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The Ornithodolite as a tool to quantify animal space use and habitat selection; a case study with birds diving in tidal waters

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Introduction

Electronic tagging can now be used to provide data on the spatial movements of animals with sub-second temporal resolution (Ropert-Coudert & Wilson 2005). Nonetheless, the size of loggers that provide reasonably high frequency data means that the use of this technology is still limited to relatively large animals (Chittenden et al. 2009; Ropert-Coudert & Wilson 2005; Wilson et al. 1986). There are also ethical considerations associated with the capture, handling and instrumentation of individuals (Wilson & McMahon 2006). Related to this, tags can also affect the behavior of the individual and hence influence the very measurements such devices are designed to make (Elliot 2016; Stothart et al. 2016). Beyond the ethical implications of instrumenting animals, biotelemetry may not be the best tool to address particular study questions. For instance, tagging tends to provide a wealth of information on a relatively small number of individuals, whereas questions such as how animals operate with respect to specific developments may be concerned with the movements of large numbers of individuals, or even different taxa, in a relatively small area. In these cases, tagging is not the ideal methodology particularly given that tagged individuals may not necessarily use the site of interest. In case were they do, estimates of spatial distribution and patterns of resource selection are likely to be based on a low number of individuals, relative to the number that are using the site.

Eulerian, or static measurements, have also been important in quantifying animal locations (Turchin 1998). Like tagging methods, the range and resolution of resulting data varies among the different techniques. Aerial surveys can provide accurate information
on the distribution of individuals over large areas (Camphuysen et al. 2004); however, the costs associated with this technique mean that few surveys tend to be run per study, limiting the ability to monitor changes in space-use. This method also provides point counts rather than movement trajectories. Radar can provide vast, high resolution datasets on space-use relative to a particular location, or series of connected locations (Chapman & Graber 1997; Eastwood 1967; Alerstam 1990). Radar can also be used to derive movement trajectories, however, it is rarely possible to automate the identification of targets or even achieve identification at all (McCann & Bell 2017). The data processing requirements (e.g. to remove signal backscatter, from the movement of non-target objects) are also substantial, although international initiatives such as the European Network for the Radar surveillance of Animal Movement may lead to advances here.

Theodolites have been used in a number of fields (Bailey & Thompson 2006; Piersma et al. 1990) and this approach combines aspects of both Eulerian and Lagrangian methods, as whilst it is place-based, individuals can be identified and, in some cases, selected according to species or behavior. Individuals can also be followed, allowing users to reconstruct movement tracks (Bailey & Thompson 2006). Theodolites are relatively straightforward when it comes to the collection and processing of data (compared to radar data for instance). They can also provide locations with high accuracy and precision when compared to land-based or seagoing surveys using grids to allocate observations to geographic areas. Traditional theodolites measure azimuth and elevation angles which are then used to estimate distance to the target (Tucker & Schmidt-Koenig 1971).
As these systems do not measure distance directly, instead requiring the height of the observer to be known, relative to the target, they can only be used for animals moving on flat substrates, such as animals on the sea surface (although estimates of distance may still become biased by swell height, for instance (Bailey & Thompson 2006)). Other non-invasive static methods like 3D video tracking can yield similar precision with finer temporal resolution than theodolites but these operate across far shorter ranges of up to a few hundred metres (Cavagna et al. 2008; De Margerie et al. 2015; Evangelista et al. 2017).

