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Route navigation in homing pigeons (Columba livia): the use of visual cues over a familiar area.

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Route navigation in homing pigeons (Columba livia): the use of visual cues over a familiar area.

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I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards. ---------- Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw'r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o'r blaen ar gyfer unrhyw radd, ac nid yw'n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

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Abstract

The use of landmarks as navigational cues used by Homing pigeons (*Columba livia*) over a familiar area remains an unresolved area of study. With evidence supporting both a visual landscape cue-only method of navigation, known as pilotage and compass-based methods using bearings to navigate from one landmark to the next known as the mosaic map, conclusions are hard to draw. Much of the evidence in support of pilotage has been seen in Oxford, with displaced birds showing a high attraction back to their established routes and idiosyncrasy, which is in favour of this hypothesis. To investigate further the use of landmarks in pigeon navigation, two sites were used in North Wales, one of which has already been used in similar homing experiments. Training releases with young pigeons were completed followed by displacement releases over an area familiar to the birds. With a lack of idiosyncrasy found in these experiments and a rather chaotic off-route release, the results presented here are not in support of pilotage. However, this does not mean that the pigeons will not develop the piloting method for navigation. Combining evidence presented here with previous work could indicate that the methods used for navigation are age-dependent and the cognitive processes may change with age.

Key Words: Pilotage, Mosaic Map, Familiar Area, Navigation, Landmarks, Displacement

Contents

Chapter One – Literature Review:

Exploring Different Navigational Mechanisms in the Animal Kingdom

1.1 Introduction

The mechanisms by which animals navigate in familiar and unfamiliar areas are diverse and complex, with many different combinations of potential navigational cues being used (Alerstam, 2006). Perhaps the most intriguing navigational feats are those performed by avian species, with many of them migrating over extensive distances within or between continents and across vast oceans (Åkesson, 2003). Homing pigeons (*Columba livia*) have long been used in avian navigation experiments and are the most comprehensively studied in terms of navigation, along with migratory songbirds (Beason, 2005; Guilford and Biro, 2014). Homing pigeons are descendants of the wild rock dove (Rose *et al*, 2004; Wallraff, 2004; Beason and Wiltschko, 2015). They were domesticated more than 4000 years ago in the times of the ancient Egyptians as message carriers, due to their accurate and reliable homing abilities (Wiltschko and Wiltschko, 2016). However, much of the navigational evidence gained from them and other birds over the past few decades, through a variety of different experiments, is contradicting (Wallraff, 2003; Holland, 2014).

Types of orientation

There are three main types of orientation in avian navigation; 1) non-compass orientation or piloting, where landmarks are followed, for example, hedgerows, coastlines, roads, and rivers. 2) compass orientation, where a route is followed based upon the cues of one or more compass mechanisms, and 3) vector orientation, generally observed in young individuals on their first migration, which is the direction taken to reach their wintering grounds (Schmidt-Koenig, 1970; Åkesson *et al*., 2014). In vector orientation, the young birds cannot correct their direction upon being displaced, unlike the adult birds. The former is generally considered for shorter distance navigation, in a familiar area and the latter two mechanisms are accepted as more long-distance navigation. When an animal can correct for a displacement, it is called true navigation (Perdeck, 1958). True navigation is described as the ability of an animal to return to a specific location (in migratory animals) or its original location (non-migratory animals) after displacement to an unfamiliar location without knowing anything about the route taken for the displacement, cues at the goal location or familiar landmarks The ‘map and compass’ hypothesis falls under the umbrella of true navigation (Keeton, 1974; Holland, 2013).

The ‘map and compass’ hypothesis.

The ‘map and compass’ model of navigation was proposed by Kramer (1958), which is a two-step model of navigation, comprising a ‘map’ step and a ‘compass’ step. The ‘compass-step’ or compass orientation is the ability of an animal to orient itself in the desired direction by using one of several compass cues available. These compass cues include the sun, the stars, and the polarization of light (celestial cues) as well as magnetic cues from the Earth (inclination and polarity of the magnetic field). Much less is known about the mechanisms involved in the ‘map-step’ and its cues, especially the long-range map of migratory species. However, magnetic inclination, olfactory gradients, landmarks,

and infrasound are all proposed (Kramer, 1958; Wiltschko and Wiltschko, 1972; Hagstrum, 2000; Lohmann *et al*., 2004; Biro *et al*., 2004; Nevitt and Bonadonna, 2005).

Here I will look at the evidence for each navigational cue and discuss the applications in terms of bird species as well as other non-avian species.

