Validating a high-throughput tracking system: ATLAS as a regional-scale alternative to GPS

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Running headline: ATLAS validation

Abstract

1. Fine-scale tracking of animal movement is important to understand the proximate mechanisms of animal behaviour. While GPS tracking is an excellent tool for measuring animal movement, it often causes a trade-off between tag weight, cost and lifespan that limits its application to relatively large individuals, a small number of individuals or short tracking durations, respectively. The reverse-GPS system – ATLAS – uses lighter, cheaper tags that last long periods of time at the similar sampling frequencies to GPS. ATLAS provides a regional-scale alternative to global GPS-based tracking with which hundreds of relatively small-bodied species can be tracked simultaneously for long periods of time.
2. Here, we test the accuracy and precision of an ATLAS system, using concurrent GPS measurements as a reference. To measure accuracy, we calculated the distance between ATLAS and GPS location estimates for a route (mobile test) and 16 fixed locations (stationary test) on the Griend mudflat, the Netherlands. This location is the focus of a large-scale ATLAS system in the Wadden Sea consisting of 26 receivers and covering 1326 km^2 of intertidal region, with almost no physical obstacles for radio signals.
3. ATLAS-derived location estimates differed on average 4.2 m from GPS-estimated stationary test sites and 5.7 m from GPS tracks taken whilst moving between them. Signals that were collected by more receiver stations were more accurate, although even 3-receiver localisations were comparable with GPS localisations (~10 m difference). Higher receiver stations detected the tag at further distances.
4. In conclusion, ATLAS provides an alternative to GPS for regional-scale animal movement studies by providing movement data of comparable spatial accuracy. The growing use of the ATLAS systems motivates further refinement of best-practice application, such as considering the height of receivers, their spatial arrangement, density and the movement mode of the study species (e.g., ground-dwelling or flying).

Introduction

Tracking animal movements is important to understand the proximate mechanisms underlying animal behaviour, with broad applications for studying key ecological and evolutionary processes (Nathan et al., 2008). Since the advent of tracking technology, insight into the often cryptic movements of animals has allowed us to understand behaviours that were never before possible, from the migration patterns of whales (Abrahms et al., 2019) and birds (Gill et al., 2009) to identifying differences between individuals in foraging strategies (Bijleveld et al., 2016; Harris et al., 2020) or confirming the cognitive mechanisms that underlie behaviour in free-ranging individuals (Beardsworth et al., *In press*; Toledo et al., 2020). In recent decades, the rapid development of global navigation satellite systems (GNSS: encompasses use of GPS, GLONAS and Galileo satellites) has led to an explosion in the number of studies in movement ecology (Holyoak et al., 2008; Joo et al., 2020). However, while GPS has become one of the primary tools of choice for monitoring movement of many species (Cagnacci et al., 2010; Hebblewhite & Haydon, 2010; Kays et al., 2015), its application is limited due to trade-offs between sampling frequency, battery size, tag weight, cost and lifespan. GPS tags require relatively large batteries to enable communication with satellites and most calculate location estimates on-board. As a consequence, tags can be too heavy for smaller species to carry (Wikelski et al., 2007). GPS tags can also be expensive; hence, many research projects with standard levels of funding are limited to tracking a small number of individuals, which might be insufficient to make appropriate inferences (Hebblewhite & Haydon, 2010). Furthermore, for studies requiring high temporal resolution of movement data (e.g., to explore biotic interactions), tracking duration of GPS devices is often limited, even with solar-charged batteries. Fortunately, alternative systems for tracking animal movement are continuously being developed in an attempt to bridge these gaps (Williams et al., 2020). These form a diverse toolset for biologging, ranging from autonomous underwater videography (Hawkes et al., 2020) to using biomarkers from tail hair to detect movement through landscapes (Kabalika et al., 2020). Despite these advances, few of these technologies can attain the fine-scale tracking of movement paths which are a necessity for identifying decision points of individuals (Collet et al., 2017; Harel et al., 2016) or groups (Strandburg-Peshkin et al., 2015), or

correlating movements with precise environmental covariates (Dickie et al., 2020; Eikelboom et al., 2020). One potential alternative for regional-scale studies is ATLAS (Advanced Tracking and Localisation of Animals in real-life Systems; Toledo et al., 2020), a high-throughput system that uses low-cost and lightweight radio-transmitters to track animals at a regional scale.

Radio telemetry has a rich history for use within animal tracking (Amlaner & Macdonald, 1980; Benson, 2010) and traditionally involved using hand-held receivers to search a landscape for signals from animal-mounted, high frequency radio-transmitters to estimate tag location through triangulation. Unlike GPS, the estimated location of a radio tag is determined at the receiver side, rather than by the tag itself, therefore alleviating energy-demanding remote data communications and enabling the almost instantaneous retrieval of tracking data. The lack of on-board computation for radio tags results in low power requirements, enabling the use of smaller batteries and thus increasing their potential for use with smaller species. However, using handheld receivers to estimate direction to the target in conventional radio telemetry can be labour intensive and produce relatively large errors that can increase with distance. Attempts to automate wildlife tracking based on standard radio tags were made as early as the 1960's (Cochran et al., 1965) and more recently implementations have estimated locations of tags using a bounding array of receivers distributed within a specific region (Kays et al., 2011).

The ATLAS system combines some of the major advantages of previous radio-telemetry solutions and GPS while resolving some of their disadvantages. First, like GPS and unlike conventional radio-telemetry, ATLAS uses time of arrival (TOA) estimation (see also MacCurdy et al., 2009), rather than approximating the angle of arrival of the signal. This means that accuracy does not decay with distance between the tag and receiver. By implementing the use of beacon tags in known locations, ATLAS can synchronise the receivers' clocks, characterise the accuracy of localisations and monitor the performance of the system (Weller-Weiser et al., 2016). Second, like conventional radio telemetry

but unlike GPS, ATLAS tags act as a transmitter, rather than a receiver and thus shift the energy-demanding task of calculating location estimates (and remote data collection) to high quality receiver stations (hence it is a "reverse-GPS" system). This enables the trade-off between battery size (and therefore tag weight) and sampling rate or tag life to be minimised and allows smaller species to be tracked using ATLAS than by GPS. ATLAS therefore provides high throughput monitoring for relatively cheap (~€50 per tag), lightweight (<1g + battery weight), and long-lasting (~8 months for 4.4g tag at 1/6 Hz) tags. However, ATLAS installation requires time, resources and expertise, and its spatial coverage is limited to a regional scale where the line-of-sight from three or more receiver stations overlap. Considering these pros and cons, ATLAS systems have recently been established in four different countries (Israel, the UK, the Netherlands and Germany), collecting rich datasets on hundreds of individuals and addressing key research questions in movement ecology (Beardsworth et al., *In press*; Corl et al., 2020; Gupte et al., 2020). Yet detailed, strategic testing of the accuracy of ATLAS and the efficacy of receiver arrays has been limited.