Theodolites that incorporate a distance measure can be used to estimate a target’s position accurately whether the animal is on the substrate or in flight (Wilson & Wilson 1988; Hedenstrom & Alerstam 1994; Piersma et al. 1990). Various researchers have developed the system further in order to estimate the airspeeds of flying animals. Double theodolite systems were first used to quantify airspeeds using triangulation of horizontal and vertical angles to resolve distance from observer, and combining positional data with measurements of wind speed (Tucker & Schmidt-Koenig 1971). This superseded previous methods where birds were followed by vehicles to estimate ground speed (Michener & Walcott 1967). A further modification was proposed by Pennycuick (1982), who added an anemometer and a coincidence rangefinder into a portable, single system, in order to track objects in flight and estimate their airspeed. This system is now based on a laser rangefinder incorporated in a pair of Vector 21 binoculars (Pennycuick et al. 2013), which builds on the optical principles used to measure distances directly and provides improved accuracy and precision. The system was therefore developed
specifically to quantify airspeed in flying birds and it is only very recently that it has been used to examine animal distributions (Hedenström & Åkesson 2016; Shepard et al. 2016). We suggest that there are potentially broad ecological applications of this technique, which have yet to be fully realised. We note, however, that the incorporation of the laser range-finder means that it is not possible to get returns from most marine mammals in the water, as the system cannot get a return from the water surface or the smooth, water-covered surfaces of most cetaceans.

In this study, we use the Ornithodolite to examine the factors affecting the fine-scale space-use of seabirds operating in a highly dynamic tidal environment. Data were collected in Ramsey Sound, Pembrokeshire, UK, where a tidal turbine is currently installed but non-operational. We use hydrodynamic numerical model simulations of current flows in the Sound to investigate the conditions that birds select during foraging. The utility and limitations of the equipment for the wider community of movement ecologists are also examined, specifically through the assessment of the measurement error and whether maximal detection distances vary according to body size. The latter was investigated using a large database of 4284 positional fixes taken from birds during migration.

**Methods**

*System performance*

The workings of the Ornithodolite have been described in detail elsewhere, in terms of the use of this equipment for the measurement of animal location and airspeed
(Pennycuick et al. 2013), hence only a summary will be given here. The ‘USMC vector 21’ is a pair of binoculars with an inbuilt laser rangefinder, digital compass (giving azimuth angle), and inclinometer, providing inclination angle to the nearest 1/6400th of a radian (Vectronix™ 2004). The user gains co-ordinates of a target by pressing and releasing two buttons when the target is between the cross-hairs in the view finder and positions are sent to a laptop via a cable. In this study a simple programme was written in Visual Basic (Microsoft) to enable users to append information including species and behavior to each set of co-ordinates.

The Vector measures distances from 5 m to over 10 km with a resolution of 0.5 m (Vectronix™ 2004). The error associated with distance measurement must be ascertained by the user. We therefore used the following protocol to quantify this: locations were taken to a fixed target, in this instance an area next to a prominent ledge, approximately 1 m² situated on Mumbles boat house (51°34′12.0″N 3°58′32.4″W) in Swansea Bay. Fixes were taken at increasing distances from 50 m to 5 km, with 10 fixes being taken at each of 12 distance intervals.

The ability to get returns from the laser (and hence record the target’s co-ordinates) is related to the target characteristics (i.e. size, color etc.) and the experience of the observer. In order to examine how maximum distance varied in relation to body size, multiple, sequential, locations of birds migrating past Ottenby observatory, southern Sweden, were collected from 2012 to 2017. The methods are detailed in full by Hedenström and Åkesson (2016). Each series of locations from an individual bird is
hereafter referred to as a ‘run’. The furthest distance measurement per run was selected for further analysis. We note that observers were not aiming to get returns from the furthest targets they could observe and the resulting distances are therefore only an indication of those that could be attained. Locations were obtained by experienced ornithologists, with one observer operating the Ornithodolite and another identifying birds using a telescope, although it is possible for a single person to operate the system, using a telescope to identify distant targets where necessary. This approach thus provides an insight into the distances that can be obtained where experience in bird identification is not a limiting factor.

