Monitoring Movement Patterns in Choughs

Jessica Stevens

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Abstract

During soft-release reintroductions, biotelemetry devices are often used to track the movement patterns of released individuals. Very high frequency (VHF) and Global Positioning System (GPS) are commonly used telemetry methods, providing accurate locations. An alternative is dead-reckoning, providing high-resolution movement paths from heading and speed measurements, showing fine-scale changes that VHF may not identify. Errors in speed estimation can accumulate, however, producing wide error margins in flight distances and locations. I assess the utility of both techniques in relation to the release of red-billed choughs (*Pyrrhocorax pyrrhocorax*) on Jersey, UK. First, I use VHF locations to examine dispersal and habitat selection. I then go on to consider the potential of dead-reckoning for future monitoring, by examining the main determinants of error in flight distance and bearing in a similar-sized bird. The reintroduced choughs undertook small movements close to the release site, with individuals travelling as a flock, and dispersal distance showing no clear increase through time. Coastal grassland was the most used habitat, despite low availability, raising the possibility that dispersal may be limited by a lack of suitable habitat. The chough's relatively short flight distances and tendency to return to a verifiable location, mean that dead-reckoning could potentially work well as a method to reconstruct their movement paths. However, drift was influenced by flight height, tailwind support and tortuosity. The effect of even low wind speeds on drift shown here suggests this would likely have an even greater influence in locations with higher wind speeds, such as Jersey. Ultimately, the use of multiple low-power telemetry systems could prove powerful, with corrected dead-reckoning providing new insight on the movement frequency, distances and paths as well as habitat selection, that could better inform conservation policy.

Declarations

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed............[redacted]...

Date.........................30/09/2022...

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. A bibliography is appended.

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I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

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Abbreviations

DD	Daily Diary
DDMT	Daily Diary Multiple Trace
DI	Dynamic Interaction
DR	Dead-Reckoning
GPS	Global Positing System
HWC	Headwind Component
IAB	Interaction of *A* and *B*
ID	Identification
RFID	Radio-Frequency Identification
SI	Spatial Interaction
VeDBA	Vectorial Dynamic Body Acceleration
VHF	Very High Frequency

Introduction

Soft-release programmes are a method of reintroduction that involve the gradual transition of captive animals into the wild through supportive measures such as supplementary feeding or predator recognition training (De Milliano *et al.,* 2016; Fernandez *et al.,* 2017; Tetzlaff *et al.,* 2019). A common technique during soft-release reintroductions is to have a period of acclimatisation in which individuals are temporarily confined to an enclosure at the release site, in order that they may adjust to the environmental conditions before release (Liu *et al.,* 2016; Knox *et al.,* 2017; Tetzlaff *et al.,* 2020). These enclosures often remain available to the individuals after release, during a period of extended acclimatisation, before gaining true independence (Blythe *et al.,* 2015). Soft-release reintroductions are widespread and form an invaluable part of many conservation management programmes (Gasparini-Morato *et al.,* 2021; Wemer *et al.,* 2022), including, famously, the reintroduction of grey wolves (*Canis lupus*) into Yellowstone National Park (Smith *et al.,* 2003; Bradley *et al.,* 2005).

An alternative to soft-release is hard-release, whereby individuals are released to their new environment without a period of accustomisation, prior training or post-release support (Richardson *et al*., 2015; Sasmal *et al.,* 2015). This technique is sometimes adopted where resources are limited as soft-release can extend over prolonged periods of time and require substantial resources, leading to considerable expense (Vieira *et al.,* 2015; Radzio *et al*., 2019). Despite the additional resources required for soft-release, most agree it is the preferred reintroduction method (Liu *et al.,* 2016; Nagata and Yamagishi, 2016) as it has proven to incur lower rates of mortality post-release due to greater resource availability and less exposure to potential threats, such as road collisions (De Milliano *et al.,* 2016; DeGregorio *et al.,* 2020).

Animal movements around and away from the release site are of critical importance in establishing the ability of released individuals to forage and avoid threats (Weise *et al.,* 2015; Cain *et al.,* 2018). The different release strategies are often characterised by different movement patterns: hard-releases often see large movements away from the release site (Swaisgood, 2010; Jung and Larter, 2017); soft-releases, in contrast, are characterised by small movements relatively close to the release site or supplementary feeding station (Attum and Cutshall, 2015; Resende *et al.,* 2021). De

Milliano *et al.* (2016) reported that, while soft-released individuals had a shorter dispersal distance, there was no detectable difference between hard- and soft-released individuals in habitat selection.

The ability to resolve movement radius, along with other more detailed movement and behavioural parameters depend on the way that movement is monitored. Animal movement is sometimes monitored through the use of camera traps for a points-based sampling system as an inexpensive, non-invasive method for determining dispersal, abundance estimation and habitat selection (Sukumal *et al.,* 2017; Sollmann, 2018; Bandyopadhyay *et al.,* 2022). Improvements in remote camera technology in recent decades has seen a marked increase in the use of camera traps for wildlife monitoring (Young *et al.,* 2018; Gilbert *et al.,* 2021), particularly for density estimates (Broadley *et al.,* 2019). Palencia *et al.* (2019) commented on how camera traps should be used in tandem with telemetry tags for monitoring movement paths and associated patterns of behaviour, as neither one individually provides sufficient information. Despite this, telemetry tags remain the most common method for tracking movements, especially for reintroduction programmes (Wilson *et al.,* 2015; Taylor *et al.,* 2017).

A common tracking method is radio telemetry or Very High Frequency (VHF) tags (Baeumker *et al.,* 2017; Desrochers *et al*., 2018). These were developed in the late 1950’s and are still widely used today as an effective, inexpensive method for tracking animal movement (Mech, 1980; Bayram *et al.,* 2016). A more recent method, also widely used, is Global Positioning System (GPS) tags, as these can give accurate location estimates within meters (Weiser *et al.,* 2016; Ironside *et al.,* 2017). Other methods include Argos Doppler (also known as Platform Transmitter Terminals) and acoustic telemetry. Argos is a satellite tracking system most commonly used for free-ranging animals, but is less accurate, giving locations within kilometres (Christin *et al.,* 2015; Lowther *et al.,* 2015; Hays *et al*., 2021). For this reason, VHF and GPS are regarded as preferred options, especially for reintroductions (Trayford and Farmer, 2012; Thomson *et al.,* 2017; Watts *et al.,* 2017). Acoustic telemetry is a rapidly developing method frequently used for tracking in underwater environments (Matley *et al.,* 2021; Reubens *et al.,* 2021) with worldwide hydrophone receiver networks (Hellström *et al.,* 2022), as other telemetry methods, such as VHF and GPS, are less effective in this medium (Teixeira *et al.,* 2015; Francisco *et al.,* 2020).

VHF tags function by emitting a high-frequency radio signal which can be tracked using a receiver and directional antenna, allowing the person to locate and observe the tagged individual (Fisher *et al.,* 2021; Nechaev and Peshkov, 2022). Triangulation, using three or more azimuths to estimate the animal's location, is often used where obstacles, such as terrain, inhibit direct observation (Hui *et al.,* 2021; Van der Meer and Dullemont, 2021). Regardless, VHF is commonly used for tracking as the lightweight tags mean animals may be equipped without substantial hindrance due to the added weight (Duda *et al.,* 2018; Smith and Pinter-Wollman, 2021). Despite the benefits associated with VHF, many choose to use other telemetry techniques as VHF is very labour-intensive, requiring persons to physically track tagged individuals throughout the deployment period, which presents a particular challenge with fast-moving animals (Desrochers *et al.,* 2018; Ross *et al.,* 2022; Saunders *et al.,* 2022). Transmitter signal may also be affected by the topography (Bassey *et al.,* 2019). Faithpraise and Bassey (2022) observed signal loss in areas of steep elevation due to multipath interference, thus restricting the ability to locate tracked animals. This is best mitigated by searching for signals from elevated locations, such as hill-tops (Nechaev *et al.,* 2021).

Developed in the early 1990's, GPS tags calculate an individual's location using a network of satellites to estimate position (Aslinezhad *et al.,* 2020; Haddad *et al.,* 2020), providing high-resolution, accurate locations with little labour (Smith *et al*., 2018; Namazi *et al.,* 2021). In order to gain high-resolution data over a long time period, a large battery is required (Morais *et al*., 2018; Hart *et al.,* 2020). GPS tags that record multiple fixes a day and last for weeks tend to have a mass around 20 g, which limits the birds that they can be deployed on as additional artificial mass deteriorates flight performance, increasing energy consumption (Portugal and White, 2022). Tomotani *et al*. (2019) also reported that larger tags resulted in slower flight speeds due to the aerodynamic drag of the device. Recently, the Atlas system has been developed (Beardsworth, 2022) that provides high-resolution tracks from miniature tags, however, this requires a costly antenna system. Many studies have commented on financial cost of GPS, noting that data collection, and therefore the conclusions drawn, may be limited through the use of only a few devices as wildlife research often works on a restricted budget (Wild *et al.,* 2022). Despite this, GPS is widely used for tracking animal movement (McGranahan *et al.,* 2018; Seidel *et al.,* 2018; Aurisano *et al.,* 2019), with many reintroduction programmes relying on GPS tags to determine survival of released individuals (Robinson *et al.,* 2021; Efrat *et al.,* 2022; Sievert et al., 2022; Skorupski *et al.,* 2022).

An alternative to these telemetry methods for analysing movement patterns is dead-reckoning (DR). DR consecutively integrates heading and speed estimates to reconstruct movement paths from a known start location, and can include pressure data to reconstruct paths in 3-D space for flying and diving species (Gunner *et al*., 2021a). This has recently been shown to be a powerful method of reconstructing fine-scale movements using lightweight tags (Gunner *et al.,* 2021a; Gunner *et al.,* 2021b), although this technique has mainly been used for terrestrial locomotion due to the particular challenges of dead-reckoning flight paths.

Flight is a fast method of travel. Errors in the estimation of flight speed can quickly accumulate to produce flight distances with a wide margin of error. Furthermore, wind speeds can be a substantial fraction of bird’s airspeeds and birds must compensate by selecting a heading that accounts for the wind vector (Goto *et al.,* 2017; Aurbach *et al.,* 2018; Bradarić *et al.,* 2020). As a result, the flight heading can be substantially different from the ground-track (that which the bird actually flies above ground). Despite this, initial analyses on tropicbirds and condors showed that tracks can be reconstructed well, when drift is corrected by GPS fixes every few minutes (Williams *et al.,* 2020; Gunner *et al.,* 2021b). For animals that undertake limited flight, and that return to a known location frequently, providing regular opportunities to correct the flight path, it may therefore be possible to obtain useful information on flight direction and distance using DR.

Here, these telemetry methods are examined in the context of a soft-release with the aim of assessing the movements and habitat use of reintroduced red-billed choughs (*Pyrrhocorax pyrrhocorax*) using biotelemetry. These birds are medium-sized (average body mass 207–375 g; Madge, 2020), providing a strong incentive for the use of lightweight telemetry devices to study their movements post-release. Red-billed choughs were reintroduced to Jersey, Channel Islands, UK, by Durrell Wildlife Conservation Trust in order to establish a free-ranging population and support coastal farmland habitat restoration (Corry, 2012). Choughs became extinct on Jersey around 1900 due to human persecution and a change in agricultural practice causing severe habitat loss (Maxwell and Corry, 2013; Corry *et al.,* 2021). In 2013, these birds were reintroduced equipped with VHF tags through soft-release. The specific objectives of this study are to (i) use this VHF telemetry data to quantify movement metrics and habitat selection post-release, and (ii) investigate the potential of dead-reckoning for the future monitoring of flight paths by examining the main determinants of error in flight distance and bearing.

