A.M. & Singh, N.J. (2016) Linking movement ecology with wildlife management and conservation. *Frontiers in Ecology and Evolution,* **3**.

Bakker, W., Ens, B.J., Dokter, A., van der Kolk, H.-J., Rappoldt, K., van de Pol, M., Troost, K., van der Veer, H.W., Bijleveld, A.I., van der Meer, J., Oosterbeek, K., Jongejans, E. & Allen, A.M. (2021) Connecting foraging and roosting areas reveals how food stocks explain shorebird numbers. *Estuarine, Coastal and Shelf Science,* **259,** 107458.

Beardsworth, C.E., Gobbens, E., Maarseveen, F.v., Denissen, B., Dekinga, A., Nathan, R., Toledo, S. & Bijleveld, A.I. (2021a) Validating a high-throughput tracking system: ATLAS as a regional-scale alternative to GPS. *bioRxiv*.

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

Bedriñana-Romano, L., Hucke-Gaete, R., Viddi, F.A., Johnson, D., Zerbini, A.N., Morales, J., Mate, B. & Palacios, D.M. (2021) Defining priority areas for blue whale conservation and investigating overlap with vessel traffic in Chilean Patagonia, using a fast-fitting movement model. *Scientific reports,* **11,** 2709.

Beukema, J. & Dekker, R. (2020) Half a century of monitoring macrobenthic animals on tidal flats in the Dutch Wadden Sea. *Marine Ecology Progress Series,* **656,** 1-18.

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. *Proceedings of the Royal Society B: Biological Sciences,* **283,** 20151557.

Bijleveld, A.I., van Gils, J.A., van der Meer, J., Dekinga, A., Kraan, C., van der Veer, H.W. & Piersma, T. (2012) Designing a benthic monitoring programme with multiple conflicting objectives. *Methods in Ecology and Evolution,* **3,** 526-536.

Boere, G.C. & Piersma, T. (2012) Flyway protection and the predicament of our migrant birds: a critical look at international conservation policies and the Dutch Wadden Sea. *Ocean & Coastal Management,* **68,** 157-168.

Börger, L., Bijleveld, A.I., Fayet, A.L., Machovsky-Capuska, G.E., Patrick, S.C., Street, G.M. & Vander Wal, E. (2020) Biologging special feature. *Journal of Animal Ecology,* **89,** 6-15.

Bowlin, M.S., Henningsson, P., Muijres, F.T., Vleugels, R.H.E., Liechti, F. & Hedenström, A. (2010) The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods in Ecology and Evolution,* **1,** 398-402.

Bridge, E.S., Kelly, J.F., Contina, A., Gabrielson, R.M., MacCurdy, R.B. & Winkler, D.W. (2013) Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology,* **84,** 121-137.

Chan, Y.-C., Brugge, M., Tibbitts, T.L., Dekinga, A., Porter, R., Klaassen, R.H. & Piersma, T. (2016) Testing an attachment method for solar-powered tracking devices on a long-distance migrating shorebird. *Journal of Ornithology,* **157,** 277-287.

Choi, C.-Y., Peng, H.-B., He, P., Ren, X.-T., Zhang, S., Jackson, M.V., Gan, X., Chen, Y., Jia, Y. & Christie, M. (2019) Where to draw the line? Using movement data to inform protected area design and conserve mobile species. *Biological Conservation,* **234,** 64-71.

Compton, T.J., Holthuijsen, S., Koolhaas, A., Dekinga, A., ten Horn, J., Smith, J., Galama, Y., Brugge, M., van der Wal, D., van der Meer, J., van der Veer, H.W. & Piersma, T. (2013) Distinctly variable mudscapes: distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *Journal of Sea Research,* **82,** 103-116.

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. *Journal of Animal Ecology,* **89,** 623-634.

Ersoy, S., Beardsworth, C.E., Dekinga, A., van der Meer, M., Piersma, T., Groothuis, T.G. & Bijleveld, A.I. (in press) Exploration speed in captivity predicts foraging specialisation in free-living red knots *Calidris canutus*. *Journal of Animal Ecology*.

Farine, D.R. & Whitehead, H. (2015) Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology,* **84,** 1144-1163.

Floor, J.R., van Koppen, C.S.A. & Lindeboom, H.J. (2013) A review of science–policy interactions in the Dutch Wadden Sea — The cockle fishery and gas exploitation controversies. *Journal of Sea Research,* **82,** 165-175.

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology,* **86,** 1320-1330.