1.2 Magnetoreception

The 'Magnetic Compass'

Unlike man-made compasses which detect the polarity (direction) of the magnetic field, the magnetic compass in birds distinguishes the equator from the poles (Wiltschko and Wiltschko, 1972). It does this by using the inclination of the magnetic field, rather than the direction of the magnetic field as in the polarity compass, which is also known as an 'inclination compass' (Wiltschko and Wiltschko, 1972, 1995; Schwarze *et al*., 2016). This method, however, is the same in both the northern and southern hemispheres, where the angle of inclination decreases towards the equator (Wiltschko and Wiltschko, 1972; Wiltschko *et al*.,1993). Whilst this does not pose a problem for shorter-distance migrants or non-migrants such as homing pigeons (Walcott and Green, 1974; Wiltschko *et al*., 1993), those trans-equatorial migrants, have to switch their compass to continue along their migratory route (Beason, 1992). Evidence shows that the use of the 'inclination compass' is light-dependent and therefore a light-dependent radical-pair mechanism has been proposed. This is a chemical-based mechanism involving photopigments in the eye, thus providing directional information for the magnetic compass sense (Ritz and Schulten, 2000; Wiltschko *et al*., 2005). Sea turtles (Lohmann *et* al., 2011), as well as bird species, are known to use the 'inclination compass' (Ritz *et al*., 2000) whereas some rodent species (Marhold *et al*., 1997) and salmon (Naisbett-Jones *et al*., 2020) use the 'polarity compass'.

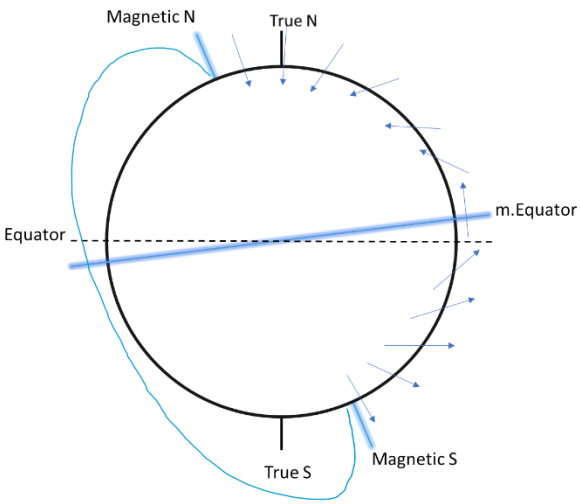

Figure 1 - based on a figure from Wiltschko and Wiltschko (2007), shows the inclination of the earth's magnetic field indicated by the arrows, the difference between the magnetic poles and the true poles. The curved line depicts the magnetic field. The angle of inclination at the magnetic equator (m. Equator) is 0°. The angle of inclination at the magnetic north and south poles are +90° and -90° respectively (Wiltschko and Wiltschko, 2007).

The 'Magnetic Map'

The inclination of the earth's magnetic field can also be used as coordinates on a "map". This differs from the magnetic compass as the inclination or intensity of the magnetic field is relatively stable, with gradual and predictable changes. Although not free of irregularities and natural anomalies, as the magnetic field varies reliably across the earth's surface, these differences in intensity act as a reliable source of positional information, like coordinates on a map (Lohmann *et al*., 2004). Perhaps the strongest evidence for cues of a magnetic map in birds is put forward by Kishkinev *et al*., (2015). The

virtual displacement of Eurasian reed warblers by 1000km eastward resulted in the re-orientation westward of the birds when tested in Elmen funnels. If the birds displayed disorientation rather than re-orientation, it would be difficult to conclude that the cause of the disorientation was the disrupted magnetic map, as there are multiple factors which could have caused it. However, the re-orientation westward supports the idea that the birds were able to identify and correct for the eastward displacement (Kishkinev *et al*., 2015). Similar experiments have been done using sea turtles off the Florida coast, with results matching those found in birds (Lohmann *et al*., 2004).

There is strong evidence for the presence of a magnetite-based mechanism to detect the cues for a magnetic map. Magnetite is the most common naturally occurring magnetic substance on earth and small amounts have been found in the skin of the upper beak of many avian species (Beason and Wiltschko, 2015). When pigeons and other migratory birds are treated with a magnetic pulse to re-magnetise the magnetite, the birds become deflected as opposed to disoriented, losing their sense of position but not direction. When tested for this, homing pigeons produced deflections in their orientation of up to 60° from their homeward direction (Beason *et al*., 1997). On their natural autumn migration, European robins were also given a magnetic pulse, gaining similar results to the pigeons, in the adult birds (Wiltschko and Wiltschko, 1995; Holland and Helm, 2013).

However, when a large number of homing pigeons were studied, the iron-rich (Fe^{3+}) cells in the upper beak turned out to be macrophages and not magnetic sensitive receptors. This, therefore, puts into question the whereabouts of the magnetite receptor (Treiber *et al*., 2012).

Sea turtles

Sea turtles are well known to swim vast distances across oceans to specific feeding sites and breeding grounds (Lohmann, 2007; Lohmann *et al*., 2008). Many studies have conclusively found that they use the earth's magnetic field to do this (Papi *et al*.,2000). As previously mentioned, sea turtles use the inclination of the magnetic field rather than the polarity (Lohmann *et al*.,2011). However, as with all navigational experiments, the question remains as to how species determine their longitudinal position based on the magnetic field since both polarity and inclination better indicate the latitudinal position (Putman *et al*., 2011).