Methods

Study Site

Jersey (49.205° N, -2.194° E) is the largest island in the Channel Islands archipelago at 120 km^2 (Statistics Jersey, 2022; Fig. 1). The majority (52%) of land area on Jersey is cultivated predominantly for the growing of crops and dairy farming; the built environment accounts for 24% land cover, while the natural environment, for example, woodland, grassland and dunes, accounts for only 18% of land cover (Statistics Jersey, 2022). The chough release site was located in the northern parish of St John, 0.6 km from the northern headland of Sorel Point (Fig. 1), as feasibility studies determined the immediate area around the release site (Corry, 2012), consisting of agricultural land, coastal grassland and open bracken, was the most suitable for red-billed choughs as these are known to be their preferred habitats (Kerbiriou *et al.,* 2006; Kerbiriou and Julliard, 2007; Burgess *et al*., 2011; Johnstone *et al.,* 2011).

Figure 1: Jersey, Channel Islands, UK, with marked release site (red). Map data: Google Satellite (2022).

VHF Data Collection

Between 2013 and 2018, red-billed choughs were reintroduced to Jersey by Durrell Wildlife Conservation Trust through seven soft-releases (Table 1). A total of 43 birds were reintroduced that were artificially incubated and hand reared at Jersey Zoo, supplemented by subadults from Paradise Park, Cornwall, UK. The release groups mimicked normal family group size for choughs with 3 - 12 individuals released each year. The initial release group in August 2013 was recaptured following two premature deaths, and re-released with additional subadults the following April. Another release in June 2018 of three male subadults addressed a gender imbalance in the established population.

Table 1: Release summary of the seven soft-releases of red-billed chough to Jersey and the data that were available to this project. Juveniles defined as <6 months, subadults 1-2 years, adults 2+ years.

Release	**Individuals**	**Life Stage**	**Tracking Period**	**Data Used Here**
August 2013	7	Subadult + Adult	30/08/13 – 20/09/13	
April 2014 *(re-release)*	8	Subadult + Adult	N/A	
July 2014	4	Subadult	10/09/14 – 08/02/15	
September 2014	6	Juvenile	10/09/14 – 08/02/15	✓
September 2015	8	Juvenile	07/09/15 – 03/03/16	✓
July 2016	12	Juvenile	21/07/16 – 27/03/17	
June 2018	3	Subadult	N/A	

On release, each bird was fitted with a coloured leg ring, metal identification ring, and tail-mounted VHF transmitter (PIP3L, Lotek, 2014) weighing 5.5 g, which represented 1.5% of the mean chough mass. The transmitters were glued to the shaft of a central tail feather and removed six months after release or at first moult (Table 1). There were no releases in 2017 and the 2018 release group were not fitted with transmitters. Staff and volunteers of Durrell Wildlife Conservation Trust conducted post-release monitoring, taking daily fixes of the bird's locations, starting from the release site then heading to high points to assist triangulation until the focal bird was found, or following up on public sightings (Birds on the Edge, 2022). Daily supplementary feeding (11:00

and 15:30) took place at the release site in order to determine condition and behaviour of the birds, and identify any health concerns.

One individual of the 2015 release group was found dead within two weeks of release so has been treated as anomalous and excluded from data analysis. It is believed the reason for this was the individual was raised separately from the rest of the release group so had not developed the same social bonds, thus increasing post-release stress. Survival rate of individuals after two years post-release was 59.6%. Known causes of death were predation by peregrine falcons (*Falco peregrinus*) and lesser black-backed gulls (*Larus fuscus*; n = 2), aspergillosis (n = 2), and starvation (n = 3). The causes of all other disappearances remain unknown. In 2021, the established population of red-billed choughs on Jersey comprised 31 individuals.

VHF Data Analysis

VHF data from the 2014 and 2015 transmitter deployments were made available to this project. Where a VHF record noted observations of specific individuals moving as a group, locations were added for all individuals in the group. Data points were removed where records did not include a verified location, and when they were duplicates. The cleaned dataset contained two fixes per individual per day for every day the individual was observed.

The dataset with a minimum of two fixes per individual per day was used to quantify movement metrics post-release. Step times and lengths were calculated using the great circle method to understand how far the release groups travelled, and to investigate whether the distance travelled by individuals post-release changed during the 6-month deployment period. Utilisation distributions (defined as the area in which the bird spent it’s time according to resource availability (Powell and Mitchell, 2012)) were calculated by kernel density estimation (Worton, 1989) at 95% using function *kernelUD()* (package ‘*adehabitatHR*’ v. 0.4.19).

The potential for interaction between the individuals of each release group was measured using three indices: spatial interaction (SI), dynamic interaction (DI), and the interaction of points *A* and *B* (IAB interaction statistic), calculated using packages *‘wildlifeDI’* v. 0.4.1 and ‘*rgeos*’ v. 0.5-9 (Long *et al*., 2014). SI relates to the intersection of two individual utilisation distributions (Millspaugh *et al.,* 2004), DI measures the cohesiveness in the speed and direction of two individuals (Long and Nelson, 2013), and the IAB statistic is an index of the distance between two simultaneous telemetry fixes of two individuals (*A* and *B*; Benhamou *et al.,* 2014).

Finally, VHF data were used to assess habitat selection. Here, random locations were generated at two scales: (i) Jersey and (ii) the surrounding area of the release site, to represent the habitats available to the choughs at the scale of the whole of Jersey and within their core movement range, determined by the 95% utilisation distribution for all individuals combined (Manly *et al.,* 2007). Points were generated in QGIS 3.20.3 (2021) by creating a random points layer within a specified polygon (e.g., Jersey; Fig. 8.1; Fig. 9). Binomial generalised linear models (Ranganathan *et al.,* 2017) were then used to determine post-release habitat selection against an equal number of random points.

Dead-Reckoning Data Collection and Analysis

The initial plan for this study was to recapture the reintroduced choughs in 2022 and equip them with two types of data loggers: a solar-powered GPS (GiPSy 6, Technosmart Europe, 2022) weighing 2 g (1% of mean body mass) and a Daily Diary (Wildbyte Technologies, 2022) weighing 5.5 g (1.5% of mean body mass), incorporating a tri-axial accelerometer, magnetometer and barometric pressure sensor, in order to reconstruct flight paths via dead-reckoning. The tags would be mounted on a leg-loop harness with the Daily Diary protected by heat-shrink. Due to personnel issues, however, this was not possible. Instead, an exploratory approach was adopted, investigating the potential of dead-reckoning for the future monitoring of flight paths using a pre-existing dataset.

Data collected by Garde *et al.* (2021) involved the release of seven homing pigeons (*Columba livia domestica*) in Bodman-Ludwigshafen, Germany (47.815° N, 8.999° E), 5.7 km north of their home loft during July 2019. Each bird was equipped with time-synchronised GPS (GiPSy 5, Technosmart Europe, 2019) and Daily Diary (Wildbyte Technologies, 2019) loggers. The units were housed together in a 3-D printed housing that was attached to the birds via a Velcro strip that had been glued to the downy feathers, following standard practise for homing pigeons (Garde *et al.,* 2021). Together the loggers weighed up to 18.0 g, which represented between 3.8% and 4.2% of the mean pigeon mass. The GPS units sampled bird location at 1 Hz. The Daily Diaries recorded acceleration at 200 Hz, geomagnetic field strength (also in 3 axes) at 80 Hz, and barometric pressure at 20 Hz. Homing pigeons are similar in size to choughs, but are heavier (350 – 500 g; Zeigler *et al.,* 1972), so are capable of carrying multiple tags to investigate drift rate.

An anemometer (Kestrel 5500 L, Kestrel Instruments, 2019) recorded weather data at the release site, including wind speed and direction, at 10 second intervals. Precise details of the data collection process can be found in Garde *et al.* (2021).

The Daily Diary magnetometer data were corrected using the in-house software Daily Diary Multiple Trace (DDMT; Holton, 2022) to offset any error caused by the hard- and soft-iron make-up of the local environment, or misalignment of the ellipsoidal fitting (Cui *et al.*, 2018; Poulose *et al.,* 2019; Morozov and Murasev, 2020). Pitch and roll were calculated by taking the arcsine of the smoothed acceleration in the surge and sway axes (Bidder *et al.*, 2015). Altitude above mean sea level was calculated from smoothed barometric pressure using Standard Atmosphere equations (Tremblay and Ainslie, 2021), once daily changes in sea-level pressure had been accounted for. The latter step used the pressure recorded at a known altitude (at the release site; Garde *et al.,* 2021).

Flight sections were identified in DDMT by identifying fluctuations in the pressure data, as well as the acceleration signal, which had peaks associated with individual wingbeats. Flight data were exported (32 flights from 7 individuals) and then dead-reckoned using R-software function *Gundog.Tracks()* (Gunner *et al.,* 2021a) in conjunction with the wind data.

A constant speed was used to dead-reckon the flight paths as no correlation has been found between the dynamic body acceleration (VeDBA), which has been used as a proxy for speed in terrestrial systems, and flight speed in birds (Gunner *et al*., 2021b). The speed was set at 25 m/s as an upper limit of speeds observed in these birds (Garde *et al.,* 2021). The particular speed selected will affect the magnitude of the distance errors (for instance, the selection of an even higher speed, such as 30 m/s would result in the need for greater subsequent distance correction). Nonetheless, this approach allows the relative importance of a range of factors to be assessed in terms of the extent to which they affect DR error.

The GPS data were used to estimate the relative error in the dead-reckoned flight paths. This was estimated as two separate components in *Gundog.Tracks()*: distance correction factor, and bearing correction factor. Distance correction factor is a coefficient that is multiplied by dead-reckoned ground speed (here, a constant of 25 m/s) to match GPS ground speed (Eq. 1) so that flight path distances align. If the GPS speed was less than the dead-reckoned speed, this would result in a distance correction factor between 0 and 1. The bearing correction factor is the difference between the dead-reckoned heading and the GPS heading at each equivalent point on the flight paths, which was scaled from -180° to 180°.

$$DR\ Speed * correction\ coefficient = GPS\ Speed \tag{1}$$

Drift in the DR track should be affected by both environmental factors and the pigeon's behaviour. The speed with which a bird flies over the ground (the ground speed) is the result of the bird's airspeed (the speed at which they move through the air) and the wind vector. Birds adjust their airspeed in relation to the strength of the head or tail wind they experience, reducing their speed with a tailwind and increasing it in a headwind. Despite this, the net effect of flight with a tailwind is for birds to cover ground more quickly, with the reverse being true for headwinds. The upshot is that the airspeed of the bird is uncoupled from their ground speed when they are flying in windy conditions. I therefore predicted that wind would be the factor that would result in the greatest difference between the fixed DR speed and the GPS speed.

The headwind component (HWC) was calculated as the component of the wind vector that was experienced as a headwind, using the approach adopted by Garde (2022). Headwinds are given positive values and tailwinds as negative values. The HWC was calculated using the angle between the wind speed vector and the GPS ground speed vector (Lempidakis, 2022).