Data analysis

Linear regressions were used to assess whether the maximum distances were affected by the mass and the wingspan of the target. As mass and wingspan are related, the residual variation from the allometric prediction of wingspan was used in the model. Specifically, the predicted wingspan was estimated as mass$^{0.39}$ for each of the 151 study species (Pennycuick 2008) and the difference between actual and predicted wingspans were used in the model. Models were constructed to assess whether the maximum distance was predicted by models containing either body mass, as a single explanatory variable, or mass and residual wingspan. Models were compared using their AIC scores which enabled us to rank them based on their statistical quality to ensure the correct model was selected. Distance and body mass were natural log transformed and regressions were run in base R (R core group 2017) and plotted using the package ‘ggplot2’ (Wickham 2009).
**Space use within Ramsey Sound**

Data collection took place in Ramsey Sound from a vantage point based near St Justinian 51°52'42.4"N 5°18'38.4"W, which provided views of the entire Sound. Data collection began on the 24th April 2017, with a total of 35 visits made to site. Surveys were conducted in periods of calm and dry weather, with good visibility where the horizon remained visible and for sea states of ≤ 2 on the Beaufort scale (corresponding to wind speeds of ~ 3m s⁻¹). The locations of seabirds within the Sound were recorded across the entire tidal cycle using the Ornithodolite. A full scan of the area was completed every 15 minutes for a minimum session length of 4 hours and the tidal state was noted (flood, ebb or slack water which occurred 2.5 hours after high water and low water respectively). Locations were recorded for all birds observed within a scan, with birds being identified to species level distance permitting. Group size and behavior were also recorded (see supplementary information). If foraging behavior was observed, individuals were followed after the main scan in order to take positional fixes at the start and end points of individual dives. Attention was taken to ensure the entire Sound was searched systematically during each 15 minute scan to reduce any spatial bias in sightings.

Azimuth, elevation angle and distance data were subsequently converted to latitude and longitude and then used to identify areas of high general use within the Sound and areas specifically associated with foraging. Distributions were plotted using fixed kernel density estimation (KDE) in the statistical analysis software R using the packages ‘ggmap’
(Khale and Wickham 2016) and ‘MASS’ (Ripley et al. 2017). An estimate of all-encompassing foraging range of great cormorants (*Phalacrocorax carbo*) (hereafter cormorant), the species diving most frequently, was provided by the 90% KDE contour (as the most frequent diving species).

To investigate how cormorants dived in relation to current vectors, the horizontal distance covered between the start and end points of a dive was calculated using the Haversine formula (Jenness 2011). The bearing was also taken, assuming the bird followed a straight line from its start to end position (Jenness 2011). Bearings were visualised using Oriana, which was also used to perform a Rayleigh’s Z test (Kovach 2011).

The Telemac-2D (v7r2) open-source hydrodynamic ocean modelling software suite was used to quantify spatial and temporal variations in current speeds (m s\(^{-1}\)), turbulent energy (J kg\(^{-1}\)) and depth (m) within Ramsay Sound spanning the entire study period. This model solves the depth integrated Saint-Venant free surface flow equations derived from the full Reynolds Averaged Navier Stokes (RANS) equations for momentum and continuity (Hervouet 2007). The finite element unstructured mesh varies from coarse (approximately 10 km at model boundaries) to fine (approximately 50 m around the North Wales coast) for a domain encompassing the Irish Sea (50°N to 56°N, 8°W to 3°W). Values of hydrodynamic conditions were provided at approximately 300 m and 10 minute resolution in Ramsay Sound. Model simulations are forced at domain boundaries with tidal harmonic constituents only and no other influences to dynamics are considered. However, in shallow coastal regions were the water column remains well
mixed, vertically homogenous velocities can be expected above the bottom boundary layer. Therefore depth-averaged approximations provide good estimation of flow characteristics. Full details of numerical model set up, calibration and validation are detailed elsewhere (Piano et al. 2017; Piano et al. 2015).