However, hatchling loggerhead turtles (*Caretta caretta*) appear to be able to distinguish their longitudinal position. When released from two sites of the same latitude, but on opposite sides of the Atlantic Ocean, they were able to re-orient themselves to account for their displacement (Putman *et al*., 2011). Another study conducted on green sea turtles (*Chelonia mydas*) provided evidence that with increasing maturity, turtles can use the magnetic information in ever-increasing complexity, compared to hatchlings (Lohmann *et al*., 2004). This could suggest that as they increase in age, their 'magnetic map' develops with increasing complexity and more information.

Both Lohmann *et al*. (2011) and Putmann *et al*. (2011) propose the use of a bicoordinate map, which does not necessarily include latitude and longitude but somehow provides the turtles with this positional information (Putmann *et al*., 2011).

1.3 Celestial navigation

Celestial navigation encompasses both the sun and the stars, the sun being used by diurnal species and the stars used to guide the nocturnal species (Sauer, 1958). The use of the sun-compass requires time compensation (Sauer and Sauer, 1958; Sauer, 1958; Wiltschko and Wiltschko, 1981). To test the presence of a time-compensated sun-compass, clock-shift experiments are most often used. In these experiments, the subject is housed in a closed room where their perception of day and night is shifted by a set number of hours to reset their internal clock to the new conditions (Wiltschko and Wiltschko, 1981).

To investigate how birds develop a sun compass experiments were carried out by Wiltschko and Wiltschko (1981) using young homing pigeons. When young inexperienced pigeons (11 weeks and younger) were clock-shifted and released from an unfamiliar area, they were unaffected, and their direction of flight did not differ from the control group. However, when older birds were released under the same conditions, they deviated significantly which is characteristic of clock-shift experiments. This strongly suggests that the older birds (12 weeks and older) rely on the time-compensated sun-compass. The younger, naïve birds on the other hand, have not yet developed a sun compass and therefore rely on other navigational mechanisms to reliably find their way home. However, when young birds were subjected to a few training flights before being exposed to clock-shifting, birds as young as 8 weeks old showed the predictable deviation consistent with that of reliance on the sun compass. Researchers concluded that experience is dominant over age for the development of the sun-compass in homing pigeons (Wiltschko and Wiltschko, 1981; Budzynski *et al*., 2000).

At high latitudes, in polar conditions, the routes provided by following the sun-compass are reminiscent of orthodromes. Orthodromes are the shortest routes between two locations on earth (Alerstam *et al*., 1999) Findings from radio-tracking data of Arctic shorebirds back this theory. The birds' internal clock becomes out of sync with the local time as they cross longitudes (Alerstam *et al*., 2001).

Sunlight Polarisation

The polarisation of light can also act as a navigational cue. Sunlight contains a combination of magnetic and electric waves which travel at 90° angles to each other, in every orientation possible. When sunlight passes through the atmosphere, some of the elements are filtered out, this is the polarisation process. Electric vectors are the result of this polarisation and produce predictable patterns in the sky. The region is known as the ‘maximal polarisation band’, depends on the azimuth of the sun. Therefore, animals who can see the light polarisation, are not required to see the sun directly to calculate its azimuth (Schmidt-Koenig *et al*., 1991; Heinze and Reppert, 2011). The patterns produced by the band of ‘maximal polarisation’ are still visible up to approximately 45 minutes after sunset. Although it seems that birds cannot substitute the sun's azimuth for the polarization of light (Schmidt-Koenig *et al*., 1991), other species can. Non-migratory bats, for example, appear to use the cues provided by the setting sun to calibrate their magnetic sense (Greif *et al*., 2014), one example is the greater mouse-eared bat, (Holland *et al*., 2010; Lindecke *et al*., 2019).

Some migratory songbirds such as the savannah sparrow calibrate their compass cues against the polarisation of light at both sunrise and sunset (Muheim *et al*., 2006).

The sun compass has also been found in marine species as well as terrestrial species. Clock-shift experiments have also been carried out on green sea turtles off the shallow reef coast of Florida. Individuals were captured at night and recorded in an outdoor pool, in which they were oriented in an eastward direction (towards deeper waters). When the same individuals were then exposed to an advancement in the day-night cycle of 7 hours in a lab and then recorded again, they displayed a significant orientation westward, very much in line with the predictable deflection from a 7h clock-shift (Mott and Salmon, 2011). There is even evidence for the use of the sun compass in the larvae of small reef fish, navigating back to their reef of birth after being exposed to the drift from the currents of the ocean (Mouritsen *et al*., 2013).

Whilst there is plenty of evidence for a time-compensated sun-compass in many bird species, there is a lack of evidence suggesting that day-migrating birds use the sun-compass. However, this seems justified when considering the sun-compass relies on the arc of the sun (Guilford and Taylor, 2014) throughout the day and this changes both geographically and seasonally. Therefore, it would make more sense for the day-migrating species to use more reliable compass cues (Munro and Wiltschko, 1993).