Here, we characterise the accuracy and precision of the largest ATLAS system to date. The Wadden Sea ATLAS system (WATLAS) has 26 receiver stations covering a total area of 1326 km^2 which are most concentrated on the Griend mudflat, an important stop-over site for many shorebird species (Piersma et al., 1993), the smaller species of which are now able to be tracked at high spatio-temporal resolution. With almost no interruptions to the flat landscape of the mudflats, the area around Griend is particularly useful to investigate the accuracy and precision of the system. We assess tag reception capabilities and the influence of receiver arrangement and concentration on the accuracy and precision of the system. We compare ATLAS localisations to GPS-derived positions at 16 test sites covering an area of 34 km^2 around the Griend mudflat. While stationary tests give a good overview of the accuracy and precision of a system, animals themselves are tracked in both stationary and mobile states. It is therefore useful to compare GPS and ATLAS while moving across a landscape, where slight variations in the array of receivers that detect the tag may occur. We therefore also calculated the difference between ATLAS and GPS en-route to each of the test sites giving us estimates for

accuracy in both stationary and moving states. We emphasise that the accuracy of neither GPS nor ATLAS localisations were tested against independent ("known") finer-scale locations, but were compared to each other. Hence, these comparisons should not be inferred as if ATLAS deviations from GPS measurements represent deviations from the true location (or vice versa), but whether these two methods are comparably accurate and precise. Finally, since movement studies frequently filter and/or smooth movement data to reduce error in location estimates (Lewis et al., 2007), and more importantly, since GPS data are provided only after intense filtering and smoothing (Kaplan & Hegarty, 2005), we assessed the accuracy of the ATLAS system both with and without applying a simple filter-smoothing process.

Methods

WATLAS - The Wadden Sea ATLAS System

The WATLAS system consist of 26 ATLAS receiver stations (Fig. 1). Components include a small computer (Intel NUC mini PC running dedicated ATLAS software, *v2020-04-19-stable*), a USRP N200 radio with a WBX40 daughterboard and a GPS disciplined oscillator (GPSDO), were housed in custom-made watertight containers. The system time/GPSDO of a receiver station is synchronized using the atomic clocks from a GPS unit which is connected to the USRP N200 radio. Receiver stations were placed around the Western Dutch Wadden sea to gain high coverage for tracking migrant shorebirds while they stopover in the area (Fig. 1). Eleven receivers were built on temporary scaffolds on the mudflats and were powered with four 100 W solar panels and a 100 W wind turbine (Ampair) connected to three (105 Ah) batteries. The remaining 15 receivers were installed in places such as on buildings and other stable structures where power was available. Each receiver had a UHF antenna connected to the radio through a custom-built front-end unit (CircuitHub) and a custom built Low-Noise Amplifier. Radio-frequency samples from tags are processed by the receiver's computer to estimate the arrival times of the signal. All receiver stations were connected to internet using a 3G cellular model (USB dongles, Huawei E3372) to send detection reports to a central server situated at

the NIOZ. In real-time, the server calculated location estimates and stored these in a MySQL (v5.7, https://www.mysql.com/) database. Seven beacons tags were placed at known locations spread throughout the study area to calibrate the system.

Data collection

To test the accuracy of the WATLAS deployment and ATLAS tracking in general, we focussed our tests on the area around Griend, where we study shorebird movement and have the highest concentration of receivers (Fig. 1). We tested reception and localisation accuracy at 16 sites around the mudflat, 9 of which were 1 km apart with an outer ring of 7 sites that were 2 km between each other and the 1 km sites (Fig. 2). Between 21st - 27th August 2020, we travelled to these sites while carrying a handheld Garmin Dakota 10 GPS (<10 m error 95% typical) – set to record tracks on 'auto' which records at a variable rate to create an optimum representation of tracks - and an ATLAS tag. The tag we used for testing emitted a radio signal at 1 Hz. It consisted of a miniature frequency-shift-keying 434MHz integrated radio transceiver and microcontroller (Texas Instruments CC1310) and a monopole ¼ λ gold-plated, multistranded steel wire antenna (Toledo et al., 2014). The tag was encased in plastic to protect it from mechanical stress. We attached the tag to the top of a 1.2m wooden pole so that we could keep the height of the tag consistent throughout the testing.

We walked to 13 of the sites during the day at low tide on the 21st, 23rd and 27th August (Fig. 2). Between sites, the pole holding the tag was kept upright meaning that the tag was consistently ~1.2m from the ground. On arrival at each of these sites, we pushed the pole into the sand so that the tag was 1m above the mudflat and attached the GPS to the pole. We collected ATLAS and GPS data at each site for 5 minutes. Due to weather and time constraints, we were unable to travel to each site on foot. On the 24th August, we sailed a rubber boat to the some of the furthest sites in the West and North mudflat (Fig. 2) and conducted the stationary test for sites 1, 4 and 12 while at anchor. The pole with the ATLAS tag and GPS tag attached was held upright on the pole in the middle of the boat therefore

the tag was ~1.3m above the water level. Despite being at anchor with a taut rope, there were waves and therefore the boat was not completely stationary during the test, therefore we expect slight overestimates in the location error and larger standard deviations for these positions.