To facilitate comparisons with the spatial and temporal distributions of dives, values of hydrodynamic conditions were transposed onto an orthogonal grid of 100 m resolution using kriging interpolation. Kriging was performed using the ‘automap’ package in R (Hiemstra et al. 2009). The spatial distribution of dives were compared to that of mean current speeds in Ramsay Sound. As tidal environments are broadly divisible into areas of comparatively fast and slow mean current speeds (Benjamins et al. 2015, Waggitt et al. 2017), such comparisons provide useful insights into general habitat-use. Furthermore, as tidal stream turbines generally occupy areas of faster mean current speeds (Fraenkel 2006), these comparisons would also identify the likelihood of interactions between diving birds and installations (Waggitt & Scott 2014). The temporal distribution of dives across tidal states (ebb-flood) within persistently used areas were examined in relation to current speeds, turbulent energy and depth. These comparisons would identify the hydrodynamic conditions experienced by individuals during dives. Values of hydrodynamic conditions were extracted using the mean coordinates of dives, which identified persistently used areas due to the aggregated distribution of recorded dives.

**Results**
**System performance**

Variance in distance measurements from fixes taken in Swansea Bay, increased with distance (Figure 1) but was low overall, being ± 0.001% of the overall distance, which is less than that suggested by the user manual (Vectronix™ 2004).

Over 4200 tracks were recorded for migrant birds in Sweden. The smallest species recorded was a goldcrest (*Regulus regulus*) weighing 5.5 g, and the maximum distance achieved for this species was 913 m. A whooper swan (*Cygnus cygnus*) with a respective weight of 8.75 Kg, was recorded 2742 m from the observer and the largest overall distance recorded was 5498 m, obtained from a migrating flock of barnacle geese (*Branta leucopsis)*.

Maximum distance recorded was best explained by a model including only the positive effect of the body mass of the recorded bird (beta = 0.12, F=120.9, df=149, p<0.001, adj $R^2 = 0.44$), with a model including also the residual wingspan receiving equivalent support ($\Delta$AIC < 2) and with a low effect size and non-significant relationship of the latter (beta < 0.001, p = 0.4).

**Space-use within Ramsey Sound**

Six seabird species were recorded in 140 hours of survey effort: common guillemot (*Uria aalge*), European shag (*Phalacrocorax aristotelis*), Northern gannet (*Morus bassanus*), great black-backed gull (*Larus marinus*), lesser black-backed gull (*Larus argentatus*) and the great cormorant (Table 1). The majority of all locations were of birds carrying out
water based behaviors e.g. loafing or diving, flight fixes were discarded for further analyses. The cormorant was the only species with > 10 dives recorded across all surveys (n = 56). Birds avoided the main channel where mean current speeds were > 1.5 m s\(^{-1}\), preferring to loaf and forage in relatively slack waters, where mean current speeds were < 0.5 m s\(^{-1}\) (Figure 3), occupying less than 40 % of the total area in the Sound available.

Cormorants foraged close to the mainland (0.1 - 0.7 km from the vantage point) in a highly restricted area of < 400 m\(^2\), which is characterised by low current speeds (min = 0.29 m s\(^{-1}\), max = 0.81 ms\(^{-1}\), mean = 0.48 ms\(^{-1}\)) and water depths of 24.5 - 26 m.

Over 80% of cormorant dives occurred 4 hours after high water or later, when tidal height was rising (Figure 4). These dive times also corresponded to periods of low current speed, relative to speeds in this location at other stages of the cycle. In fact 40 % of the dives occurred in current speeds of < 0.4 m s\(^{-1}\), when the current speed varied from ~ 0.2 - 1.0 m s\(^{-1}\) across the tidal cycle (Figure 4). Dive times also coincided with periods of falling turbulence, with dives occurring when the turbulence was < 0.02 J kg\(^{-1}\) (with it increasing up to a mean of 0.04 J kg\(^{-1}\)).