Flights were characterised by an initial period of circling where birds are thought to be establishing the orientation of the loft (Gagliardo *et al.,* 2001; Jandačka *et al.,* 2022), followed by a relatively straight section (Fig. 10). I hypothesised that the tortuosity of the flight track might also affect the correction factors. To assess this, I used the standard deviation of the turning angles, calculated using function *earth.bear()* (package '*fossil*' v. 0.4.0). In order to capture the tortuosity within the different sections of the flight, the mean tortuosity index was calculated for 15 second flight segments (Fig. 2).

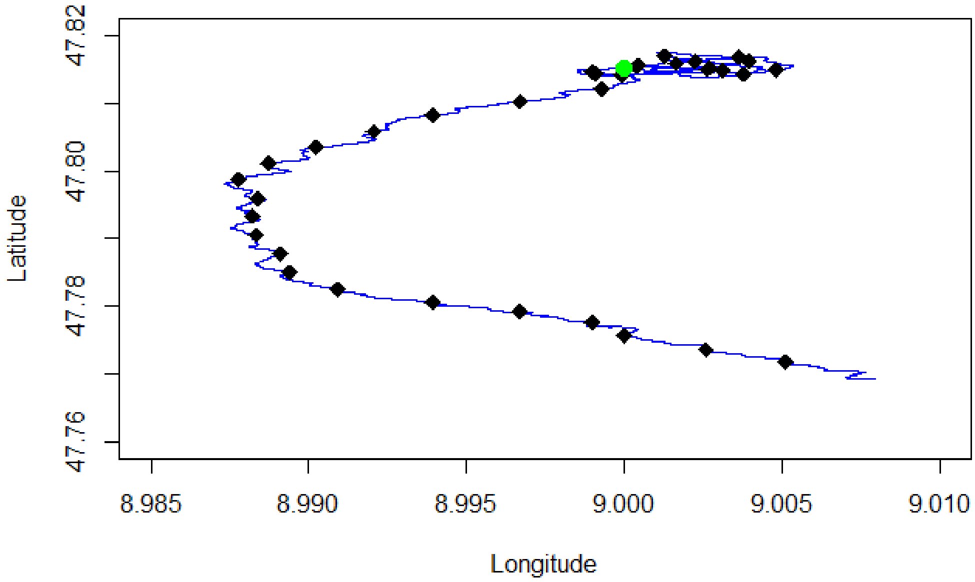


Figure 2: 15-second segment creation (black) of an example dead-reckoned flight path to enable calculation of a continuous tortuosity index (release site = green).

Two linear mixed-effects models were used to investigate the effect of HWC, altitude and flight path tortuosity on the extent to which (i) the distance and (ii) the bearing of the DR paths needed adjusting (the correction factors) in order for them to correspond with the GPS track. The models also included the interaction of HWC and altitude to account for the potential impact of altitude on wind speed experienced by the birds. The model included bird ID as a random intercept to account for repeated measurements of the same individual over multiple flights, and flight ID to account for repeated measurements within the same flight. Models were run using packages '*lmerTest*' v. 3.1-3, '*lme4'* v. 1.1-30, and '*MuMIn'* v. 1.46.0. Model outputs were checked using residual and QQ plots to verify no assumptions had been violated. All analyses were run using R v. 4.2.0 and R-Studio v. 2022.2.3.492 (R Project, 2022; RStudio Team, 2022).

Results

VHF Results

The time between VHF locations (n = 2,555) for a given individual across birds in the 2014 and 2015 releases (appendix 1.0) ranged from 5 minutes to 6.95 days, with a mean of 26.3 hours (Fig. 3, red). The mean step time for individuals with locations recorded twice per day (48% of records) was 10.6 hours (Fig. 3, blue; this dataset was used for subsequent analyses of step length). The majority of locations (84.8%) were derived from triangulation with line-of-sight confirmation, 10.4% from direct observation with handheld GPS, and 4.8% from triangulation only.

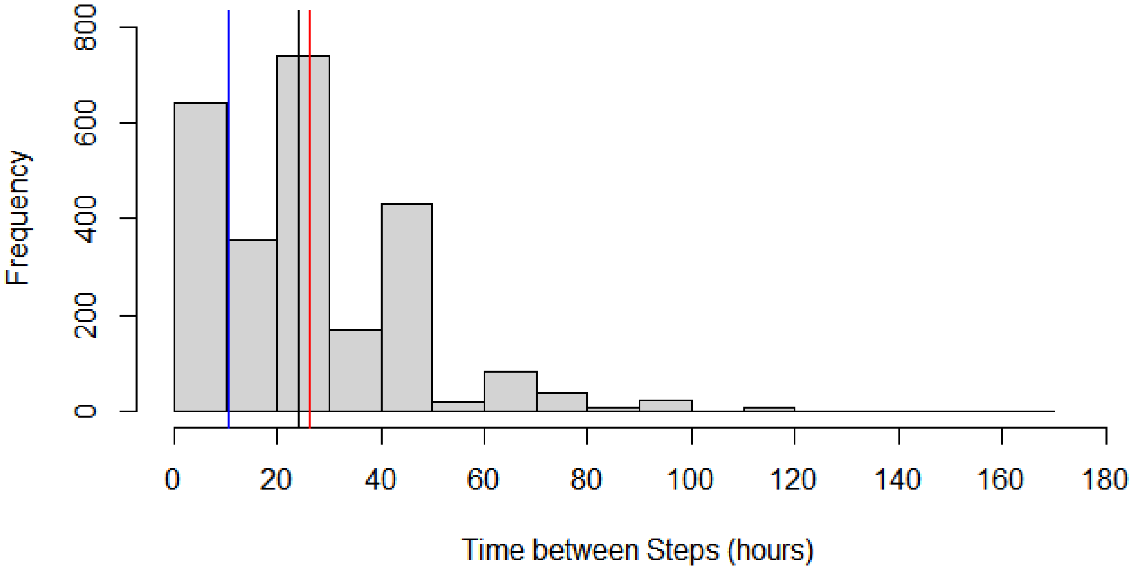


Figure 3: Step times within each individual's flight paths. Min = 5 minutes; max = 6.95 days; overall mean = 26.3 hours (red); mean within 24 hours = 10.6 hours (blue; 24-hour mark = black line).

The mean daily step distance (the distance between two consecutive locations on an individual's movement path) for all released individuals during their respective tracking periods was 763.3 m, as both release groups maintained small movements around the release aviary. The maximum daily step distance of any individual in the 2014 release group during their post-release tracking period was 10.1 km from the release site on the northern coastline of Jersey to the south-west headlands of the island (Fig. 5) in early November (~2 months post-release; Fig. 4). The group was recorded on one occasion in mid-November (Fig. 4) on the north-west coastline (6 km from the release site), but the majority of fixes (92%) were located on the northern coastline near the release site (Fig. 5). The maximum daily step distance of any individual in the 2015 release group during their post-release tracking period was 2.7 km from the release aviary, south-west along the coastline (Fig. 6) with a mean circular direction of -95.9° in early December (~3 months post-release; Fig. 4), repeating on a number of occasions until February (~5 months post-release, Fig. 4).

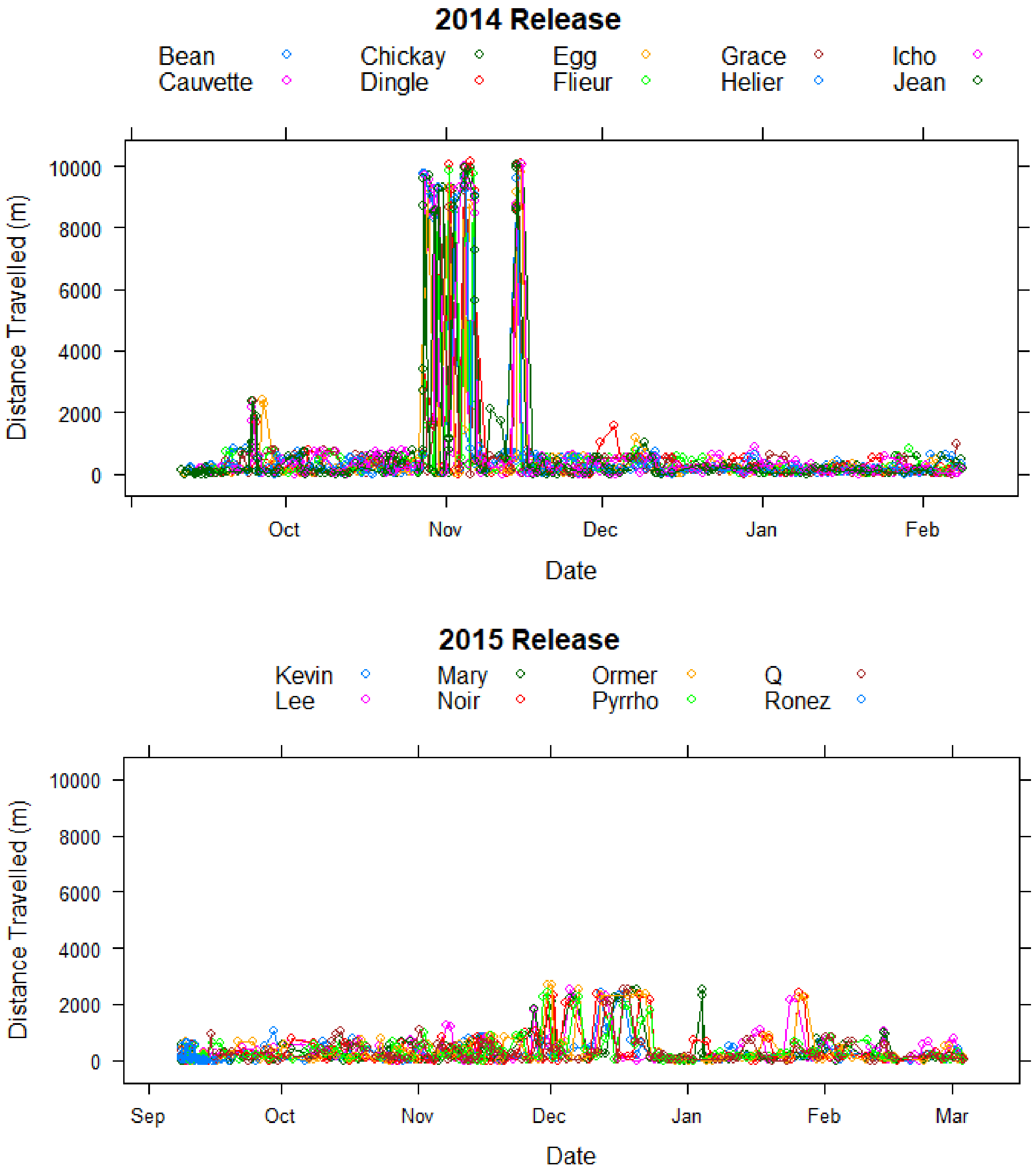


Figure 4: Step distances of the 2014 and 2015 release groups over the course of their respective 6-month tracking periods.

Visual assessment of these data did not show a systematic change in step distance with time after the release. Instead, there were distinct periods of 1 to 11 days when birds undertook longer movements away from the release site (Fig. 4). There was no marked similarity in the timing that these occurred between years in terms of the month (October – November in 2014 and November – February in 2015) or time since release (1.5 and 2.5 months respectively, Fig. 4).