Gill, R.E., Tibbitts, T.L., Douglas, D.C., Handel, C.M., Mulcahy, D.M., Gottschalck, J.C., Warnock, N., McCaffery, B.J., Battley, P.F. & Piersma, T. (2009) Extreme endurance flights by landbirds crossing the Pacific Ocean: ecological corridor rather than barrier? *Proceedings of the Royal Society B: Biological Sciences,* **276,** 447-457.

Guilford, T. & Biro, D. (2014) Route following and the pigeon's familiar area map. *Journal of Experimental Biology,* **217,** 169-179.

Gupte, P.R., Beardsworth, C.E., Spiegel, O., Lourie, E., Toledo, S., Nathan, R. & Bijleveld, A.I. (in press) A guide to pre-processing high-throughput animal tracking data. *Journal of Animal Ecology*.

Harten, L., Katz, A., Goldshtein, A., Handel, M. & Yovel, Y. (2020) The ontogeny of a mammalian cognitive map in the real world. *Science,* **369,** 194-197.

Hays, G.C., Bailey, H., Bograd, S.J., Bowen, W.D., Campagna, C., Carmichael, R.H., Casale, P., Chiaradia, A., Costa, D.P., Cuevas, E., Nico de Bruyn, P.J., Dias, M.P., Duarte, C.M., Dunn, D.C., Dutton, P.H., Esteban, N., Friedlaender, A., Goetz, K.T., Godley, B.J., Halpin, P.N., Hamann, M., Hammerschlag, N., Harcourt, R., Harrison, A.-L., Hazen, E.L., Heupel, M.R., Hoyt, E., Humphries, N.E., Kot, C.Y., Lea, J.S.E., Marsh, H., Maxwell, S.M., McMahon, C.R., Notarbartolo di Sciara, G., Palacios, D.M., Phillips, R.A., Righton, D., Schofield, G., Seminoff, J.A., Simpfendorfer, C.A., Sims, D.W., Takahashi, A., Tetley, M.J., Thums, M., Trathan, P.N., Villegas-Amtmann, S., Wells, R.S., Whiting, S.D., Wildermann, N.E. & Sequeira, A.M.M. (2019) Translating marine animal tracking data into conservation policy and management. *Trends in Ecology & Evolution,* **34,** 459-473.

Hertel, A.G., Royauté, R., Zedrosser, A. & Mueller, T. (2021) Biologging reveals individual variation in behavioural predictability in the wild. *Journal of Animal Ecology,* **90,** 723-737.

Joo, R., Boone, M.E., Clay, T.A., Patrick, S.C., Clusella-Trullas, S. & Basille, M. (2020a) Navigating through the R packages for movement. *Journal of Animal Ecology,* **89,** 248-267.

Joo, R., Picardi, S., Boone, M.E., Clay, T.A., Patrick, S.C., Romero-Romero, V.S. & Basille, M. (2020b) A decade of movement ecology. *arXiv preprint arXiv:2006.00110.*

Kabat, P., Bazelmans, J., van Dijk, J., Herman, P.M.J., van Oijen, T., Pejrup, M., Reise, K., Speelman, H. & Wolff, W.J. (2012) The Wadden Sea Region: Towards a science for sustainable development. *Ocean & Coastal Management,* **68,** 4-17.

Kays, R., Crofoot, M.C., Jetz, W. & Wikelski, M. (2015) Terrestrial animal tracking as an eye on life and planet. *Science,* **348,** aaa2478.

King, A.J., Fehlmann, G., Biro, D., Ward, A.J. & Fürtbauer, I. (2018) Re-wilding collective behaviour: an ecological perspective. *Trends in Ecology & Evolution,* **33,** 347-357.

Kraan, C., van Gils, J.A., Spaans, B., Dekinga, A., Bijleveld, A.I., van Roomen, M., Kleefstra, R. & Piersma, T. (2009) Landscape-scale experiment demonstrates that Wadden Sea intertidal flats are used to capacity by molluscivore migrant shorebirds. *Journal of Animal Ecology,* **78,** 1259-1268.

Lindström, Å., Alerstam, T., Andersson, A., Bäckman, J., Bahlenberg, P., Bom, R., Ekblom, R., Klaassen, R.H.G., Korniluk, M., Sjöberg, S. & Weber, J.K.M. (2021) Extreme altitude changes between night and day during marathon flights of great snipes. *Current Biology,* **31,** 3433-3439.

MacCurdy, R.B., Bijleveld, A.I., Gabrielson, R.M., Cluderay, J., Spaulding, E.L., Oudman, T., van Gils, J.A., Dekinga, A., Piersma, T. & Winkler, D.W. (2015) Automatic, intensive wildlife radiotracking. *Untying the knot: Mechanistically understanding the interactions between social foragers and their prey*, pp. 41-56.