The mean axial orientation of cormorant dives (mean=168.8 ± 8.3°) was into the flow of the current (Figure 5) and was not uniformly distributed (n= 40, Rayleigh's Z 5.503, p< 0.005). Birds covered short distances during dives (mean = 44.5 m, median = 17.8 m, max = 261 m, min = 0.6 m) suggesting that birds are most likely to be orientating into the flow on the majority of dives and being drifted backwards through the motion of the current,
effectively producing a bearing that is coincident with the current vector.

**Discussion**

**System performance**

Our results demonstrate how the Vector Ornithodolite can be used to investigate mechanisms underpinning habitat selection at fine-scales. We show that the system can be used to provide positional data for birds moving within a radius of > 5 km from an observer, with measurement error of ≤ 4 m within this distance range, in accordance with and exceeding the indications of the Ornithodolite. The measurement error is therefore less than that generally accepted for GPS data, which is estimated to be in the range of 3 - 28 m (Frair et al. 2004), with also modern animal-borne GPS systems seldom exceeding an accuracy < 5 m. The spatial error in tagging technology can lead to the misrepresentation of behaviors in a scale-dependent manner (Browning et al. 2017; Costa et al. 2010). In contrast, the fact that the Ornithodolite is operated by a user means that animal locations can be coded according to behavior (as well as species, age, and other factors that may be of interest), with the downside being that it has relatively intensive requirements when it comes to survey effort.

The “maximum” distance recorded to birds migrating past the Swedish coast increased with bird body mass, which most likely reflects a combination of two factors. Firstly, if we assume that birds of all sizes were equally likely to migrate at any distance from the coast (and consequentially the observer), our results suggest that larger birds are detected more readily at greater distances, which could lead to some sampling bias in
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studies recording locations of smaller species. Beyond this, experiences during data collection also suggest that it can be difficult to obtain a fix from species at the smaller end of the size spectrum, even when they have been detected with optics and are within range. Nonetheless, a location was obtained from the smallest species (5.5 g) when it was ~ 1 km from the observer and there were several instances where birds weighing 50 - 100 g were recorded ~ 2 km away, demonstrating that small birds (including those too small to be tagged) can be detected and recorded at substantial distances.

Spatial bias is well documented for land-based surveys, which use distance bands or grid systems for assessing the locations of birds foraging in near-shore tidal habitats (Waggitt et al. 2014; Waggitt et al. 2016a), with birds being less likely to be detected if they forage further from the shore. However, it seems unlikely that this has affected the results in the present study, given that the full length of Ramsey Sound (1.9 km) is less than the distance over which large birds such as seabirds can be detected and recorded, and that surveys were conducted in periods of low swell height. Therefore, while some of the general limitations of shore-based surveys still apply to the use of the Ornithodolite in a general sense, with both being based on the use of a tele-scope and binoculars to scan for birds, we consider it unlikely that we have underestimated the usage of fast flowing currents that lie further from the coastlines.

Like GPS tagging and land-based surveys, the Ornithodolite can be affected by environmental conditions. The probability of detecting a target or getting a return with the Ornithodolite may be influenced by sea state and surface conditions (although these
factors were not investigated directly here), false returns can be given from fog or cloud, although spurious returns are easy to identify and remove, and the system can also be affected by high winds that make the equipment unsteady to hold and difficult to obtain a fix on the target bird.

Many studies have discussed the potential impacts of bird capture and recapture and the deleterious effects of tags (Bennisson et al. 2017; Calvo & Furness 1992; Götmark 1992; Phillips et al. 2003; Vandenabeele et al. 2011; Wilson & Vandenabeele 2012). The Ornithodolite has advantages here, as it does not involve marking animals and in fact observers can be placed at a vantage point away from breeding colonies, thereby reducing disturbance. The operational range of the system also far exceeds predicted flushing distances, which can be a factor in other surveys, including boat-based work (Schwemmer et al. 2011). Finally, the Ornithodolite uses a laser tachometer to measure distance. It seems unlikely that this could have adverse effects on target animals, as medical literature citing retinal injuries from handheld laser devices indicates that risk of injury is high if the primary light source is in the ‘green’ end of the light spectrum and if pointed directly at the eye from less than one metre away (Luttrull & Hallisey 1999; Mainster et al. 2004; Wyrsch & Baenninger 2010).