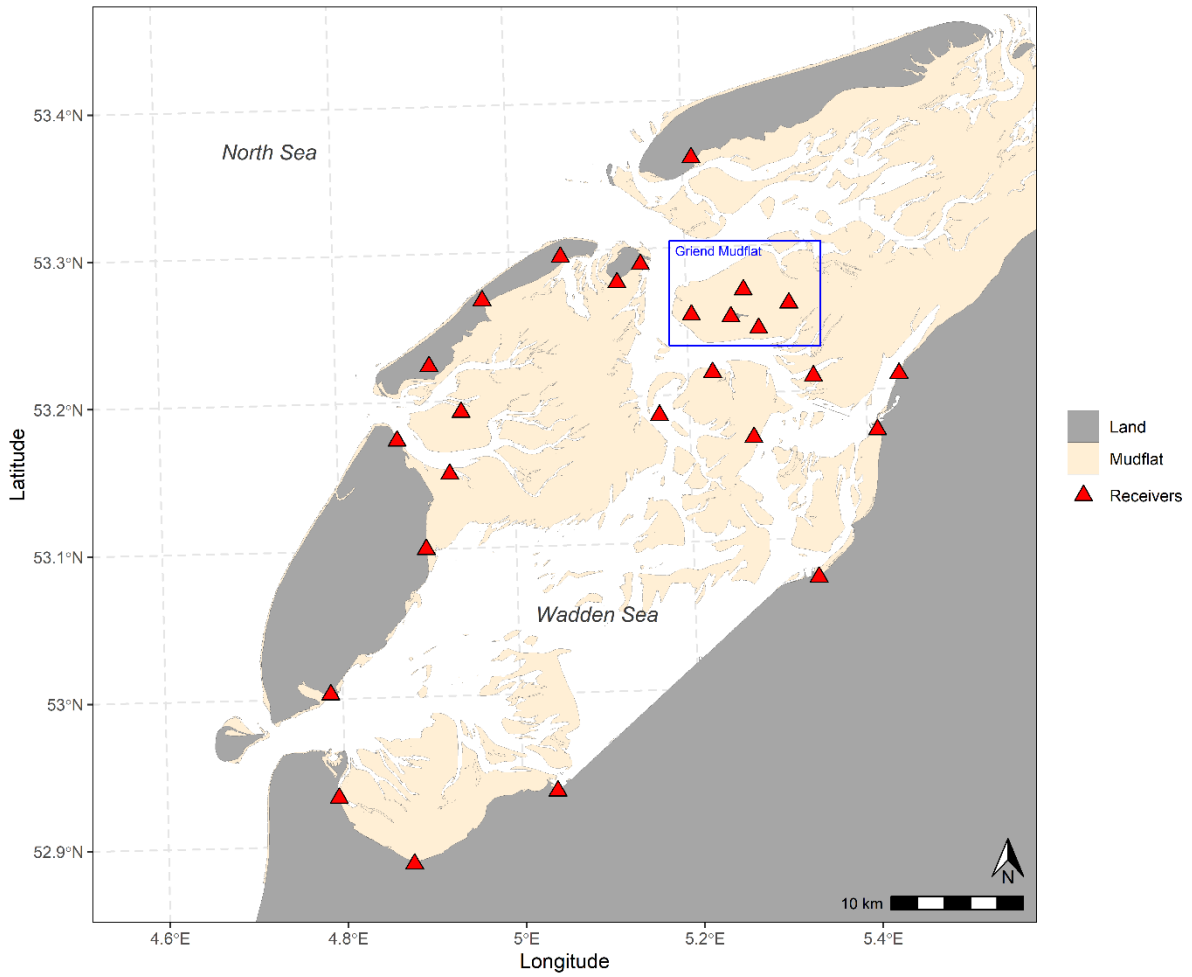


Figure 1. Configuration of receiver stations in 2020 around the Western Wadden sea. The blue rectangle indicates the island of Griend, whose surrounding mudflat provides rich foraging opportunities for many shorebird species and where our receivers are most concentrated. Land is shown in grey and the exposed mudflat at -144 NAP is shown in beige. The locations of receiver stations are shown as red triangles.

Filter-Smoothing

Many biologists choose to filter and/or smooth their data before use to reduce errors in positioning estimates (Bjørneraas et al., 2010; Gupte et al., 2020). As GPS data are regularly smoothed without a practical option to retrieve the raw data (Kaplan & Hegarty, 2005), we used a simple filter-smoothing process on the raw data. ATLAS provides some error estimates automatically, namely variance in the

Easting and Northing (VARX and VARY). We removed localisations that had high VARX and VARY (>2000) and then smoothed the data by computing a 3-point median smooth across the localisations (Appendix S1).