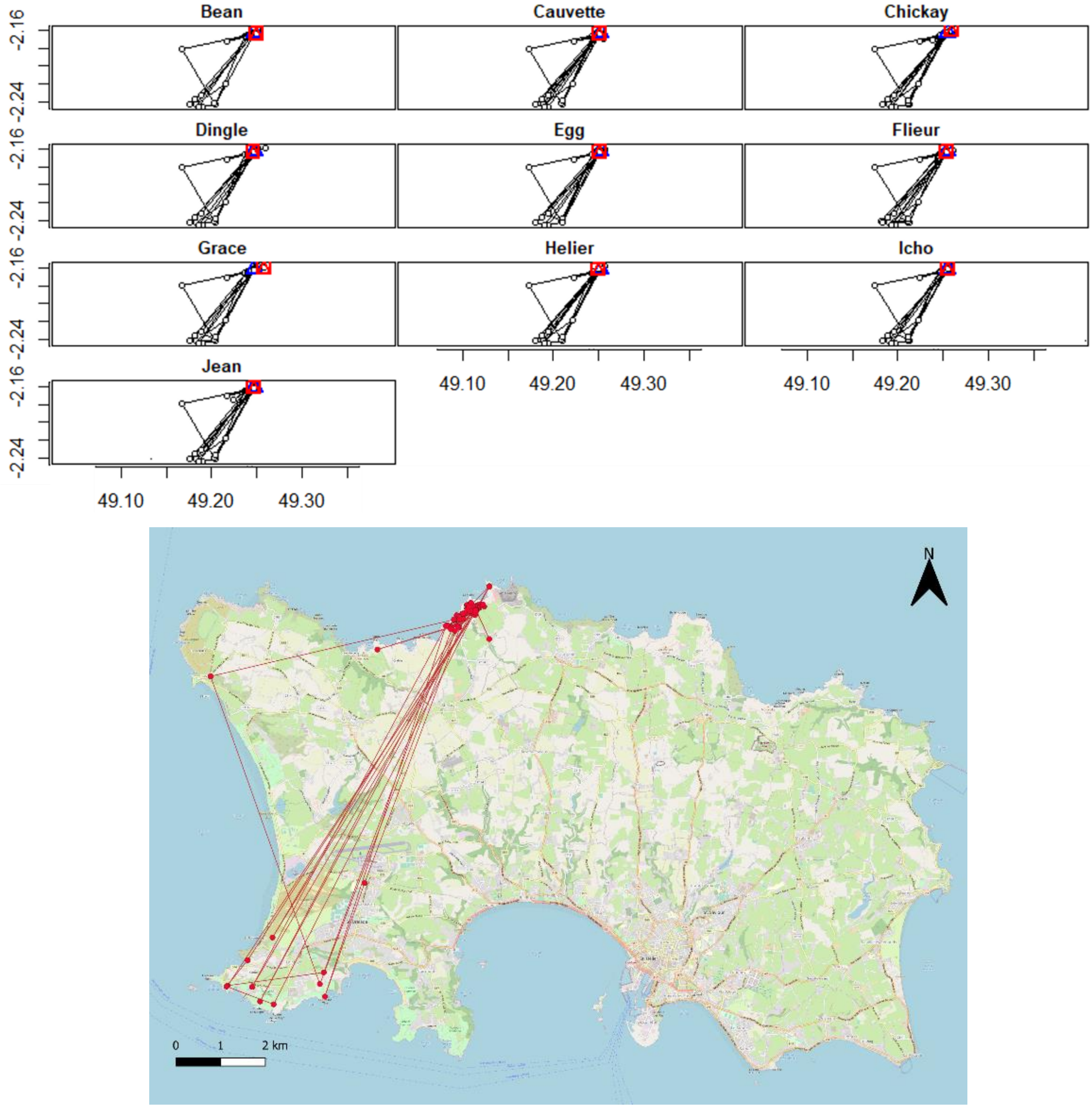


Figure 5: Trajectories of the 2014 release group during their 6-month tracking period with start (blue) and end (red) points. One individual (Cauvette) plotted on OpenStreetMap (2022) using QGIS 3.20.3 (2021).

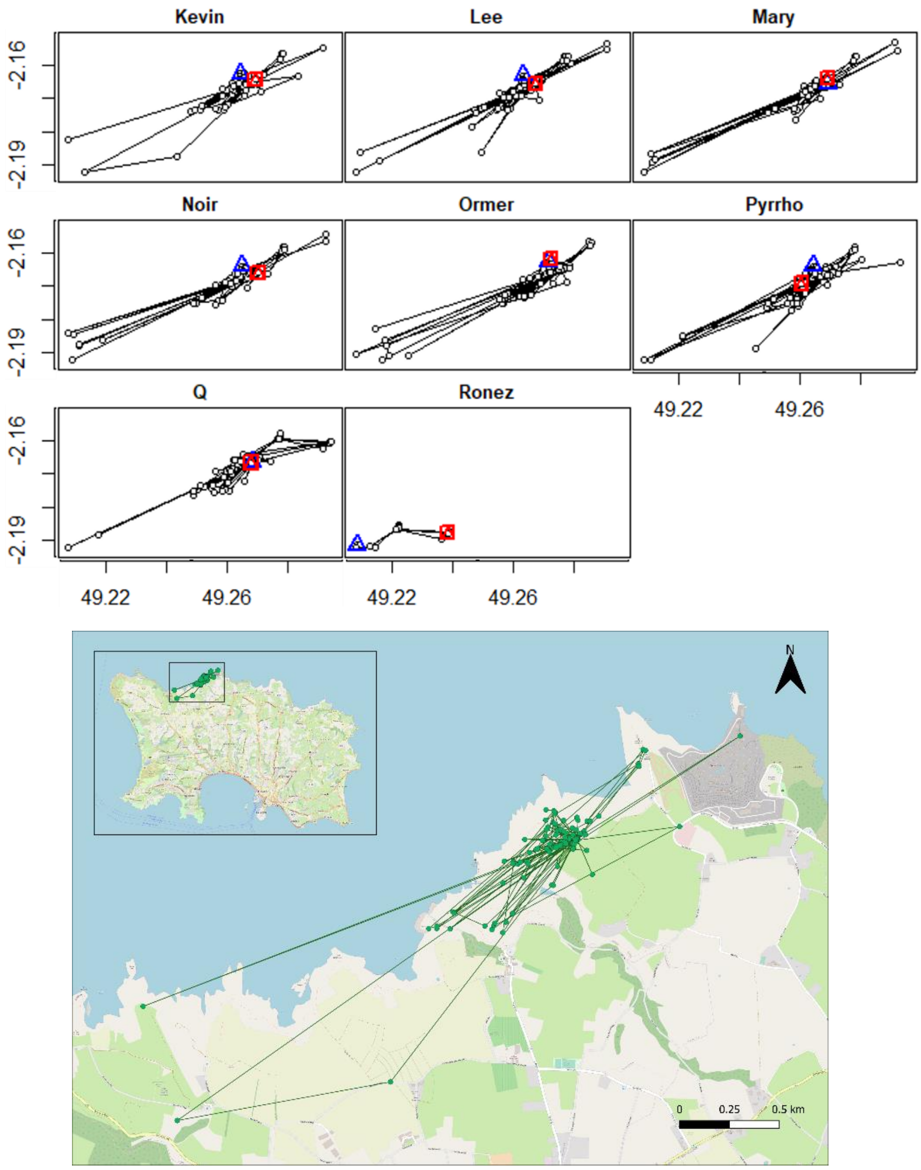


Figure 6: Trajectories of the 2015 release group during their 6-month tracking period with start (blue) and end (red) points. One individual (Kevin) plotted on OpenStreetMap (2022) using QGIS 3.20.3 (2021).

There was considerable overlap in the kernel density utilisation distributions of the released individuals each year (Fig. 7; 2014: SI = 75.8 – 97.8, mean = 88.4; 2015: SI = 57.7 – 85.5, mean = 70.5), with 91.9% of data points falling within the utilisation distribution contours for the 2014 release and 96.9% of data points for the 2015 release, indicating that there was probable dynamic interaction between the birds.

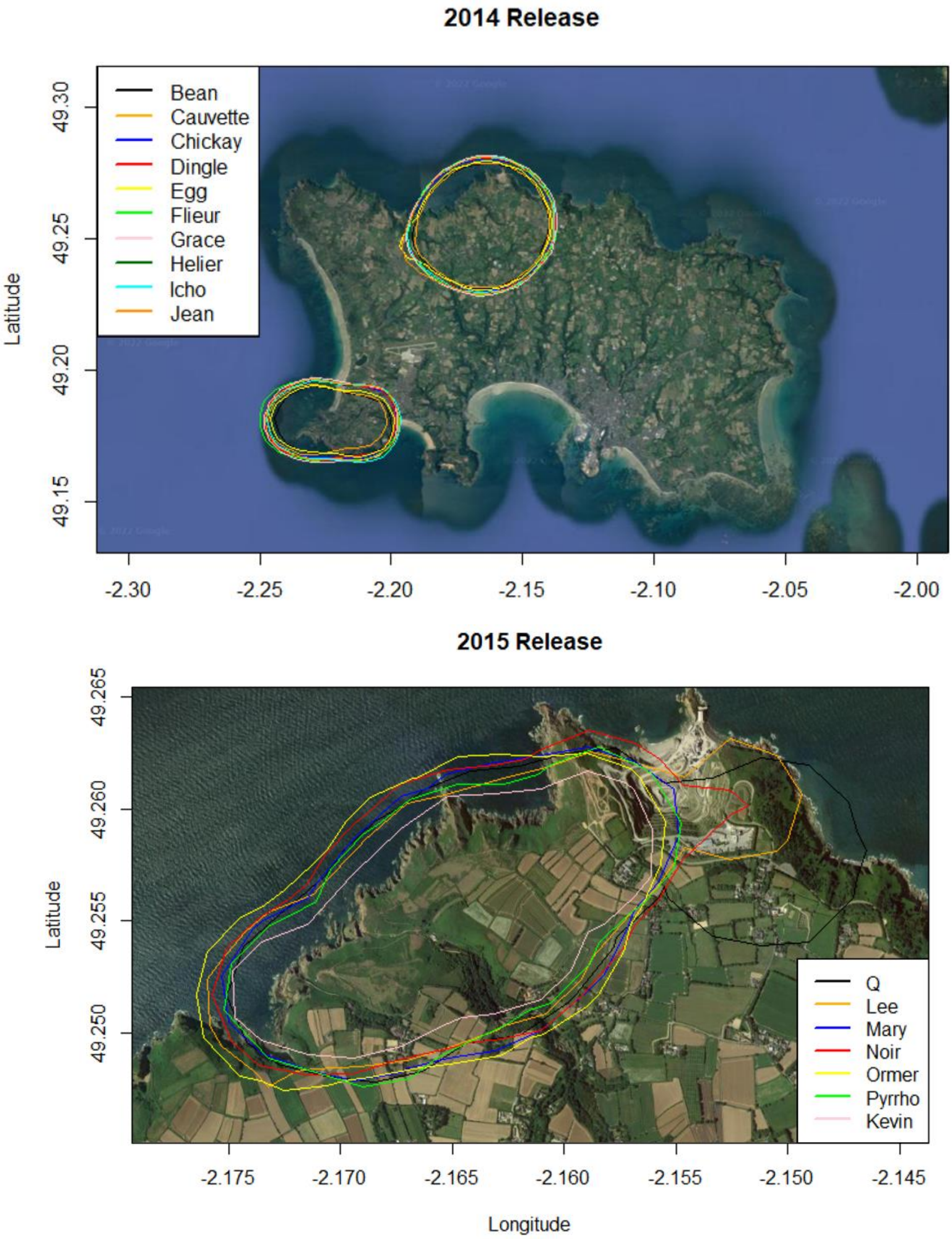


Figure 7: Utilisation distribution contours of all choughs from the 2014 and 2015 releases during their respective tracking periods. Map data: Google Satellite (2022).