**Habitat Selection**

Relatively few studies have quantified habitat use at very fine scales in seabirds (Holm & Burger 2002; Waggett et al. 2016a; Waggett et al. 2016b; Zamon 2003). Here we show that cormorants were highly selective in terms of both the foraging area and the time in
the tidal cycle when they chose to dive. Ramsey Sound experiences extreme tidal variation with current speeds $> 3.5 \text{ m s}^{-1}$ and strong eddy formation over the rocky reefs. Cormorants dived in a highly localised area of the Sound, showing a general avoidance of high current speeds in the main channel and areas of high turbulence caused by rocky reefs at ‘the Bitches’ and ‘Bishop’s and Clerks’. While we did not test whether current speed was the ultimate driver of space-use, it seems likely that birds were responding to low current speed, prey availability, or a combination of both these factors. This follows from the observation that birds were orientating into the current during their dives, as has been hypothesised by previous studies (Heath & Gilchrist 2010), and travelling short distances. This pattern of diving repeatedly in the same place, suggests that cormorants are more likely to be foraging mid-water, as the rate at which benthic prey would be replenished by the changing tide would be negligible (Rahel 1988; Schneider & Piatt 1986). Furthermore, the sea bed in Ramsey Sound consists of gravel and hard rock which is less suitable for benthic fish species (Fischer 2000). It therefore seems likely that cormorants were targeting shoaling fish, in highly specific areas of the Sound.

Pelagic fish tend to shoal in areas of minimal water turbulence where current speeds are relatively low (Cury & Roy, 1989; Fréon & Misund 1999), which generally accords with the conditions that cormorants selected. As stated above, the area where birds were diving was characterised by a relatively low current speed compared to the main channel. Within this, and over the changing conditions of the tidal cycle, birds showed less selectivity of current speed, diving over a reasonably wide range of available speeds, up to $\sim 0.75 \text{ m s}^{-1}$, only appearing to avoid the strongest currents of $\sim 1 \text{ m s}^{-1}$. What was
striking, however, was the tendency to dive on the flood tide, which appeared to be strongly related to turbulence levels, with birds selecting times of low turbulence.

Overall therefore, when and where cormorants dive appears to be influenced by a hierarchy of factors operating in space and time. In contrast to these findings, Holm and Burger (2002) showed that pelagic cormorants (*Phalacrocorax pelagicus*) showed no significant response to tidal height or current strength. In fact, individuals were more likely to dive in areas of high turbulence within eddies (although values of current speed and turbulence coefficients are not known) (Sealy 1975). Whilst Waggitt *et al.* (2017) found that European shags *Phalacrocorax aristotelis* generally associated with areas of slow mean currents among five locations in Scotland, there were exceptions to this rule. These differences may well be driven by patterns of prey availability, which can vary between sites and predator species. Nevertheless, this study agrees with a growing consensus that associations with areas of fast mean currents are comparatively rare among UK cormorant species (*Waggitt et al.* 2017).

The need for detailed information on foraging patterns, including how tidal stream features contribute to foraging success and the direction of travel in relation to currents, has been highlighted in a recent review by Benjamins *et al.* (2015), as these factors will ultimately influence the likelihood of animals exploiting particular hydrodynamic features. Such associations are important in advancing our understanding of the species and sites where collisions between seabirds and tidal turbines are most likely (Benjamins *et al.*. 2015; Waggitt & Scott 2014). Overall, there are a number of indicators that the
tidal turbine may represent a relatively low risk to seabirds in Ramsey Sound. The Sound appears to be used by relatively few seabirds, at least during the course of the sampling in this study, despite the fact that around 2,000 pairs of auks breed on Ramsey (Mitchell et al. 2004). Furthermore, seabirds tended not to use the main channel, which has the greatest current speeds, making it most suitable for marine energy (ME) installations (Mueller & Wallace 2008; Pelc & Fujita 2002; Piano et al. 2017).