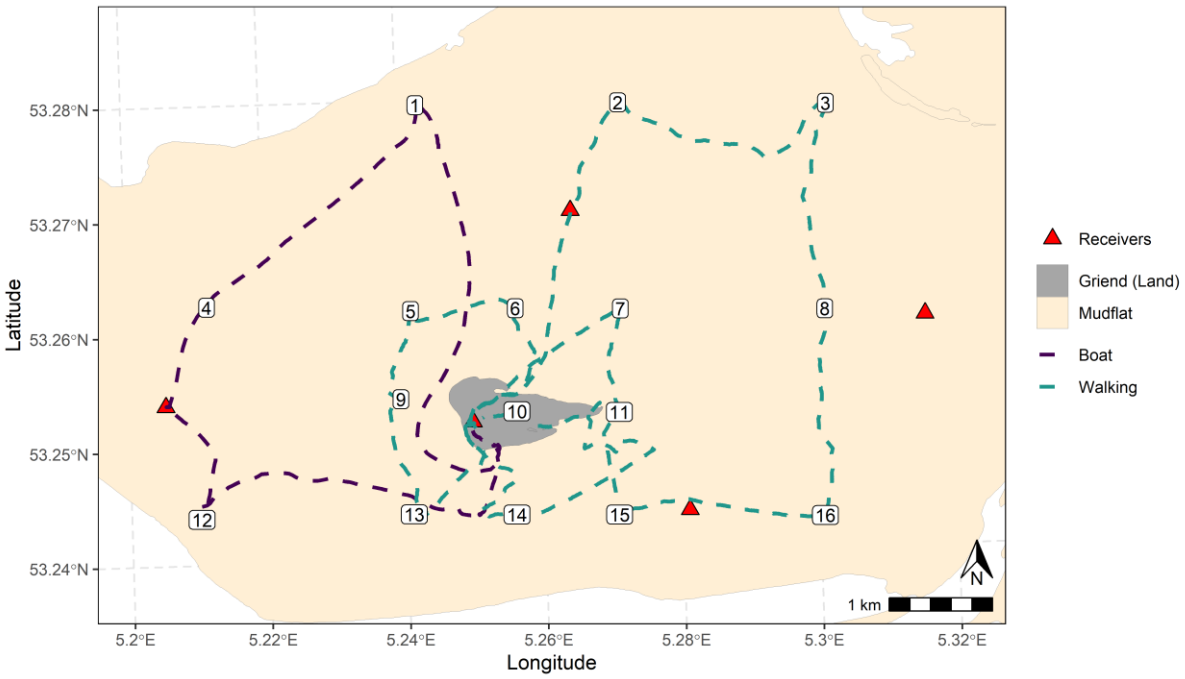


Figure 2. Map of the routes travelled to each stationary test site (numbered) around the Griend mudflat. Routes are mapped using GPS data. Due to time and weather constraints, we used a boat to test the western side of the mudflat (purple) but the rest was walked.

Accuracy Analysis and Tag Reception

We split the analysis into two parts, analysing data at test sites (stationary test) and between test sites (mobile test) separately.

Stationary Test

For the stationary test, we calculated the mean GPS-derived location estimate at each of the 16 test sites and compared it to the ATLAS-derived location estimate; hence, our measure of accuracy (which we henceforth call ‘error’) refers to the difference in meters between the two estimated locations. For each site, the mean error (m), standard deviation, the median error (m) and the 95th upper and lower percentiles. We investigated the tag reception at each location by calculating the fix rate (number of

localisations/300 (max possible localisations in 5-minute period at 1Hz) and the mean and standard deviation of the number of receivers that contributed to each location estimate.

Mobile Test

When the tag was mobile, we compared each ATLAS-derived location estimate to the nearest (in time) GPS-derived location estimate. We removed pairings of location estimates where the smallest time difference between an ATLAS location estimate and a GPS location estimate was > 2 seconds. We calculated the distance (m) between the remaining paired locations to determine 'error'. As in the stationary test, we calculated the mean error (m), standard deviation, the median error (m) and the 95th upper and lower percentiles to assess accuracy. We aggregated these summary statistics by the number of receivers that contributed to each location estimate to assess the influence of the number receiver stations on accuracy and investigate the overall coverage of our system. To assess tag reception around the mudflat for specific receivers, we plotted each receiver station and the location estimates that they contributed to on separate maps.

Results

Stationary Test

For the stationary test, we calculated a median error [2.5-97.5%] of 4.2 m [0.6-110.1] over all sites, which reduced to a median 3.1 m [0.5-27.5] after filter-smoothing the data (Fig. 3). When analysed individually, we found that the least accurate sites were the three most Northern sites (1-3). These sites were outside of the array of receivers and each had a mean of <4 receiver stations detecting them (Fig. 3, Table 1). Fifteen out of sixteen sites had a fix rate of >90%. One site (site 2) had a fix rate of 73% and the lowest accuracy (median error = 110.5 m [5.5-1059.4]) and mean number of receivers detecting the tag there (mean error ± s.d. =3.4 ± 0.8). This low accuracy was able to be mitigated by applying the filter-smooth, which increased accuracy to 28.2 [7.6-67.5]. It should be noted however that for this particular site the number of location estimates that remained after smoothing was only

9.7% of the expected number of points, which is equivalent to an average sampling interval of ~100 seconds.