The global dynamic interaction values (2014: DI = 81.9 – 1 (mean = 94.9); 2015: DI = 36.8 – 80.1 (mean = 53.8)) show that there was significant cohesion (2014: *p* = 0.018 – 0.02; 2015: *p* = 0.019 – 0.024) in the movement patterns of the choughs of both release groups, with stronger cohesion seen in the 2014 release group. This cohesiveness is corroborated by looking at the movement displacement (DI_d) and direction (DI_θ) of the birds (2014: DI_d = 86.5 – 1 (mean = 95.6), DI_θ = 89.2 – 1 (mean = 96.9); 2015: DI_d = 61.3 – 89.3 (mean = 70.4), DI_θ = 33.6 – 82.7 (mean = 55.4)), as well as the significant attractions presented from the IAB test (2014: *p* = 0.018 – 0.02; 2015: *p* = 0.019 – 0.023), with no avoidance (*p* = 1), as it shows that the individuals of each release group moved at similar speeds and directions at similar times, suggesting that the choughs from each release travelled together as a flock.

Habitat Selection

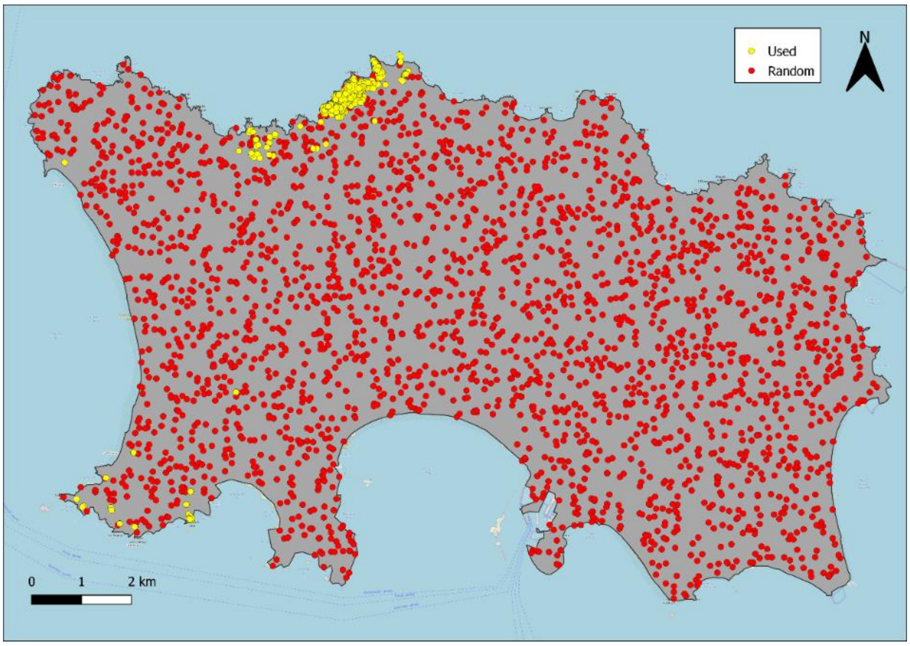


Figure 8.1: Verified used points of red-billed choughs across Jersey from 2014 and 2015 release groups compared to an equal number of random points (n = 2,555) in the same available area. Modelled on OpenStreetMap (2022) using QGIS 3.20.3 (2021).

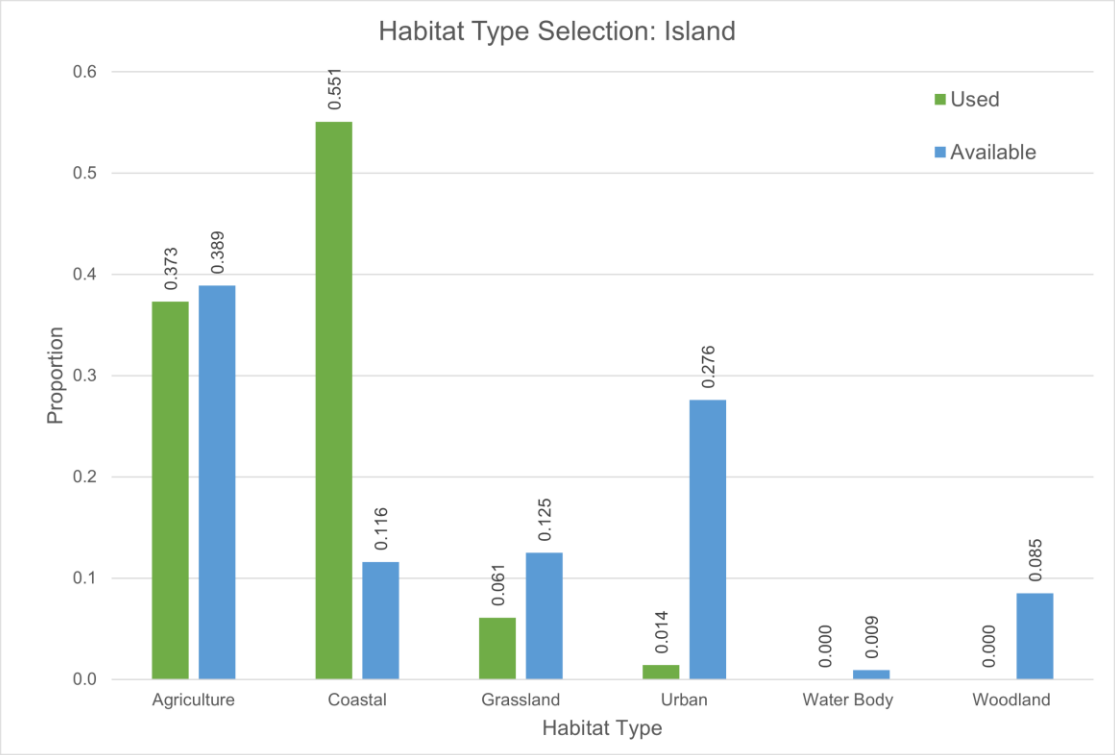


Figure 8.2: Proportion of used and available habitat types for red-billed choughs across the island of Jersey. Classification of habitat types can be found in appendix 2.0. Phase I habitat survey data provided by Jersey Department of the Environment (States of Jersey, 2011).

Coastal grassland was the most significantly used habitat by the choughs of both release groups across the island (coefficient estimate = 7.57 ± 0.41 S.E., $p < 0.001$), with coastal habitats making up 55.1% of the used habitat types, despite an availability of only 11.6% (Fig. 8.2). Agricultural land was the most available habitat type across the island (38.9%) and also significantly used (37.3%; coefficient estimate = 3.33 ± 0.29 S.E., $p < 0.001$). While the urban environment made up 27.6% of all available habitat across the island, it was not significantly used (coefficient estimate = -14.19 ± 220.81 S.E., $p > 0.1$), making up only 1.4% of the used habitat (Fig. 8.2). Water bodies and woodland were not used at all, however, together they make up only 9.4% of available habitat (Fig. 8.2).

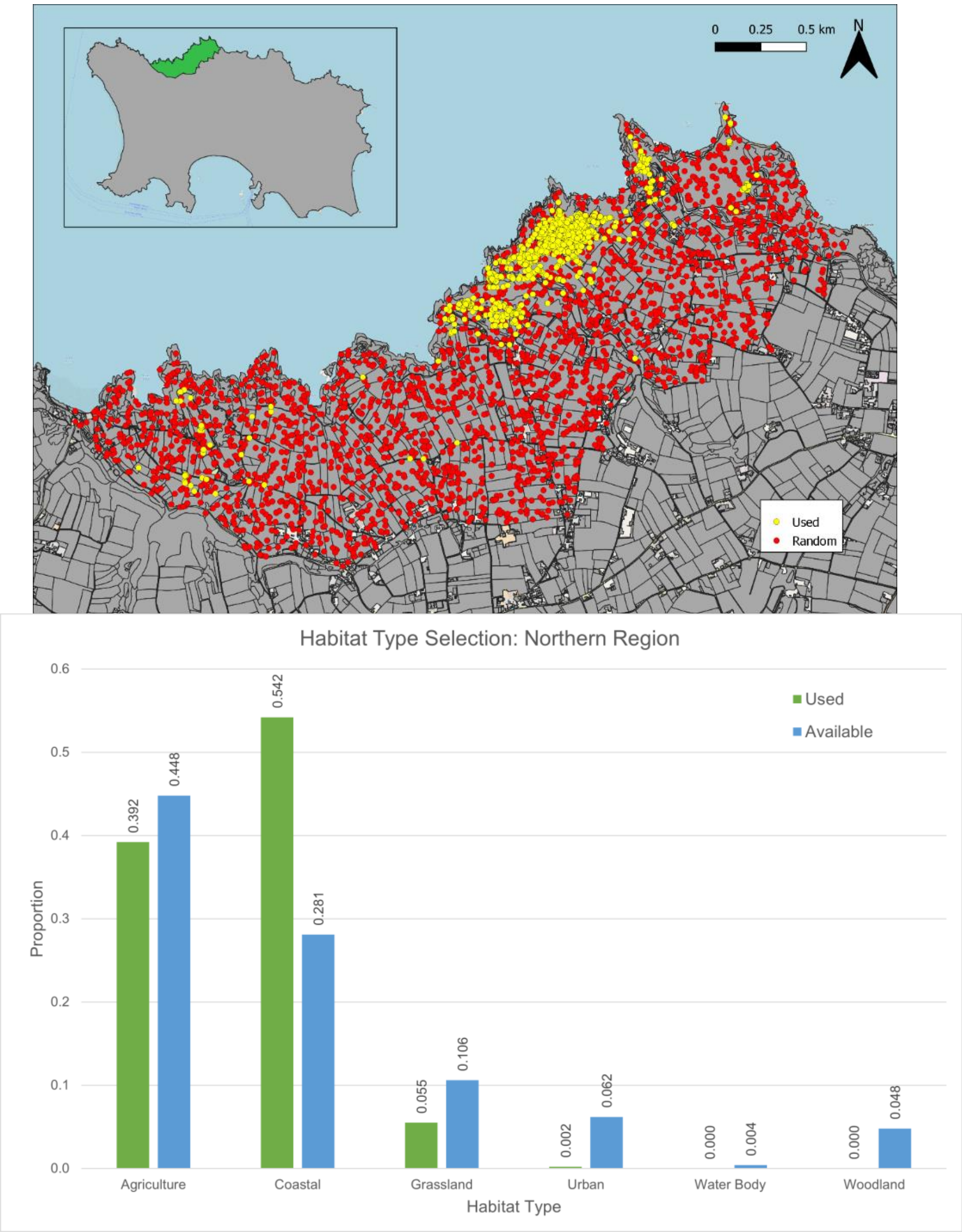


Figure 9: Verified used points of red-billed chough around the release site (area = 4.34 km^2), of 2014 and 2015 release groups compared to an equal number of random points (n = 2,424) in the same available area, and the relative proportion habitat selection. Borders defined by existing habitat separation, e.g., roads. Modelled on OpenStreetMap (2022) using QGIS 3.20.3 (2021). Phase I habitat survey data provided by Jersey Department of the Environment (States of Jersey, 2011). Classification of habitat types can be found in appendix 2.0. Phase I habitat survey data provided by Jersey Department of the Environment (States of Jersey, 2011).