Cormorants have previously been identified as one of the species most at risk from tidal turbine developments (Furness et al. 2012; Langton et al. 2011) due to their high usage of tidal races for foraging and their propensity to forage on benthic prey (Furness et al. 2012; Garthe & Hüppop 2004). Cormorants were the birds most commonly diving in Ramsey Sound, despite the fact that no cormorants are recorded as breeding on Ramsey and the nearest sizeable colony (Thorn Island, 32 pairs) is located 25 km away (Mitchell et al. 2004). Therefore the cormorants observed in our study were likely to be non-breeding individuals or those choosing to forage some distance away from the main colony. These individuals may be exposed to lower risk of collision with tidal turbines than would have been predicted based on previous studies, due to their tendency not only to forage in areas of low current strength, but also to cover far less distance than is typical of cormorants diving in other areas (Holm & Burger, 2002; Schneider & Platt 1986). Finally, if these birds are avoiding areas of high turbulence, then this would also tend to keep them away from operational turbines, which will produce a turbulent wake (Chen et al. 2015). However, further research is required to ascertain whether
cormorants show a general avoidance of turbulence, or whether this represents a site, or individual-specific phenomenon.

In conclusion, we suggest that the Ornithodolite is a potentially valuable addition to the armoury of tools being used to quantify animal responses to specific, small-scale anthropogenic impacts, such as renewable energy devices. The system provides 3-d coordinates within a radius of several kilometres with a measurement error that is lower than many GPS tags. Though the initial start-up costs for the Ornithodolite are relatively high ($18900), there is no requirement to pay data subscriptions over the lifetime of the product or recover any technology from animals to access data. The variety and quantity of data that can be collected mean that it is likely to prove cost effective in the longer term, particularly when compared to animal-borne tags, with GPS tags costing around $70 - $800 depending on the method of data transmission and the hardware itself (Hebblewhite et al. 2007). The system itself has relatively low training requirements and simple post-processing of the resulting data, but above all, it represents a method of tracking animals that has little to no ethical implications for the target animals. Finally, the ability to track even the smallest passerines means that it opens up opportunities to assess how a wide range of animals may respond to developments on land, as well as at sea, from patterns of land use to the installation of wind farms (Hedenström & Alerstam 1994; Piersma et al. 1990).
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Table 1. The number of individual seabird locations recorded with the Ornithodolite in Ramsey Sound. Locations are given for behaviors where birds were on the water surface (n=218 positional fixes).

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<td>Cormorant</td>
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Figure legends

Figure 1. The residual variation of range measurements as a function of distance to a fixed, 1m² target area as measured by the Ornithodolite (n = 120 fixes, 10 fixes per distance interval).

Figure 2. The maximum range of avian targets as measured by the Ornithodolite as a function of species body mass.

Figure 3. Kernel density contours showing distributions for i) all seabird species observed either loafing or diving and ii) all cormorant dives. Both datasets are plotted against mean horizontal current speed for all survey days in Ramsey Sound.

Figure 4. The times when cormorants were diving are given in relation to i) tidal height, ii) current strength and iii) turbulence, as modelled using the hydrodynamic model. Each red line represents a 15 minute interval in which a minimum of one dive occurred.

Figure 5. i) Dive bearings for cormorants foraging in Ramsey Sound in relation to the mean current direction for flood tides. The strategy of orientating into the flow resulted in birds travelling relatively low horizontal distances during dives as displayed in ii).
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214x120mm (150 x 150 DPI)
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154x74mm (150 x 150 DPI)