MacCurdy, R.B., Bijleveld, A.I., Gabrielson, R.M. & Cortopassi, K.A. (2019) Automated wildlife radio tracking. *Handbook of position location: theory, practice, and advances* (eds S.A. Zekavat & R.M. Buehrer). John Wiley & Sons, Inc., Hoboken, New Jersey, USA.

MacCurdy, R.B., Gabrielson, R.M. & Cortopassi, K.A. (2011) Automated wildlife radio tracking. *Handbook of position location: theory, practice, and advances* (eds S.A. Zekavat & R.M. Buehrer), pp. 1129-1167. John Wiley & Sons, Inc., Hoboken, New Jersey, USA.

MacCurdy, R.B., Gabrielson, R.M., Spaulding, E., Purgue, A., Cortopassi, K.A. & Fristrup, K.M. (2009) Automatic animal tracking using matched filters and time difference of arrival. *Journal of Communications,* **4,** 487-495.

Melamed, I. & Toledo, S. (2017) A robust, selective, and flexible RF front-end for wideband sampling receivers. *ICT Express,* **3,** 96-100.

Middleton, A.D., Sawyer, H., Merkle, J.A., Kauffman, M.J., Cole, E.K., Dewey, S.R., Gude, J.A., Gustine, D.D., McWhirter, D.E. & Proffitt, K.M. (2020) Conserving transboundary wildlife migrations: recent insights from the Greater Yellowstone Ecosystem. *Frontiers in Ecology and the Environment,* **18,** 83-91.

Murgatroyd, M., Redpath, S.M., Murphy, S.G., Douglas, D.J.T., Saunders, R. & Amar, A. (2019) Patterns of satellite tagged hen harrier disappearances suggest widespread illegal killing on British grouse moors. *Nature Communications,* **10,** 1094.

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. *Proceedings of the National Academy of Sciences of the United States of America,* **105,** 19052-19059.

Oudman, T., Piersma, T., Ahmedou Salem, M.V., Feis, 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. *Movement Ecology,* **6,** 24.

Pekarsky, S., Schiffner, I., Markin, Y. & Nathan, R. (2021) Using movement ecology to evaluate the effectiveness of multiple human-wildlife conflict management practices. *Biological Conservation,* **262,** 109306.

Piersma, T., Hoekstra, R., Dekinga, A., Koolhaas, A., Wolf, P., Battley, P.F. & Wiersma, P. (1993) Scale and intensity of intertidal habitat use by knots *Calidris canutus* in the Western Wadden Sea in relation to food, friends and foes. *Netherlands Journal of Sea Research,* **31,** 331-357.

Piersma, T. & Lindström, Å. (2004) Migrating shorebirds as integrative sentinels of global environmental change. *Ibis,* **146,** 61-69.

Preisler, H.K., Ager, A.A. & Wisdom, M.J. (2013) Analyzing animal movement patterns using potential functions. *Ecosphere,* **4,** 1-13.

Rakhimberdiev, E., Duijns, S., Karagicheva, J., Camphuysen, C.J., Dekinga, A., Dekker, R., Gavrilov, A., Ten Horn, J., Jukema, J. & Saveliev, A. (2018) Fuelling conditions at staging sites can mitigate Arctic warming effects in a migratory bird. *Nature Communications,* **9,** 1-10.

Robitaille, A.L., Webber, Q.M.R. & Vander Wal, E. (2019) Conducting social network analysis with animal telemetry data: applications and methods using spatsoc. *Methods in Ecology and Evolution,* **10,** 1203-1211.

Schlägel, U.E., Grimm, V., Blaum, N., Colangeli, P., Dammhahn, M., Eccard, J.A., Hausmann, S.L., Herde, A., Hofer, H. & Joshi, J. (2020) Movement-mediated community assembly and coexistence. *Biological Reviews,* **95,** 1073-1096.

Shaw, A.K. (2020) Causes and consequences of individual variation in animal movement. *Movement Ecology,* **8,** 12.

Signer, J., Fieberg, J. & Avgar, T. (2019) Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and Evolution,* **9,** 880-890.

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.

Strandburg-Peshkin, A., Farine, D.R., Crofoot, M.C. & Couzin, I.D. (2017) Habitat and social factors shape individual decisions and emergent group structure during baboon collective movement. *Elife,* **6,** e19505.

Taylor, P., Crewe, T., Mackenzie, S., Lepage, D., Aubry, Y., Crysler, Z., Finney, G., Francis, C., Guglielmo, C. & Hamilton, D. (2017) The Motus wildlife tracking system: a collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology,* **12,** 8.

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.

Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown, D., de Bruyn, P.J.N., Cagnacci, F., Calabrese, J.M., Camilo-Alves, C., Chamaillé-Jammes, S., Chiaradia, A., Davidson, S.C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C.H., Ford, A.T., Fritz, S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.J.M., Hof, C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J.D.C., López-López, P., Markham, A.C., Mattisson, J., Medici, E.P., Mellone, U., Merrill, E., de Miranda Mourão, G., Morato, R.G., Morellet, N., Morrison, T.A., Díaz-Muñoz, S.L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., O'Hara, R.B., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., Cunha de Paula, R., Pedrotti, L., Reineking, B., Rimmler, M., Rogers, T.L., Rolandsen, C.M., Rosenberry, C.S., Rubenstein, D.I., Safi, K., Saïd, S., Sapir, N., Sawyer, H., Schmidt, N.M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J.P., Singh, N., Solberg, E.J., Spiegel, O., Strand, O., Sundaresan, S., Ullmann, W., Voigt, U., Wall, J., Wattles, D., Wikelski, M., Wilmers, C.C., Wilson, J.W., Wittemyer, G., Zięba, F., Zwijacz-Kozica, T. & Mueller, T. (2018) Moving in the anthropocene: global reductions in terrestrial mammalian movements. *Science,* **359,** 466-469.

van de Kam, J., Ens, B., Piersma, T. & Zwarts, L. (2004) *Shorebirds. An illustrated behavioral ecology.* KNNV Publishers, Utrecht, The Netherlands.

van de Pol, M., Ens, B.J., Heg, D., Brouwer, L., Krol, J., Maier, M., Exo, K.M., Oosterbeek, K., Lok, T. & Eising, C.M. (2010) Do changes in the frequency, magnitude and timing of extreme climatic events threaten the population viability of coastal birds? *Journal of Applied Ecology,* **47,** 720-730.

van der Veer, H.W., Dapper, R., Henderson, P.A., Jung, A.S., Philippart, C.J., Witte, J.I.J. & Zuur, A.F. (2015) Changes over 50 years in fish fauna of a temperate coastal sea: Degradation of trophic structure and nursery function. *Estuarine, Coastal and Shelf Science,* **155,** 156-166.

van Gils, J.A., Piersma, T., Dekinga, A., Spaans, B. & Kraan, C. (2006a) Shellfish dredging pushes a flexible avian top predator out of a marine protected area. *PLoS Biology,* **4,** 2399-2404.

van Gils, J.A., Spaans, B., Dekinga, A. & Piersma, T. (2006b) Foraging in a tidally structured environment by red knots (*Calidris canutus*): ideal, but not free. *Ecology,* **87,** 1189-1202.

van Roomen, M., Laursen, K., van Turnhout, C., van Winden, E., Blew, J., Eskildsen, K., Günther, K., Hälterlein, B., Kleefstra, R., Potel, P., Schrader, S., Luerssen, G. & Ens, B.J. (2012) Signals from the Wadden sea: population declines dominate among waterbirds depending on intertidal mudflats. *Ocean & Coastal Management,* **68,** 79-88.

Verhoeven, M.A., Loonstra, A., Senner, N.R., McBride, A.D., Both, C. & Piersma, T. (2019) Variation from an unknown source: large inter-individual differences in migrating black-tailed godwits. *Frontiers in Ecology and Evolution,* **7,** 31.

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. *15th International Conference on Information Processing in Sensor Networks*, pp. 1-12. IEEE.

Wikelski, M., Kays, R.W., Kasdin, N.J., Thorup, K., Smith, J.A. & Swenson, G.W. (2007) Going wild: what a global small-animal tracking system could do for experimental biologists. *Journal of Experimental Biology,* **210,** 181-186.

Williams, H.J., Taylor, L.A., Benhamou, S., Bijleveld, A.I., Clay, T.A., de Grissac, S., Demšar, U., English, H.M., Franconi, N. & Gómez-Laich, A. (2020) Optimising the use of biologgers for movement ecology research. *Journal of Animal Ecology,* **89,** 186-206.

Wolff, W.J. (2005) The exploitation of living resources in the Dutch Wadden Sea: a historical overview. *Helgoland Marine Research,* **59,** 31-38.

Xia, H., Bertoni, H.L., Maciel, L.R., Lindsay-Stewart, A. & Rowe, R. (1993) Radio propagation characteristics for line-of-sight microcellular and personal communications. *IEEE Transactions on antennas and propagation,* **41,** 1439-1447.

Zwarts, L., Blomert, A.-M. & Wanink, J.H. (1992) Annual and seasonal variation in the food supply harvestable by knot Calidris canutus staging in the Wadden Sea in late summer. *Marine Ecology Progress Series***,** 129-139.