Star Compass

For night-migrating birds (in particular, songbirds), using the stars as a compass is much simpler than using the sun as there is no need for a ‘time sense’ (Sauer, 1958; Foster *et al*., 2017). Night migrating songbirds use the orbital poles as their compass, in which they are not required to compensate for time as the pole star (Polaris in the northern hemisphere) remains at the same azimuth every night for the entire night, it never moves (Emlen, 1967, 1975). Many of these studies have been conducted in planetariums, where these artificial skies can be manipulated to emulate different conditions (Sauer and Sauer, 1958) or in funnel-shaped cages outside, where the field of view of the birds can be altered (Emlen, 1967).

The first experiments, which identified the use of the centre of celestial rotation were carried out with these night-migrating passerines. Perhaps the most crucial being indigo buntings conducted by Emlen (1967, 1975). Indigo buntings were placed in Emlen funnels outside under clear skies. Only the sky directly above them was visible. The birds oriented in the funnel in the same direction as they would on their annual migrations. In autumn they oriented southward, and, in the springtime, they oriented in a northeast direction. Further experimentation, carried out in a planetarium, where the polestar (Polaris) was changed to Betelgeuse (in the constellation of Orion) provided very strong evidence that young Indigo buntings rely on celestial rotation rather than the patterns of the stars as they were completely unfazed by the change, orienting in their correct migratory direction (Emlen, 1975). The learning of the patterns of stars appears to develop later in adult birds, with celestial rotation becoming a secondary navigational mechanism. Adult birds were still able to orient themselves under motionless skies (Emlen, 1975). Many birds set off on their migration at sunset, which they use to

‘calibrate’ their magnetic compass. Once calibrated, they can then maintain their direction from the use of their star compass (Moore, 1986; Muheim *et al*., 2006, 2009).

There is some evidence to suggest that the harbour seal (*Phoca vitulina*) can navigate by the same mechanism as Polynesian sailors, by using a ‘lodestar’. A lodestar is a single star, which has a distinguishable position in the sky, and can be used as a navigational point (Foster *et al*., 2017). Mauk *et al*. (2005) showed that harbour seals can see celestial objects, by teaching the seals to identify Venus and the star Sirius. Using artificial stars, they then identified the minimum brightness of 4.4 stellar magnitudes that could be detected by the seals. The researchers then trained two harbour seals to identify Sirius in a planetarium. They rewarded the seals when they touched the wall directly beneath the projection of Sirius (Mauck *et al*., 2008). Although this looks promising, there needs to be more research into this as stated by Foster *et al*. (2017), as this could be an example of landmark navigation rather than true lodestar mapping.

Interestingly, it is not just celestial rotation and star patterns that can act as navigational cues. A species of Dung beetle, *S. satyrus*, of South Africa, relies on the Milky Way as a compass to orient themselves whilst rolling their dung-balls. When a planetarium was manipulated, firstly only displaying the milky way, and secondly hiding the streak of the Milky Way, the beetles oriented in the same fashion to viewing the natural starry sky in the first case and took longer to orient themselves in the second case Dacke *et al*., 2013).

1.4 Landmarks

Whilst there is general agreement that homing pigeons use landmarks within their familiar area, it is often disputed as to how they use them and to what extent they are used (Biro *et al*., 2004). There are two proposed mechanisms for the use of landmark navigation. Firstly, there is piloting, whereby the birds navigate using the landmarks as reference points, traveling from one to the next (Füller *et al*., 1983; Biro *et al*., 2006). Secondly, there is the theory of the ‘mosaic map’, where birds retain the directional information and the topography of the landmarks to create a map of the local area and use compass cues to navigate between them (Biro *et al*., 2004, 2007). One piece of evidence in support of piloting is route loyalty to a particular flight track, even when this track might be longer or more inefficient (Biro *et al*., 2004; Fuiman *et al*., 2020).

To determine the importance of landmarks, experiments on homing pigeons have been conducted using frosted lenses. In these experiments, the birds were able to still navigate to within 1km of the home loft and in some cases were able to enter the loft (Schmidt-Koenig and Schlichte, 1972). Many have used the results of these experiments as arguments against the use of landmarks in pigeon navigation. However, in further experiments where the birds were split into two different groups, the birds allowed to view their surroundings before being released were able to home faster than those deprived of this early visual opportunity of the landscape. Several of the pigeons wearing the frosted lenses would not fly at all, which indicates the lenses had strong implications for the birds' navigational abilities (Gagliardo *et al*., 2020).