Similar to the habitat selection across the island as a whole, coastal grassland was the most significantly used habitat by the choughs of both release groups around the release site (coefficient estimate = 3.86 ± 0.27 S.E., $p < 0.001$), with area borders defined by existing habitat separation, such as roads and villages (Fig. 9). Coastal habitats made up 54.2% of the used habitat types in the northern region, with a higher availability of 28.1% compared to the whole island at 11.6% (Fig. 8.2; Fig. 9). Coastal heathland, however, while significantly used across the whole island (coefficient estimate = 2.89 ± 0.49 S.E., $p < 0.001$), was not significantly used around the release site (coefficient estimate = -12.69 ± 333.64 S.E., $p > 0.1$). Agricultural land was again the most available habitat type in this northern region (44.8%) and was also used significantly (39.2%; coefficient estimate = 1.73 ± 0.25 S.E., $p < 0.001$). The urban environment made up comparatively little of the available habitat (6.2% compared to 27.6% availability across the whole island; Fig. 8.2; Fig. 9), but made up only 0.2% of the used habitat (Fig. 9). Again, water bodies and woodland were not used by the choughs, with availabilities of 0.4% and 4.8% respectively (Fig. 9).

Dead-Reckoning Results

Overall, dead-reckoning produced tracks that appeared similar in heading and tortuosity to the GPS tracks and the major inflection/turn points were also well-represented (Fig. 10). Nonetheless, the dead-reckoned and GPS tracks diverged with time due to the cumulative impact of drift on the estimated position. This resulted in distance errors of up to 5.8 km between the end points of the GPS and DR paths (mean end point distance error = 1.7 km; Fig. 11). The dead-reckoned positions also required substantial bearing correction to align them with GPS positions, with modes -40° and 50° depending on the direction in which the correction was made in relation to the bird's direction of travel (Fig. 11).

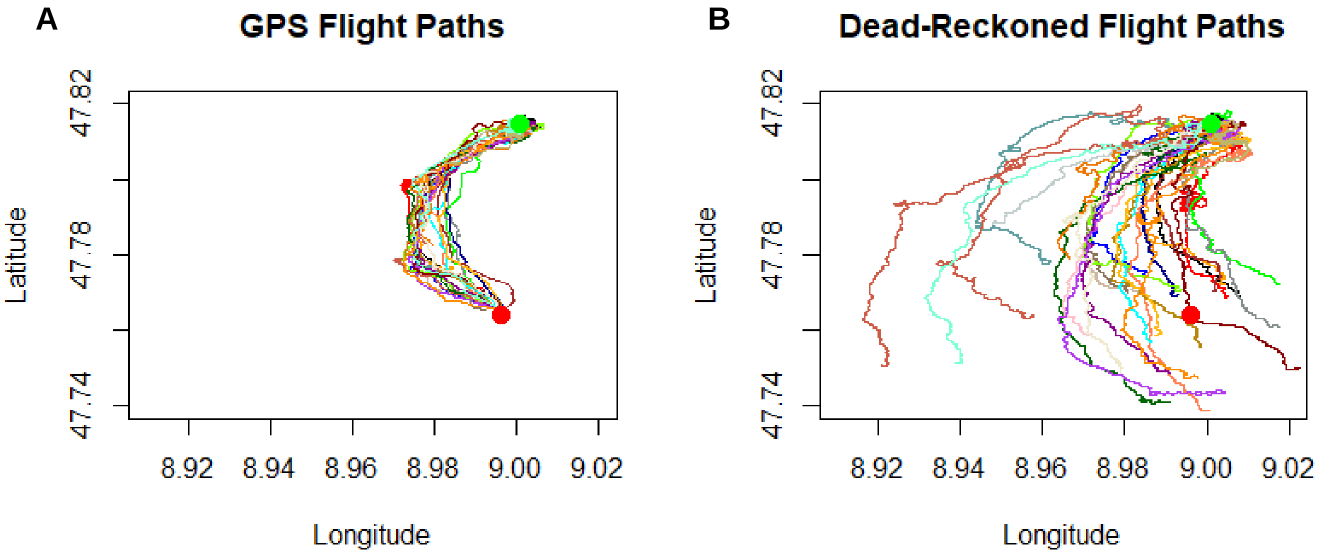


Figure 10: All (A) GPS and (B) DR tracks from 32 flights (release site = green circle; home loft = red circle), coloured according to the flight ID.

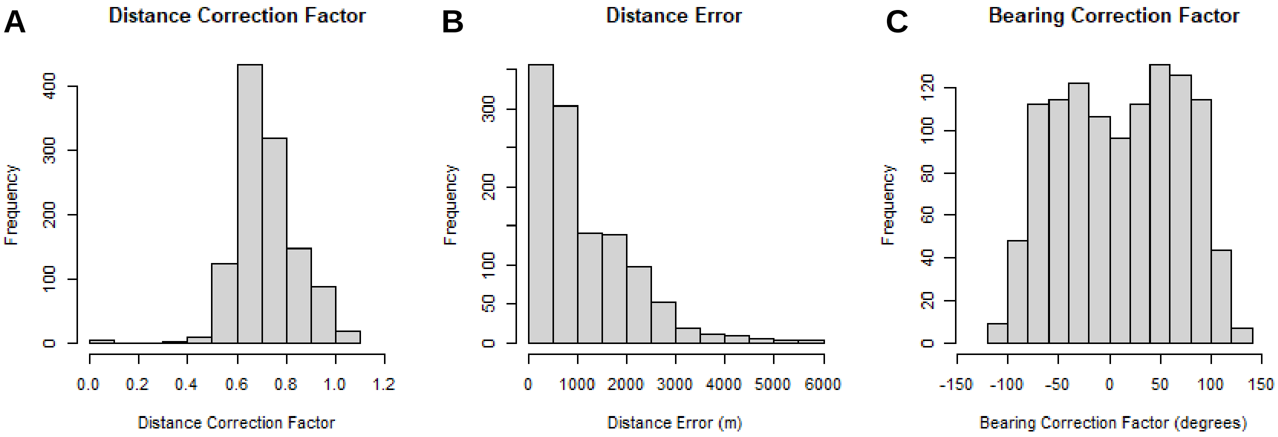


Figure 11: Frequency histograms of the DR to GPS (A) distance correction factor, (B) distance error between each equivalent GPS and DR point along the flight paths, and (C) bearing correction factor for 32 flights.

The distance correction factor needed to match DR speed to GPS speed was negatively affected by HWC and flight path tortuosity, and positively affected by altitude, with altitude having the highest estimate (Table 2). The interaction of HWC and altitude negatively affected distance correction factor and had the lowest estimate, but was not significant (Table 2). Distance correction factors closer to 1 correspond to GPS speeds being closer to the constant DR speed. Stronger tailwinds therefore required less correction for the DR path to match the GPS track (Fig. 12, *A*; Fig. 13).

While tortuosity was significant in the model, this relationship may be unduly influenced by a relatively low number of values with higher tortuosity (Fig. 12, *C*). The R^2 values show that almost the same amount of variance is explained by the fixed and random effects ($R^2_m = 0.28$, $R^2_c = 0.48$). QQ and residual plots indicated that model assumptions were met.

Table 2: Regression estimates, standard errors, t-values and p-values for a linear mixed-effects model measuring the effect of different scaled variables on the dead-reckoned distance correction factor. Conditional R^2 is estimated at 0.48, and marginal R^2 at 0.28.

	Estimate	**Std. error**	***t* value**	***p* value**
Intercept	7.186e-01	1.007e-02	71.348	<2e-16
HWC	-2.990e-02	3.285e-03	-9.100	<2e-16
Altitude	4.760e-02	3.325e-03	14.314	<2e-16
Tortuosity	-8.596e-03	3.023e-03	-2.843	0.005
HWC : Altitude	-4.828e-04	2.647e-03	-0.182	0.855

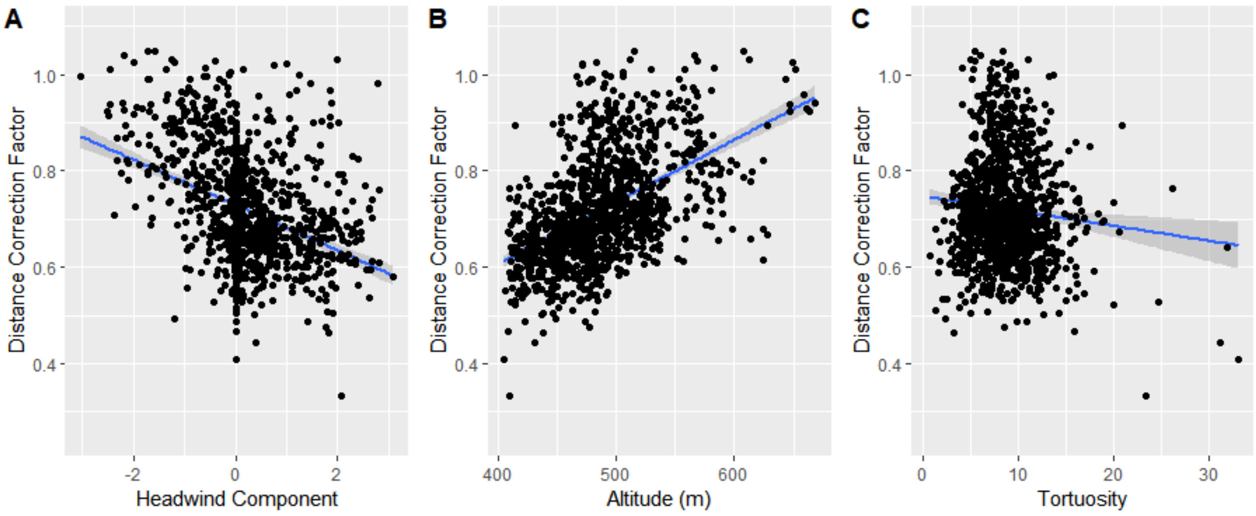


Figure 12: The effect of unscaled (A) headwind component, (B) altitude, and (C) flight path tortuosity on the distance correction factor needed for the dead-reckoned path to match the GPS path.