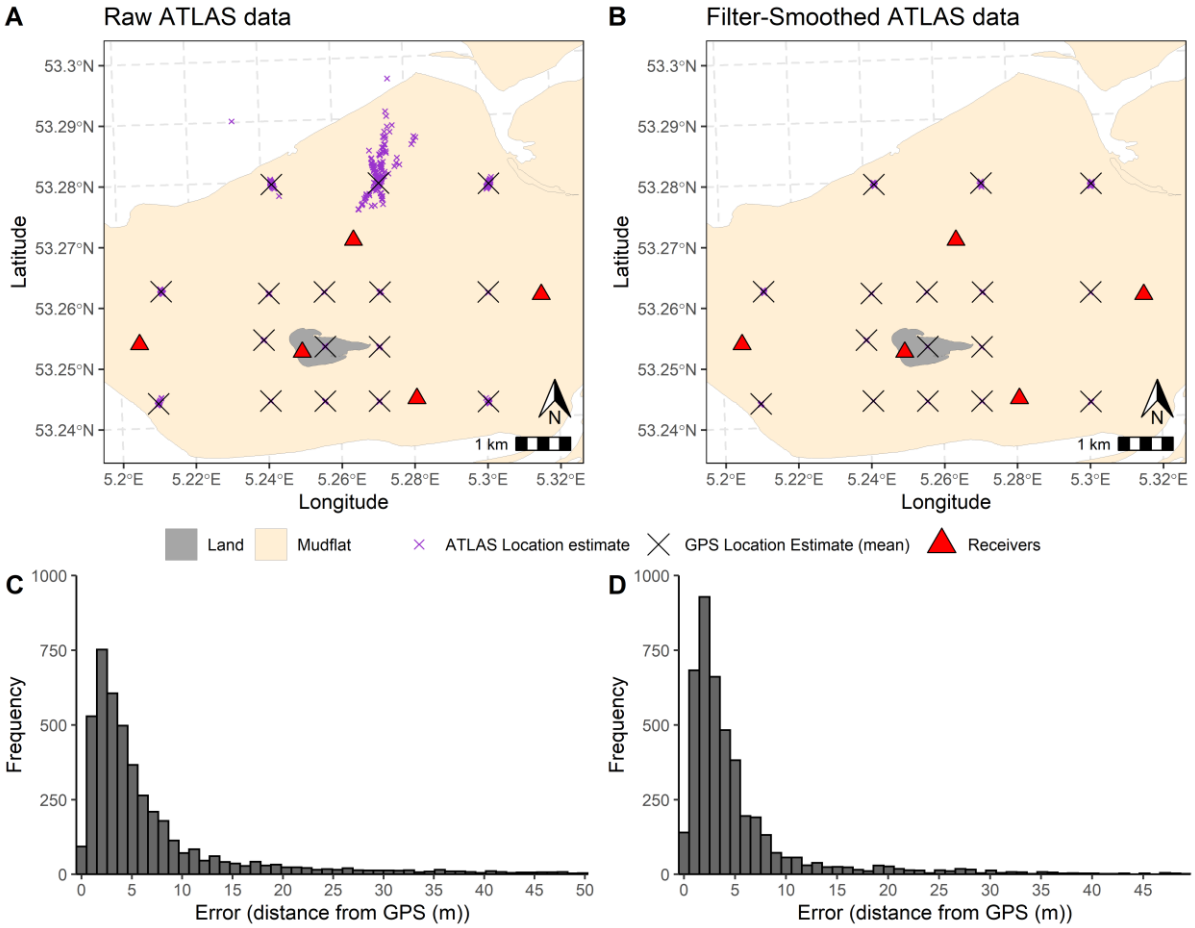


Figure 3. Comparison between ATLAS and GPS derived localisations for raw (A & C) and filter-smoothed (B & D) data. Purple crosses denote positions calculated by ATLAS over a 5-minute period and larger, black crosses indicate the GPS-derived location estimate. The histograms (C & D) show the error in positions at all stationary sites combined, indicating with a peak in accuracy < 5m for both raw and filter-smoothed data.

Table 1. Accuracy (error = distance (m) to GPS-derived location estimate) and fix rate (% localisations at 1Hz, max 300) of ATLAS tags (both raw data and filter-smoothed data) that were stationary over five minutes. IDs relate to locations on Fig. 2. ID1, ID4 and ID12 (boxed) were taken on an anchored boat, therefore we may expect higher standard deviations on these results.

	Raw					Filter-Smoothed				
ID	**N**	**Fix Rate (%)**	**Mean N Receivers (SD)**	**Mean Error (m) (SD)**	**Median Error (m) [95%]**	**N**	**Fix Rate (%)**	**Mean N Receivers (SD)**	**Mean Error (m) (SD)**	**Median Error (m) [95%]**
1	276	92	3.8 (0.8)	23.8 (83.8)	13.9 [1.5-59.5]	265	88.3	3.8 (0.8)	11.7 (8.3)	9.1 [1.2-30.1]
2	219	73	3.4 (0.6)	248.2 (299.6)	110.5 [5.5-1059.4]	29	9.7	3.6 (0.8)	28.8 (15.1)	28.2 [7.6-67.5]
3	299	99.7	3.8 (0.4)	29.5 (19.9)	26.3 [4.1-77.6]	282	94	3.8 (0.4)	21 (12.0)	19.4 [4.3-47.8]
4	298	99.3	3.4 (0.6)	12.5 (9.9)	9.4 [1.6-40.6]	298	99.3	3.4 (0.6)	8.2 (6.1)	7 [1.3-28.5]
5	300	100	4.6 (0.7)	3.2 (2.4)	2.9 [0.3-8.5]	300	100	4.6 (0.7)	2.3 (1.5)	2 [0.3-6.2]
6	300	100	5.3 (0.7)	3.1 (1.7)	2.8 [0.7-7.4]	300	100	5.3 (0.7)	2.7 (1.4)	2.5 [0.8-5.9]
7	299	99.7	3.8 (0.4)	5.3 (3.8)	4.1 [0.7-14.3]	299	99.7	3.8 (0.4)	3.4 (2.4)	2.9 [0.4-8.8]
8	300	100	4 (0.1)	4.7 (2.3)	4.4 [1-9.7]	300	100	4 (0.1)	4.2(1.6)	4.2 [1.6-7.5]
9	300	100	5.7 (0.5)	3.9 (2.5)	3.4 [0.7-9.7]	300	100	5.7 (0.5)	3.2 (1.9)	2.8 [0.7-7.9]
10	295	98.3	3.9 (0.4)	2.4 (1.7)	2.2 [0.5-6]	295	98.3	3.9 (0.4)	2.1 (1.1)	2 [0.5-4.5]
11	279	93	4.8 (1.0)	3 (2.4)	2.3 [0.5-9.6]	279	93	4.8 (0.4)	2.1 (1.4)	1.8 [0.4-5.4]
12	281	93.7	4 (0.9)	8.1 (11.6)	5.4 [0.8-24.3]	274	91.3	4 (1.0)	4.6 (3.6)	3.9 [0.5-16]
13	282	94	5.8 (0.8)	2.2 (1.3)	2 [0.3-4.8]	282	94	5.8 (0.8)	1.7 (0.9)	1.6 [0.2-4]
14	300	100	5.2 (0.4)	4.8 (3.1)	4.4 [0.4-12.5	300	100	5.2 (0.4)	4.3 (2.5)	4.1 [0.6-9.7]
15	300	100	5.8 (0.4)	3.6 (2.6)	3.1 [0.5-9.2]	300	100	5.8 (0.4)	2.7 (1.8)	2.2 [0.2-7.0]
16	299	99.7	5.2 (0.8)	7.3 (6.9)	5.7 [0.9-20.5]	299	99.7	5.2 (0.8)	4.8 (2.8)	4.6 [0.6-11.3]

Mobile Test

ATLAS location estimates had an overall median [2.5-97.5%] of 5.7 m [0.9-63.3] when compared to GPS. In general, localisations where only 3 receiver stations detected the tag were the least accurate and accuracy increased with receiver number (Table 2). Larger errors were more likely to occur on the edges and outside of the receiver array (Fig. 4). The filter-smoothing that we implemented decreased overall error to a median of 4.4 m [0.7-27.4] (Table 2, Fig. 4B). Ten receiver stations received tag signals during the moving test and ranged from detecting 0.58% of signals to 97.87% (Fig. 5). The furthest distance at which a receiver detected a signal was 14,764 m, but this was the highest of the receivers (44.4 m) and only contributed to 1.17% of localisations. The receivers that detected >90% of signals were within 5 km of their furthest detection.