However, the evidence from displacement experiments over familiar territory, where birds are displaced to a new release site from one where they have extensive experience showed the birds deflecting back to their established route. This route loyalty would unlikely be observed if the birds used compass cues in preference to landmark cues over familiar territory (Biro *et al*., 2004, 2006). These routes that the birds remain loyal to are very individually distinct and are not the most direct or efficient (Biro *et al*., 2004; Meade *et al*., 2005). Given that even in clock-shift experiments, where the compass component is out of sync with the visual cues, birds who were familiar with the release site, showed no effect of the clock-shift, which demonstrates a strong reliance on the visual landmarks over the compass cues. Another key piece of evidence in support of piloting in homing pigeons is that in one experiment, the only bird to not develop a strong route loyalty and therefore not recapitulate turned out to be blind in one eye (Meade *et al*., 2005).

Landmarks do not include only singular structures, both natural or man-made, but also include linear landmarks such as roads, rivers, and the coastline (Zaleshina and Zaleshin, 2020). Landmarks are not necessarily visual but could also comprise geomagnetic anomalies and specific sources of infrasound (Wiltschko and Wiltschko, 2015) as well as gradients of light, such as different levels of snow coverage for Antarctic marine species (Fuiman *et al*., 2020). This leads to an interesting example of piloting by the Weddell Seal (*Leptonychotes weddellii*) when diving under the Antarctic ice. GPS trackers provided 'strong evidence' for the use of piloting by above-ice visual features to find their way home. When individuals were displaced to an unfamiliar site, they partook in several short-distance dives before committing to their long-distance dives (Fuiman *et al*., 2020).

Most penguins are considered a pelagic foraging species; however, the yellow-eyed penguins (*Megadyptes antipodes*) are benthic foragers (Mattern *et al*., 2007). When fitted with GPS trackers, it was revealed that the penguins travelled to their foraging sites at distances between 12-20km. The penguins displayed a very strong route loyalty which noticeably changed direction at specific points along their route. In a further study, Mattern *et* al., (2013) attached GPS trackers to Yellow-eyed penguins foraging in the South New Zealand mid-continental shelf. The penguins were found to forage in lines following the continental shelf. At least some of the foraging paths also coincided with a shallow groove in the seafloor, likely caused by a small trawler (Mattern *et al*., 2013; Fuiman *et al*., 2020). As a benthic forager who does not migrate, the use of visual cues on the seafloor would also allow them to develop a 'mosaic map' of the area (Mattern *et al*., 2013).

1.5 Olfactory map

Possibly the most explored method of navigation in avian species is olfaction (Kishkinev *et al*., 2019). Homing Pigeons are the most researched species in terms of olfactory cues and orientation (Nevitt and Bonadonna, 2005). Based on the "olfactory navigation hypothesis" proposed by Papi (1971) pigeons learn the odours and wind directions around their loft. When they are taken to a release site, whether that be familiar or not, they detect the changes in the odour gradients with reference to home, thereby orienting themselves in the homeward direction (Zannoni *et al*., 2020). There has been extensive research demonstrating anosmic individuals fail to orient themselves and therefore their

navigational abilities are compromised, for both homing pigeons as well as in wild species (Zannoni *et al*., 2020). The issue with the olfactory navigation hypothesis is that it is difficult to identify, quantify and map which odours birds use as their orientational cue (Ganzhorn and Paffrath, 1995; Wallraff, 2005; Wiltschko and Wiltschko, 2015).

However, research into other species such as the procellariiform seabirds (albatrosses and petrels), has demonstrated the use of dimethyl sulphide (DMS) as an orientational cue used for foraging across the vastness of the Southern Ocean (Nevitt *et al*., 1995). DMS has been studied widely as a regulator for the Earth's climate (Nevitt *et al*., 1995). It is produced when zooplankton feed on a select few classes (Keller *et al*.,1989) of phytoplankton (Nevitt *et al*., 1995; Wright *et al*., 2011). The plumes of DMS can provide a 'map' of the otherwise featureless ocean, showing beneath the surface structures such as shelf edges and seamounts (Nevitt and Bonadonna, 2005).

Penguins (Sphenisciformes) were commonly thought to lack a sense of smell despite being closely related to the procellariiform seabirds and are known to be visual hunters (Cunningham *et al*., 2008; Wright *et al*., 2011). Cunningham *et al*. (2008), demonstrated that African Penguins can detect DMS on land and further research into this has provided evidence that African Penguins can detect DMS out at sea, which they likely use to locate their prey from a distance (Wright *et al*., 2011). Chin-strap Penguins were also tested for their sensitivity to DMS on land, which yielded the same results as those for the African Penguins (Amo *et al*., 2013). This phenomenon is not unique to marine bird species. The Harbour Seal (*Phoca vitulina vituline*) has demonstrated a high sensitivity to DMS, likely used for orienting towards highly rich food sources underwater (Kowalewsky *et al*., 2006).

So far, the olfactory detection of dimethyl sulphide appears to apply only to marine species. However, rather interestingly, a recent study conducted in Arnino, Tuscany, a rural coastal region in northwest Italy demonstrated that homing pigeons can use DMS gradients to orient themselves homeward. In this case, the Tyrrhenian Sea was located to the west of the home loft. According to the "olfactory map hypothesis" the young birds likely learned the familiar odours around their loft so when displaced, they were able to compare the levels of odour compounds at the release site to those learned at their loft. The release sites were all to the east of their loft, therefore the DMS gradient would become weaker the further inland (east) you go (Zannoni *et al*., 2020).