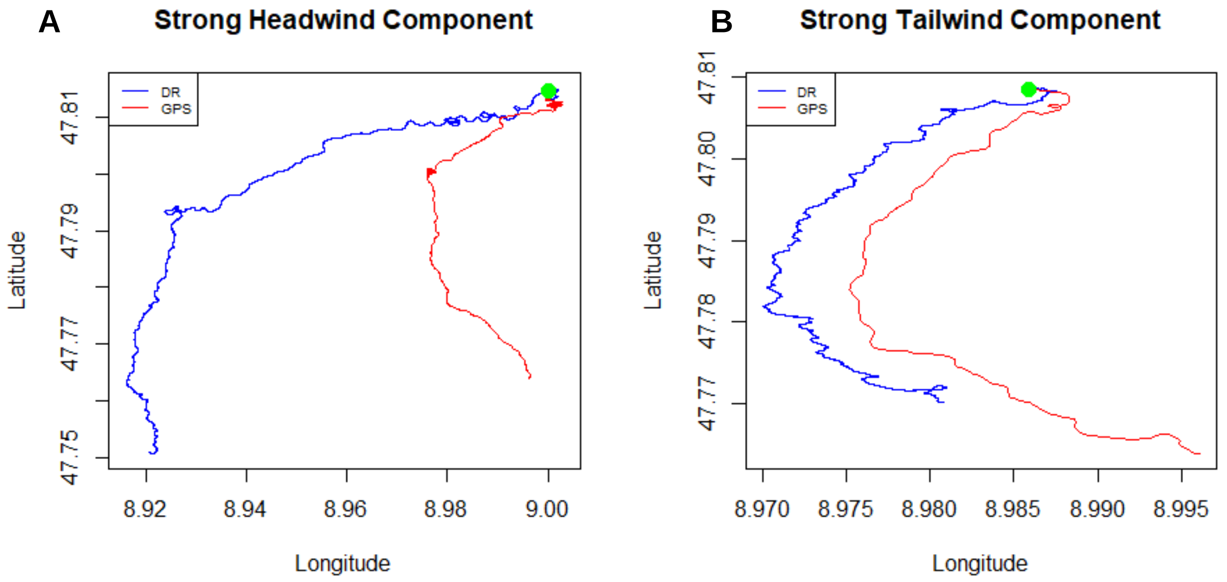


Figure 13: DR and GPS flight paths for (A) a single flight with a headwind of 3 m/s at the release site (green circle), and (B) a single flight with a tailwind of 3 m/s at the release site (green circle).

The bearing correction factor was negatively affected by HWC, altitude and flight path tortuosity, as well as the interaction of HWC and altitude (Table 3). Variance in the bearing correction factor is explained more at the individual and flight level than by the environmental variables ($R^2_m = 0.028$, $R^2_c = 0.081$), however, despite the significance found in altitude, tortuosity and the interaction of HWC and altitude, the R^2 of the global model (R^2_c) is extremely low.

Table 3: Regression estimates, standard errors, t-values and p-values for a linear mixed-effects model measuring the effect of different scaled environmental variables on the dead-reckoned bearing correction factor. Conditional R^2 is estimated at 0.081, and marginal R^2 at 0.028.

	Estimate	**Std. error**	***t* value**	***p* value**
Intercept	8.570	3.037	2.822	0.009
HWC	-2.699	1.995	-1.352	0.177
Altitude	-7.941	2.042	-3.889	0.0001
Tortuosity	-4.013	1.887	-2.127	0.03
HWC : Altitude	-6.489	1.647	-3.940	8.76e-05

Discussion

This thesis examines two different types of biotelemetry and their ability to provide insight into the post-release movements of a small population of reintroduced red-billed choughs. Daily VHF locations revealed that the choughs primarily remained in a limited area close to the release site (mean daily step distance = 763.3 m) with occasional movements up to 10.1 km. This could be due to the supplementary feeding at the release site, the habitat availability and/or social factors, each of which I will consider below. VHF can potentially be used to provide more detailed movement paths (Edelhoff *et al.,* 2016; Fisher *et al.,* 2021), however, this requires the continued presence of observers to triangulate their changing locations through time, or a single observer using VHF to locate the birds and then manually mark their position with a GPS unit (as used here). I go on to consider the potential utility of dead-reckoned flight paths for this system, where birds undertake relatively short flights and return to the release point (and feeding station) on a daily basis (outside the breeding season).

VHF Tracking of Reintroduced Choughs

One of the primary drivers of the chough's limited dispersal could be the provision of food at the release site. This means that dispersal may have been reduced, due to the motivation of guaranteed resource availability. Many studies have remarked on the influence of supplementary feeding, maintaining this same conclusion (Mitchell *et al.,* 2011; Madden *et al.,* 2018; Tetzlaff *et al.,* 2019; Resende *et al*., 2021). Knox and Monks (2014) tested this as their hypothesis and found soft-release greatly reduces dispersal, but increases post-release survival. In contrast, Bannister *et al.* (2020) and others (De Milliano *et al.,* 2016; Deguchi *et al.,* 2022) reported release method and supplementary feeding had minimal impact on dispersal.

In this case, the provision of food could also be acting in concert with a limited availability of feeding opportunities, e.g., due to the limited extent of their preferred foraging habitat. The results here show that coastal habitats, such as coastal heathland, were positively selected for by the choughs but had low availability across the island. As such, the birds may have had restricted dispersal due to a lack of suitable coastal habitat beyond the northern release region. However, ultimately, knowing whether the choughs are limited by the extent of available coastal habitat would require data on the prey density within these habitat patches, which is also likely to show seasonal variation. Urban areas may also restrict dispersal as choughs did not occupy these spaces. Increasing urbanisation (Reynolds *et al.,* 2019; Fingland *et al.,* 2022) may therefore further compromise the long-term establishment of choughs on Jersey.

Pre-release feasibility studies (Corry, 2012) and existing literature on preferred chough habitat (Gilbert *et al.,* 2019; Jonsson *et al.,* 2020; Braunisch *et al*., 2021) show that the surrounding area of the release site had suitable habitat for choughs, most notably, agricultural land. Considering the habitat selection presented here, it is therefore possible that, rather than dispersal restriction, the chough population established around the release site as their ecological needs were met, so were not motivated to disperse further, suggesting that the release site was indeed located in suitable chough habitat. Anderson *et al.* (2022) recommended further reintroductions at different sites in order to assist dispersal away from the initial release site, suggesting that natural repopulation and extended dispersal is unlikely without population reinforcement elsewhere.

The reduction in dispersal distance of the 2014 release group in the second half of their tracking period suggests that they settled around the release site. The movement patterns observed among the 2015 release group throughout their tracking period mirrored the latter movement patterns of the 2014 release group, as is evident in their step distances and trajectories, with the 2015 release having a lower maximum step distance (2.7 km) than the 2014 release (10.1 km). While there aren't sufficient data for a formal analysis, the movement patterns of the 2015 release group were potentially influenced by the 2014 release group, as they were already established in the area around the release site.

The results show that social bonds developed within the two release groups, which may have influenced the likelihood of the latter release group remaining local due to social bonds forming between the two groups. This is clear in the cohesion amongst the release groups, combined with the knowledge of chough social bonds from existing literature (Fenn *et al.,* 2021; Leon *et al.,* 2022). White *et al.* (2021) reported this tendency in soft-released Puerto Rican parrots (*Amazona vittata*), while Garnier *et al.*

(2021), studying Iberian ibex (*Capra pyrenaica*), noted that dispersal reduced in areas where conspecifics were already present as conspecifics acted as possible indicators of favourable habitat. Richardson and Ewen (2016) suggested dispersal is influenced by social behaviour, particularly where there are multiple releases, but suggested that integration of birds from subsequent releases with resident birds was unlikely.

Overall, therefore, this study adds to the extensive literature showing that VHF can be an effective method for tracking animal movement and space use. While some argue VHF underestimates home range estimates and habitat preference, suggesting GPS as the preferred tracking system (Agan *et al*., 2021; Kobryn *et al*., 2022), VHF can achieve greater accuracy, particularly in closed habitats such as woodland where GPS access to the sky is limited (Wilson, 2020). In addition, VHF tracking allows additional observational information to be gathered on the behaviour of the tracked individuals, which may assist in the interpretation of movements and behaviours post-release, which can be informative for shaping reintroduction techniques and post-release monitoring (Rodgers *et al.,* 1996; Oswald *et al.,* 2019; Fisher *et al.,* 2021). White and Garrot (2012) argued that, due to point error margins of up to a kilometre, triangulation may be adequate for tracking seasonal herd migrations, for example, but should not be employed where precise locations are necessary, such as analysis of habitat selection. O'Gara *et al.* (2020), however, concluded that triangulation provides an accurate and precise method for determining location of tracked animals.

However, the benefits of VHF are tempered by the high levels of observer effort (Ross *et al.,* 2022; Saunders *et al.,* 2022), making it unfeasible to gain high frequency data without the support of a large team (Latham *et al.,* 2015; Skupien *et al.,* 2016). In this study, two locations per day were obtained for 48% of the data points within the 6-month tracking period. While this provided valuable data on habitat selection, locations outside the core area on the northern coastline may have been missed if, for instance, observer effort was limited on a given day when some individuals were not observed close to the release site. Indeed, data were collected by following the transmitter signal of a focal bird. The movements of other birds may therefore have been missed if they were not present with the focal bird (Muller *et al.,* 2019). Furthermore, VHF tracking may be limited by animals intentionally avoiding human interaction, making line-of-sight confirmation impossible (Hirakawa *et al.,* 2018; Thorsen *et al.,* 2022). This was the case on occasion during data collection in Jersey (Corry, 2022, personal communication), further increasing the labour required to collect the data as more time would be spent on searching for the birds. Other biotelemetry techniques are therefore better suited to the collection of continuous movement data. In this study, such tags could provide valuable insight into the frequency and timing of longer-range movements. If multiple birds were equipped with such tags, this would open up further possibilities, such as identifying which individual initiated the movement.

Dead-Reckoning

Dead-reckoning movement paths incur drift, where the estimated position drifts away from the true location due to the difficulties of accurately estimating animal speed and heading (Gunner *et al.,* 2021a). These factors are particularly pertinent for swimming and flying animals, which vary their movement speed and heading in relation to the current or wind vector (Gunner *et al.,* 2021b). In this study, I assessed the relative importance of the physical environment and the bird's movement decisions (namely, flight altitude and tortuosity) in affecting drift. The complexity of these relationships means that it is not possible to produce an algorithm that corrects for them (such an approach would also likely be species-specific). Instead, the aim was to explore the need for verified positions and the potential insight that corrected dead-reckoned movement paths could provide in this, and potentially other, soft-release system(s).

Despite the relatively small range in wind speeds recorded throughout the data collection period (0 – 4.8 m/s), wind still had a strong impact on the need for speed adjustment. Tailwinds are known to increase ground speed in flight (Fan *et al.,* 2020; Nussbaumer *et al*., 2022), which likely explains why the GPS speeds (ground speeds) were close to matching the constant DR speed, as the latter was set at a high level (25 m/s). A reduction in the tailwind component resulted in the DR rapidly diverging from the GPS track (Fig. 13). This demonstrates how even winds corresponding to a gentle breeze (Beaufort scale; Forrester, 1986) could result in substantial drift given that a fixed wind speed will be experienced as a head or tailwind depending on the bird's direction of travel. Given that Jersey has an annual mean wind speed of 6.2 m/s with gusts up to 16.5 m/s (Windfinder, 2022), it is clear that wind would cause substantial drift if the flight paths of choughs were reconstructed using dead-reckoning without correction.

Wind speed increases with height above ground. It was therefore surprising that the interaction between the headwind component and the flight altitude was not significant as this suggests that the importance of altitude in the need for speed correction was not driven by wind. Birds flew faster at higher altitudes, consistent with results from birds flying over a much greater altitudinal range (Bishop *et al.,* 1997). This follows from the lower air density at higher altitudes, which results in reduced lift (as well as drag). Birds must therefore increase their airspeed in order to increase the lift. Nonetheless, birds in this study operated over flight heights of 405 - 677 m above sea level. This small altitudinal range suggests that other factors may also influence the relationship between speed and height. For instance, the fastest speeds occurred as birds lost altitude (Garde *et al.,* 2021), which tended to occur once they had flown over the highest elevation on the route (Garde *et al.,* 2021). The relationship between speed and altitude may therefore vary with location, as well as species.