Table 2. Accuracy of tag when moving according to the number of receiver stations that detected the tag. Error is calculated by measuring the distance between the ATLAS localisation and the (temporally) closest GPS localisation (if <2 seconds difference).

	Raw			Filter-Smoothed		
NBS	**N**	**Mean Error (m) (SD)**	**Median error [95%]**	**N (N removed by filters)**	**Mean Error (m) (SD)**	**Median error [95%]**
3	4285	24.1 (44.8)	10.7 [1.3-150.1]	3850 (-435)	11.1 (19.0)	6.3 [1-47.6]
4	8712	9.9 (15.4)	5.6[0.9-50.3]	8464 (-248)	6.5 (7.5)	4.3 [0.7-25.9]
5	4379	5.9 (6.4)	4.4[0.7-18.9]	4378 (-1)	4.9 (4.2)	3.8 [0.6-15.3]
6	1358	5.3 (3.9)	4.2 [0.7-15.8]	1358 (0)	4.6 (3.4)	3.6 [0.6-14.2]
7	53	4.4 (3.5)	3.4 [1.1-13.1]	53 (0)	3.4 (3.0)	2.3 [0.8-10.5]

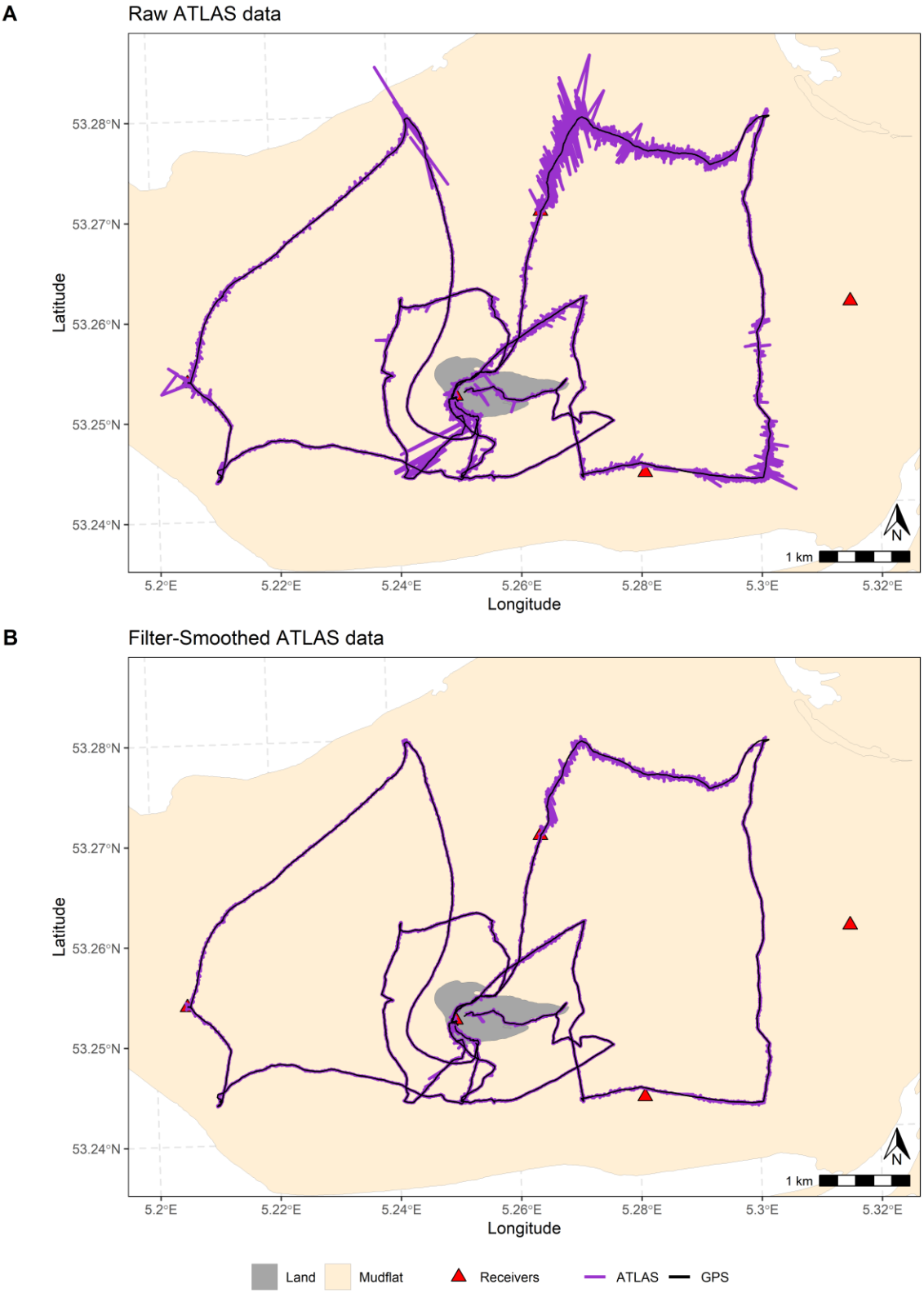
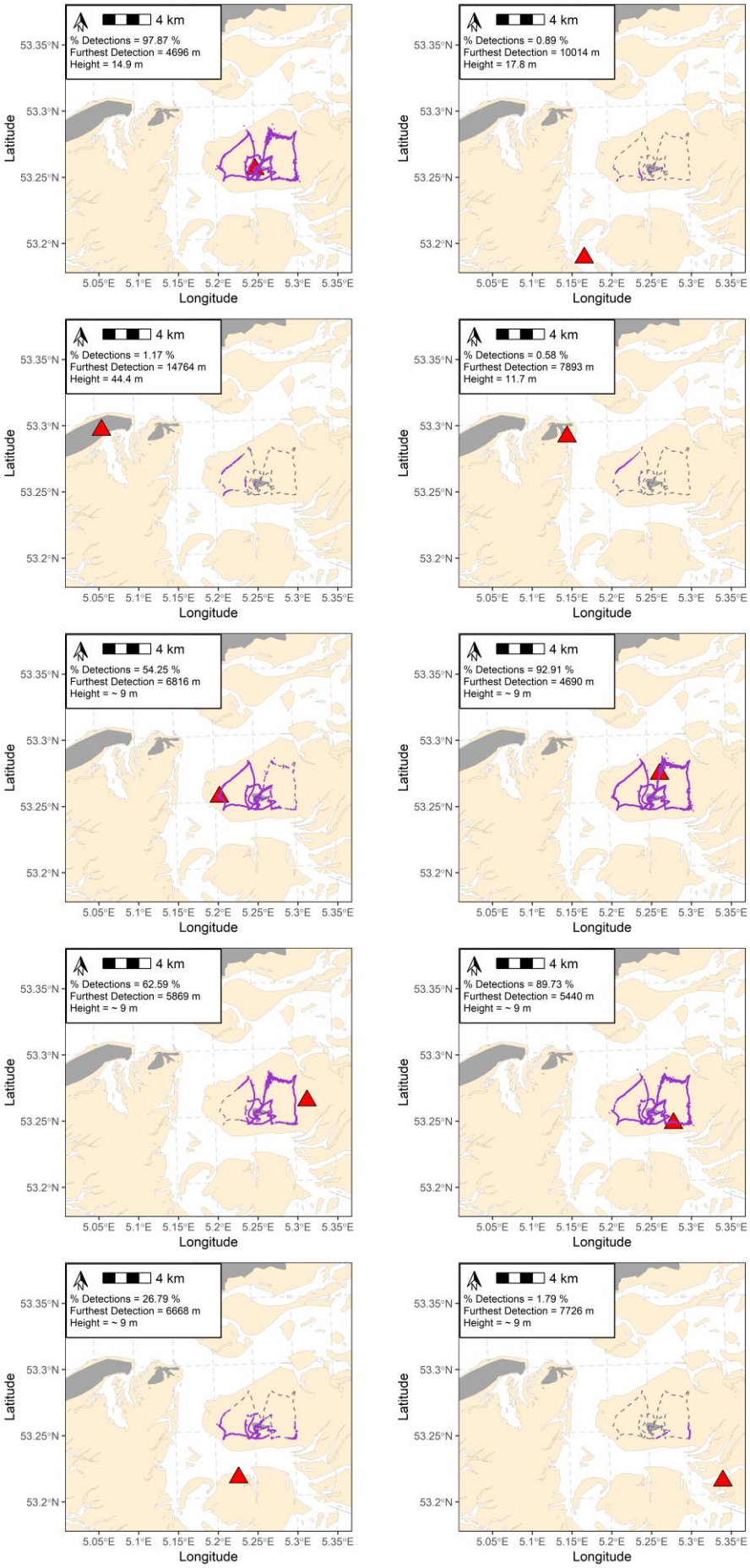