However, olfaction is not necessarily a key component of all bird species' orientation and navigation. Kishkinev *et al*. (2019) provide evidence that the Eurasian Reed Warbler, a migratory species, does not require the olfactory map for navigation purposes. By displacing both anosmic and control birds from the eastern Baltic to Moscow, a displacement of 1000km, both groups of birds were able to re-orient themselves and correct the displacement.

1.6 Infrasound

Elephants are well known for their infrasonic and ultrasonic communications across vast distances (McComb *et al*., 2003; Garstang, 2015) as well as some whale species (McComb *et al*., 2003); however, some research suggests that infrasound can be used as a navigational cue for other

species. This method is very controversial as it doesn't quite fit the mould of the more accepted methods for navigation i.e., the 'map and compass' model (Beason and Wiltschko, 2015).

Navigational sources of infrasound include oceanic waves and atmospheric storms. Low-frequency sounds travel much further than high-frequency sounds, hence the ability of animals such as elephants, to communicate over vast distances (Beason and Wiltschko, 2015). This detection of seismic signals from the earth has been suggested for the Asian elephants (*Elephas maximus*) of Sri Lanka and Thailand, when, during the 2004 Sumatran earthquake, they were able to detect the crashing of the tsunami wave hitting the shore at distances of 1000km away. African elephants (*Loxodonta Africana*) have also been shown to detect distances of other herds up to 2.5km away (Garstang, 2015).

Homing pigeons once again take the experimental spotlight for many of these investigations. In the 1990s pigeon races across Europe and northeast America were significantly disrupted with no explanation. Very few pigeons arrived on time with many of them being delayed by hours to days and the majority did not make it back to their home lofts. The common factor in all these situations was the scheduled flight of Concorde from Paris to New York. The timings of the pigeon locations were consistently coordinated with the timing of Concorde going supersonic. In one case with two pigeon races happening in Virginia and Pennsylvania, which started at different times on the same day, the delayed Concorde flight from Paris to New York was predicted by the disruption of the two pigeon races (Hagstrum, 2000).

In further experimentation, Hagstrum proposes that the atmospheric background noise, which is in the infrasonic band, provides navigational cues. Evidence for this includes the annual variation in homing performance by birds released in summer versus winter, correlating with annual variation in seismic background noise. In winter, the homing ability of the birds decreases as observed at locations in Germany, which coincides with the higher amplitude of seismic background noise. This has been aptly termed the 'Wintereffeckt' and is observed across both mature and young birds (Hagstrum *et al*., 2016). This variation could be due to the impact of storms coming across the Atlantic Ocean. More evidence for infrasound and the interaction of atmospheric conditions includes a study in Switzerland, where pigeons only flew under temperature inversions. If it is the case that infrasound is a strong navigational cue, then the avoidance of large water bodies by pigeons could also be explained (Hagstrum, 2015).

1.7 Conclusion

There is no disagreement that the mechanisms of navigation are extremely complex. To summarise, there are three types of orientation 1) non-compass or piloting, 2) compass orientation, and 3) vector orientation, of which the latter is not considered true navigation. The 'map and compass' theory encompasses magnetic, solar, celestial, infrasound, visual and olfactory cues.

From the evidence reviewed here, conclusions could be made that there is a hierarchy of navigational cues used by pigeons as there is at least some evidence for each type of 'map cue' and 'compass cue'. Are the navigational mechanisms used by homing pigeons universal or location-dependent?

There appears to be more evidence to suggest that the latter could be the case, certainly in terms of which map cues are used. Coastal populations of homing pigeons may use olfactory odour cues as their principal ‘map’, due to the more predictable sea breeze and dimethyl sulphide plumes from the plankton. Inland populations may use a magnetic inclination map as it could be unlikely that olfactory cues would be reliable enough to produce the highly accurate route loyalty that is observed in the homing pigeon’s familiar area (Meade *et al*., 2005).

With evidence from pigeons and the use of the olfactory map, as well as green sea turtles and their use of magnetic cues, it can be concluded that, at least in some species, navigational cues are learned. This is especially the case for map cues but also appears true for some compass cues as well.

In the broader sense of animal navigation, it appears that some species are more loyal to one or two navigational cues, for example, dung beetles using celestial cues for their orientation. Whilst others such as sea turtles, appear to use a combination of navigational cues. In terms of homing pigeons, there is evidence for all but celestial navigational cues, which potentially indicate a much higher level of complexity than we have identified thus far.