The main effect of flight tortuosity on the need for speed correction is consistent with previous studies that have reported lower flight speeds during periods of tortuous flight (Dehnhard *et al.,* 2021; Gilmour *et al*., 2021; Rodríguez *et al.,* 2022), although the highest tortuosity values were represented by relatively few data points in this study. The broader point is that the flight style of free-living birds could also influence the error in dead-reckoned flight paths. Choughs are known for their particular flight style, which can involve aerobatic displays and manoeuvres, as well as switching between soaring and flapping flight (Flight, 2017; Glaeser *et al.,* 2017). These are likely to be associated with changes in airspeed (Hedenström *et al.,* 2002), and hence departure from a dead-reckoned flight path where a fixed speed is used. This may be most marked where choughs use updrafts over cliffs to maintain a fixed position. In this instance the ground speed is reduced to zero.

Finally, the model R^2 values recorded here show that it is important to consider model variance at the individual and flight level, as individual traits often account for a substantial portion of the model variance. Fisher *et al.* (2015), measuring multiple behavioural traits, showed that there is increasing among-individual variation over time within each of the different behaviours. Muff *et al.* (2020) explained how this individual-specific behavioural variation can explain movement patterns and habitat selection at a fine scale where results would otherwise show optimistic confidence intervals and standard errors.

While the R^2 values of the distance correction factor model show that equal variance can be explained by the fixed and the random factors, the R^2 values of the bearing correction factor model are too low to draw any meaningful conclusions, as only 8% of the variation seen in the bearing correction factor can be explained by the predictor variables. This was initially surprising, as a bird must adjust it's heading in relation to the wind vector if it is to successfully arrive at its goal destination (here, the loft). However, it may be that the crosswind component would be more pertinent than the headwind component when it comes to predicting the bearing correction.

Choughs appear to be flying shorter daily distances than the pigeons (here, choughs had a mean daily step distance of 763.3 m, compared to the pigeon flights of 5.7 km), so overall drift may be low. Dead-reckoning provides greater insight into the small-time changes in an individual's movement patterns, with lower power requirements than GPS (Smith *et al.,* 2018). DR also represents heading well, in a broad sense, so even uncorrected flight paths would provide information on the extent and timing of daily movements, as well as their direction.

While dead-reckoning provides extensive insight into movement patterns, it is not best deployed for analyses of habitat selection. DR does not produce multiple verified points in the same manner as VHF and GPS so could not be used against a generation of random points to determine habitat use and availability. Verified points are essential for DR to correct for drift, especially in faster animals or where there are long periods between verified points, as drift accumulates over time. The highly heterogenous and human-modified habitat matrix of Jersey means that uncorrected DR is unlikely to be useful for habitat selection analyses, as estimated positions could be in a different habitat type to the true locations.

Dead-reckoning has the potential to become a powerful tool, especially for soft-release reintroductions, as the release site provides a verified point to correct for drift for individuals consistently returning for supplementary feeding, allowing fine-scale movement paths to be produced for released individuals. In contrast to VHF, DR requires far less labour to collect data, making it a more feasible telemetry option for smaller teams of data collectors or when tracking elusive animals. Radio-Frequency Identification (RFID) systems could be integrated at feeders to record when birds are back at the aviary. This would provide known verified locations and additional information about how often birds are using supplementary feed.

Corrected DR using verified fixes could provide insight into fine-scales changes in flight paths, habitat selection, and which birds may lead longer-range movements. Here, error was analysed by correcting for drift at each fix along the movement path, providing insight into the relative importance of altitude, wind speed and flight path tortuosity. Were drift to be corrected by taking a known location each day (e.g., the release site/feeding station) and applying a constant correction factor across the track, the error would be different, as changes in speed within and between daily flights would not be taken into consideration. Overall, this study is an early exploration into the use of dead-reckoning for flight. Initial results show that dead-reckoning has extensive potential, however, further research needs to be conducted before the method is feasibly applicable to soft-release systems.

Conclusion

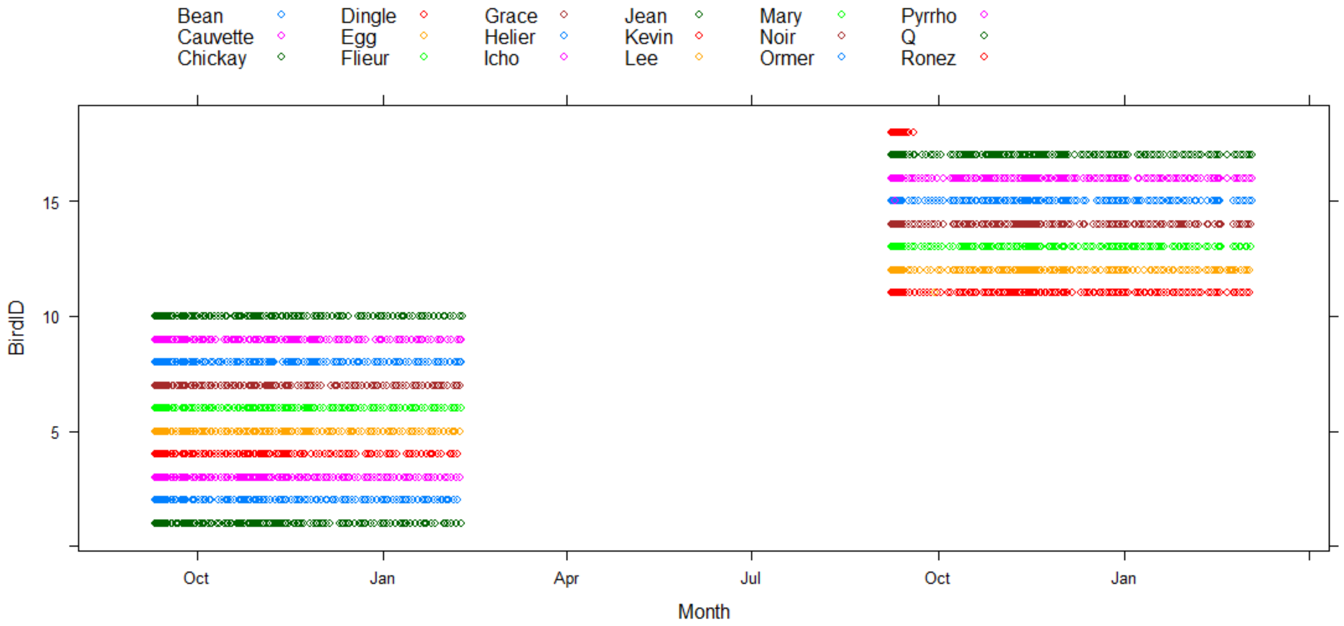
This study aims to assess the movements and habitat use of reintroduced red-billed choughs using biotelemetry. Red-billed choughs were soft-released on Jersey between 2013 and 2018 by Durrell Wildlife Conservation Trust. A total of 43 choughs were reintroduced to Jersey equipped with VHF transmitters and tracked over a period of 6 months after each release. Despite the relatively low frequency of these VHF locations (twice a day), this dataset provided valuable insight into the movements and habitat selection of the choughs. These data demonstrated that choughs remained very close to the release site, as the mean daily step distance for all released individuals was 763.3 m. Furthermore, the interaction statistics showed choughs from each release travelled together. Binomial generalised linear models showed that coastal grassland was the most used habitat by the choughs of both release groups across the island and at the release site, with coastal habitats making up 55.1% of the used habitat types, despite an island availability of only 11.6%. This raises the question of whether dispersal may be limited by a lack of suitable habitat. Agricultural land was also used and was the most available habitat at both scales, while urban areas were widely available but not used, bringing into question the future of these birds with increasing urbanisation.

While the VHF data indicate a strong tendency for birds to remain close to the release site, the low sampling frequency will underestimate the daily movement distance, and potentially the frequency and extent of less-frequent, longer-range movements. Thus, dead-reckoning allows the opportunity to monitor movement patterns by providing high-frequency flight paths showing fine-scale changes in movement. Data collected by Garde *et al.* (2021) of homing pigeons equipped with GPS and Daily Diary devices were analysed here to investigate the effect of headwind component, altitude and flight path tortuosity on the distance and bearing correction factors of the DR paths using two linear mixed-effects models. Stronger tailwinds required a greater distance correction factor (and therefore less correction in this study as the default speed was high), as a bird will cover ground faster with a tailwind, thus providing less opportunity for DR path drift. The marked effect of low wind speeds on DR drift shown in this study provides an initial insight into how drift may be affected when applied to locations with higher wind speeds, such as Jersey.

Many studies conclude that using multiple telemetry types simultaneously gains better results (Henderson *et al.,* 2018; Smith *et al*., 2018; Brownscombe *et al*., 2019). Indeed, here, and in other systems using soft-release, the use of multiple low-power systems could prove very powerful. Dead-reckoning can produce high-resolution movement paths but requires verified positions, such as VHF or GPS, to correct for drift. Once corrected, DR paths could also then provide information on habitat selection. Understanding the fine-scale changes of animal movement within different habitats would be an important tool in informing conservation policy that could ensure species habitat requirements are met, thus contributing to the long-term establishment of reintroduced animals.

Appendix

1.0 Verified points of all red-billed choughs released in September 2014 (tracking period: 10/09/214 – 08/02/2015, mean number of fixes = 145.3) and September 2015 (tracking period: 07/09/2015 – 03/03/2016, mean number of fixes = 152.4).



2.0 Habitat type classification, as defined by Phase I Habitat Survey data provided by Jersey Government Environment Agency (States of Jersey, 2011).

Agriculture	Arable land
	Arable land, *short term ley*
Coastal	Bracken, *open and scrub underlay*
	Coastal grassland
	Coastal heathland
	Dense scrub, *blackthorn, bramble, gorse, sallow and other*
	Dune dwarf scrub
	Dune grassland

	Dune marram dominated
	Hard cliff
	Open dune
	Rock
	Shingle
Grassland	Amenity grassland
	Bare ground
	Gardened
	Grassland, *improved and semi-improved*
	Parkland
Urban	Brown-field site
	Road
	Urban
Water Bodies	Marshy grassland, *Oenanthe dominated and semi-improved*
	Saltmarsh
	Standing water
	Swamp
Woodland	Planted coniferous
	Woodland, *plantation (orchard, etc.)*
	Woodland, *planted broadleaved*
	Woodland, *planted mixed*
	Woodland, *semi-natural, broadleaved*

Glossary

Bearing Correction Factor	The difference between dead-reckoned heading and GPS heading at equivalent points on a flight path, in the range of -180° to 180°.
Daily Diary	Biotelemetry tag incorporating a tri-axial accelerometer, magnetometer and barometric pressure sensor, designed by Wildbyte Technologies (2022).
Daily Diary Multiple Trace (DDMT)	Swansea University in-house software for the analysis of Daily Diary tag data.
Distance Correction Factor	A coefficient that is multiplied by dead-reckoned ground speed to match GPS ground speed.
Distance Error	Distance in meters between equivalent points on GPS and dead-reckoned tracks for a single flight.
Dead-Reckoning	The method by which flight paths are reconstructed by consecutively integrating heading and speed estimates from a known start location.
Headwind Component (HWC)	The component of a wind vector experienced as headwind, calculated as the angle between the wind speed vector and the GPS ground speed vector.
Vectorial Dynamic Body Acceleration (VeDBA)	A proxy for speed calculated from the dynamic acceleration values of each axis (x, y, z).
Very High Frequency (VHF)	A high-frequency radio signal which can be tracked using a receiver and directional antenna.

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