Figure 4. Comparison between ATLAS- (purple line) and GPS- (black line) derived localisations for raw (A) and filter-smoothed (B) data.


4 km
% Detections = 97.87 %
Furthest Detection = 4696 m
Height = 14.9 m
% Detections = 0.89 %
Furthest Detection = 10014 m
Height = 17.8 m
% Detections = 1.17 %
Furthest Detection = 14764 m
Height = 44.4 m
% Detections = 0.58 %
Furthest Detection = 7893 m
Height = 11.7 m
% Detections = 54.25 %
Furthest Detection = 6816 m
Height = ~ 9 m
% Detections = 92.91 %
Furthest Detection = 4690 m
Height = ~ 9 m
% Detections = 62.59 %
Furthest Detection = 5869 m
Height = ~ 9 m
% Detections = 89.73 %
Furthest Detection = 5440 m
Height = ~ 9 m
% Detections = 26.79 %
Furthest Detection = 6668 m
Height = ~ 9 m
% Detections = 1.79 %
Furthest Detection = 7726 m
Height = ~ 9 m
Latitude
53.35°N
53.3°N
53.25°N
53.2°N
Longitude
5.05°E 5.1°E 5.15°E 5.2°E 5.25°E 5.3°E 5.35°E

261

Figure 5. Detections for each of the contributing receiver stations and information on the percentage of total localisations that the receiver detected, the furthest detection from the receiver and the height of the receiver. Purple crosses denote location estimates that each receiver (red triangle) contributed to. The grey dashed line shows the path (tracked by GPS) of the researcher during the tests.

Discussion

We found the ATLAS system is highly comparable to GPS in terms of accuracy. The median difference (in meters) between raw ATLAS-derived location estimates and GPS location estimates was 4.2 m for stationary tags and 5.7 m for moving tags. Accuracy was higher if more receivers detected the tag. However, the tag's location in respect to the receiver array configuration also had a large effect, with less accurate estimates occurring when the tag was on the outskirts or outside the array of receivers. As is common procedure (Gupte et al., 2020), we show that these errors can be mitigated through a simple filter-smoothing process, as is routinely and intensively applied to raw GPS location estimates (Kaplan & Hegarty, 2005). Therefore, ATLAS provides an accurate alternative to GPS for regional systems, and more accurate ATLAS localisations can be achieved through strategic placing of receiver stations.

We found the most extreme errors occurred when the tag outside of the receiver array, matching the results seen in another ATLAS system (Beardsworth, 2020). This is a well-understood phenomenon in TOA systems where error scales as a function of array geometry and location estimates are less reliable outside the array (MacCurdy et al., 2018). Specifically, for the sections of the study that occurred in the most northern part of the mudflat, all detecting receiver stations were located to the South of the tag, outside the core array of receiving stations. While one receiver station was situated to the north of Griend, on Terschelling, 10 km away, this seems to be outside the range of reception, despite another receiver to the West, on Vlieland, detecting the tag 14.8 km away. The range at which receivers can detect transmissions can differ markedly between habitat types and topography, therefore this is highly site dependent (MacCurdy et al., 2009). For instance, detections of an ATLAS

tag have been previously shown to differ over short distances due to the signals being blocked by hills (Beardsworth, 2020). However, the WATLAS system has very few topographical obstacles that limit reception of transmissions by receivers. It is therefore likely that other factors, such as height of the tag and/or receiver play an important role in reception.