Future studies could take a more holistic approach or a comparative approach to investigating the individual navigational mechanisms and cues. For example, comparatively looking at two populations of the same species at two different geographical locations, in an attempt to identify whether they use the same navigational cues in the same way, or whether they rely on different cues in the primary sense. For example, a coastal population and an inland population. Alternatively, do long-distance migrants change their primary navigational cues depending on their geographical location along their migratory route as opposed to relying on just one primary cue the whole length of their migrations? Another important question is how do the navigational cues work together to create a more complex system than we have thus far discovered?

Chapter Two

2.1 Introduction

The ability of species to navigate over a familiar area is quickly becoming a key study point in the realm of avian navigation. Homing pigeons (*Columba livia*) play a lead role in these navigational experiments due to their reliable homing abilities (Bingman and Ioalè, 1989; Guilford and Biro, 2014). The mechanisms used for navigation over short distances in a familiar area remain inconclusive. Kramer's (1953) map and compass hypothesis for navigation, proposes the use of a map sense to determine where the bird is in relation to its destination, and a compass cue, for the bird to orient itself in the correct direction of its destination, this is evident in long-distance navigation from unfamiliar areas. There are two models for the use of landmarks as visual cues in navigation over a short distance in a familiar area, firstly "pilotage" where familiar landmarks are navigated one after the other, with no dependence on compass cues (Biro *et al*., 2004; Biro *et al*., 2007). Secondly, the "mosaic map" model where compass cues are used to get from one landmark to the next (Wiltschko and Wiltschko, 2003; Biro *et al*., 2004, Meade *et al*., 2005). The mosaic map model falls into Kramer's (1953) map and compass hypothesis as a two-stage mechanism. There is much debate as to which method of navigation homing pigeons prefer when navigating over a familiar area (Holland, 2013).

The time-compensated sun-compass is widely accepted as the dominant compass cue in homing pigeons (Biro *et al*., 2007). With manipulations of the time compensated sun-compass by using clock-shifting methods, the birds' internal clock is shifted by a given number of hours, perceiving sunrise a few hours ahead or behind actual sunrise time. This deliberately sets their internal clock in conflict with the external cues given by the sun, therefore providing a predictable angle of deflection to be seen if the birds are relying on the sun compass to navigate (Bingman and Ioale, 1989).

Early work disregarded the use of visual cues such as landmarks as unimportant for navigation. However, more recent research is indicating a crucial role for visual cues in navigating over a familiar area (Meade *et al*., 2005). Before the development of GPS navigational systems, homing experiments used vanishing bearings to determine the initial orientation of the birds' flight home, and the time it took for the birds to reach home as a measure of efficiency. These methods, however, are a rather inaccurate measure as the exact direction home for the entire flight cannot be recorded, nor can the inaccurate speed show how idiosyncratic, or efficient the birds are (Meade *et al*., 2005). Now that experiments use GPS loggers, we can get more insight into the methods of navigation, which is yielding even more contradicting results (Meade *et al*., 2005).

Studies depriving pigeons of sensory navigational cues, such as olfactory cues and magnetic cues have shown that the birds' can still navigate home using just their visual sense (Meade *et al*., 2005). However, Koenig-Schmidt and Schlichte (1972) used frosted lenses on pigeons, depriving them of their visual cues, and yet the birds were still able to navigate within range of their home loft. This suggests that visual cues may be necessary for the birds to fly back into the loft, but not used to fly from their release site to the vicinity of the loft (Schmidt-Koenig and Schlichte, 1972; Schmidt-Koenig

and Walcott, 1978; Füller *et al*., 1983) This evidence combined with clock-shift studies, where birds released from a familiar site show the predicted angle of deflection in initial orientation and seemingly disregard their familiar landscape cues, has been enough evidence for many researchers to reject the hypothesis of visual cues being necessary for navigating over a familiar area (Bonadonna and Gagliardo, 2021). This conflicting evidence for exactly how homing pigeons navigate over a familiar area has proven to be rather controversial.

Numerous studies conducted in Oxford show that when birds are released from a training release site multiple times, the efficiency of their routes home increases with an increasing number of releases (Meade *et al*., 2005; Biro *et al*., 2006; Flack *et al*., 2012; Guilford and Biro, 2014). The routes are also highly stereotyped and individual to each bird (Biro *et al*., 2004, 2006). Although the efficiency increases, it never reaches full efficiency with the birds' never flying the most direct route home, which suggests a reliance on landmarks for piloting (Biro *et al*., 2004; Meade *et al*., 2005). These experiments also showed that when displaced to an unfamiliar release site a few kilometres away from the training release site, the birds fly back to their established route home and follow it from the point at which they intersect it. When the birds were deprived of their other sensory cues, with one group wearing magnets on their heads for the duration of the flight to exclude magnetic cues, and another group made anosmic to exclude olfactory cues, all the birds bar one still produced the highly idiosyncratic routes. The bird that didn't follow this trend was blind in one eye, again, strong evidence for visual cues being dominant here (Meade *et al*., 2005). Conclusions from these results are that pilotage is favoured rather than the mosaic map for navigating the short distances of a familiar area (Biro *et al*., 2004).