Signal detection requires a clear 'line of sight' between the receiver and the tag. Because of the effects of reflections from ground and sea, higher receiver stations can typically continue detecting tags at larger distances than receivers that are closer to the earth's surface (Xia et al., 1993). This may also explain why the highest receiver station (44.4 m high on Vlieland) was able to detect the tag almost 15 km away, but the Terschelling receiver station (35.1 m) was unable to detect the tag 10 km away. While receiver height is important, tag height also affects the reception of a signal. Tags attached to animals in flight can have much larger detection ranges than animals on the ground (Xia et al., 1993); for instance, localisations of Egyptian fruit bats (*Rousettus aegyptiacus*) during flight were based on receiver detections from up to 40 km away in the Hula ATLAS system (Toledo et al., 2020). If flight locations (as opposed to ground locations) are sufficient for a particular study, a sparser array of receivers may be appropriate to maximise coverage of an area. Ground locations can instead be inferred from take-off and landing locations. Similar inferences are made in marine systems, where diving behaviour prevents satellite tracking, thus movement tracks are reconstructed between surfacing events (Hussey et al., 2015). For systems that track ground-dwelling animals, receivers should be positioned <5 km away from the study area as we (with the tag 1.2 m above the ground) found the most successful receivers (>90% of signals detected) were within 5 km from the test locations.

While we did not specifically assess signal strength in this study, this also has a strong influence on the accuracy of a location estimate. Signal strength can be affected by multiple causes. For instance, the height of the receiver's antenna, the height of the tag antenna and the distance between them

influences the strength of the signal at the receiver. Another factor that affects the signal strength is the transmitter power. While the transmitters in ATLAS tags have a power of 10mW, the relatively short tag antenna (which is necessary for use with animal-borne tags) reduces efficiency. Ping duration (8ms) and bandwidth (1MHz) also influence accuracy (Weller-Weiser et al., 2016). However, these values are typical for ATLAS and are optimized for miniature tags. Finally, interference from other transmitters, such as radio remote controls, can degrade the performance of the system. Due to the remoteness of the Wadden sea, there is little interference in the 434MHz band. This is evident from the fact that the gain, moderated by automatic gain control (AGC) at each receiver, is often very high, unlike in heavily populated areas. Nevertheless, this level of interference is site dependent and should be considered when establishing an ATLAS system.

One further element that we found influenced the localisation accuracy of ATLAS was the number of receivers detecting a tag. Tag signals detected by ≥ 4 receivers had a median error of ≤ 5.6 m while signals detected by 3 receiver stations had a median of 10.7 m error. This result may tempt users of ATLAS systems to use the number of receivers that contribute to a location estimate to filter movement data, removing locations that are created with only 3 receivers. Indeed, this has previously been suggested (Weller-Weiser et al., 2016). However, despite ten (out of a potential 26) different receiver stations detecting the tag at various positions on the mudflat, 22.8% of signals were detected by only three receivers. Implementing such a broad filter may be detrimental to the amount of data retained about the animal's movement. Furthermore, while an error of 10.7 m is acceptable in many cases, our simple filter-smoothing process reduced the error of 3-receiver location estimates to 6.3 m. We refer the reader to Gupte et al. (2020) for an in-depth assessment of filtering and smoothing techniques for ATLAS data.

It is important to note again that throughout this study, we based measures of accuracy on GPS location estimates yet GPS itself is susceptible to errors (Hofman et al., 2019). According to its

specification, our particular GPS unit gives location estimates of <10 m error, therefore it is possible that ATLAS could be more or less accurate than this GPS device. For studies with no true location with which to measure accuracy, standard deviation in fixed locations gives an indication of the precision of a system. The standard deviation for 10 of the 16 stationary test sites was under 5 m and thus, apparently similar to GPS (Forin-Wiart et al., 2015; Frair et al., 2010; Tomkiewicz et al., 2010). After filter-smoothing, 12 of the 16 sites had a standard deviation of < 5 m. In these locations, the mean number of receivers detecting the tag signal ranged from 3.8-5.8 but all locations were central in the array, indicating that arrangement of receivers may be more important than concentration of receivers. Even the least accurate test location (Site 2: which was outside the receiver array and detected by only a mean of 3.4 receiver stations), had a standard deviation of 15.1 m after filter-smoothing. Since most environmental covariates are measured at larger scales than this, ATLAS gives an appropriate level of accuracy and precision for many study species.

In summary, we provide evidence for the high accuracy and precision of a relatively novel localising system, ATLAS. ATLAS provides an opportunity to track animals remotely at high spatial and temporal resolution that rivals GPS technology. This system is most useful for regional-scale studies, where animals can be surrounded by an array of receiver stations and is effective even while only 3 receiver stations detect the tag. However, the clear advantages of GPS tracking should not be neglected, namely, its capacity to track animals at much larger scales, and the fact that the researcher is not responsible for installing and maintaining the system's infrastructure (satellites in orbit for GPS, an array of receivers for ATLAS). In the design of an ATLAS system, we suggest that receiver stations are placed as high as possible and surround the study site with a direct line of sight. The density of receivers in an area is also important but depending on the number of receivers available for a study, trade-offs may have to be made between coverage and density of receivers. Considerations should be made according to the height of the tag, with low-ground dwelling species requiring a dense receiver array than species that may fly between places of interest. We note that, unlike military and commercially motivated multipurpose development of GPS, the ATLAS system

was developed and is being applied by multidisciplinary teams of scientists for movement ecology research. We encourage further use of this high-throughput wildlife tracking system, which can provide accurate high-resolution data on the movement of multiple interacting individuals of various species including small ones, at a regional scale, with low costs and for long durations.

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Authors' contributions

CEB and AIB conceived the idea for the manuscript; CEB, EG and AIB collected the data; CEB and EG analysed the data; CEB led the writing of the manuscript; RN and ST developed the ATLAS system and provided support throughout data collection; AIB, BD, AD and FvM built and maintained the WATLAS system and tags, and provided local support throughout data collection; all authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data and relevant code for this research are stored in GitHub: https://github.com/CBeardsworth/watlas_validation and have been archived within the Zenodo repository: https://doi.org/10.5281/zenodo.4527614

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