However, more recent work in Bangor, North Wales, found different behaviours to those in Oxford. Whilst the bird's flight efficiency also increased with an increasing number of training flights, and route stereotypy was also identified, they found different methods for navigation when the birds were displaced. Rather than flying to their already established route home, they tended to either parallel it, find a completely new route home, or follow the coast home (Griffiths *et al*., 2021). With evidence both for and against the use of visual cues, either for pilotage or as part of a mosaic map, it is difficult to draw firm conclusions.

This experiment aims to look at how homing pigeons navigate over a familiar area from two locations around the Bangor area, North Wales. The experiment focuses on visual cues rather than compass cues. Efficiency, idiosyncrasy, and off-route releases will be used to identify whether the birds appear to rely on the visual cues presented to them from the landscape, or on compass cues most likely being the time-compensated sun compass. Firstly, a replication of the original Bangor study (Griffiths *et al*., 2021) will be done with the exception of only carrying out 5 training releases to identify whether this is sufficient training to reach peak efficiency which is what the previous study finds. Here, the same training release site will be used in Y Felinheli and the same off-route release sites. Secondly, the methods again will be replicated from the original Bangor study, this time with a change in release site at a location near Pentraeth, Anglesey. This new release site is perpendicular to the Y Felinheli

release site. This is to determine whether birds will demonstrate the same behaviours as before in (Griffiths *et al*., 2021) or whether those results were site-specific.

Hypotheses

The efficiency of individual birds will increase as experience increases with repeated releases from the same site

Five training releases will prove to be sufficient for peak efficiency to be reached, based on previous efficiency experiments where the efficiency levelled off after 5 training releases.

The birds will develop individually unique routes home to the loft from the training release sites.

When released from an off-route site, the birds will not be attracted back to their established routes, as has been observed in previous experiments in the area.

2.2 Methods

Release Sites

Two different locations were chosen for the training release sites, firstly a site just outside of Y Felinheli along the Menai Straits, and secondly a site just outside of Pentraeth on Anglesey.

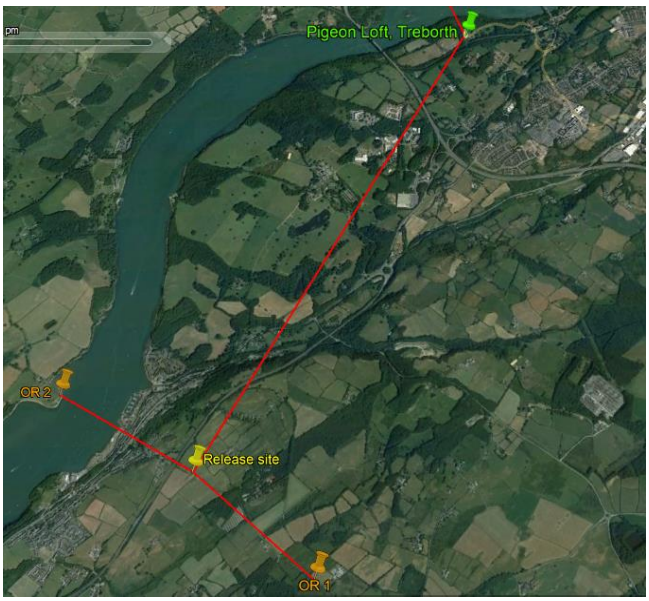

Figure 2. Map showing the locations of the home loft in Treborth botanic gardens, the training release site in Y Felinheli and the two off-route release sites.

Firstly, a group of 30 homing pigeons all one-year-old and previously the subject of homing experiments, were trained with flock releases to refamiliarise themselves with the area. These birds were used in experiments the previous year so had prior experience flying in the area. They were given training flights at 4 sites around the loft. First, the Treborth playing fields (53.2153427, -4.1753522), followed by Parc Menai (53.2081619, -4.1865424) and Bangor Football Club (53.2251625, -4.1470955) and finally the Menai Bridge Viewpoint on Anglesey (53.2225215, -4.1835577). The training release site chosen here was the same as in the previous study (Griffiths *et al*., 2021) just outside of Y Felinheli, North Wales (53.181583, -4.202611) which is 4.39km away from the loft. This same site was chosen to allow for a comparison between the first 5 releases in the previous experiment with the 5 training releases presented here and therefore identify whether 5 releases are

sufficient for peak efficiency to be reached. Despite the short distance from the loft, it is still unlikely that the birds could see it directly from the release site, given the terrain of the area and the fact the loft is surrounded by trees.

Figure 3. Map showing the locations of the home loft in Treborth botanic gardens, the training release site outside Pentraeth and the two off-route release sites.

Secondly, Following the same methods as in Y Felinheli, a different group of 15 first-year homing pigeons were used here as test subjects. Their training consisted of flock releases from Treborth playing fields (53.2153427, -4.1753522), Parc Menai (53.208000, -4.186487), Anglesey viewpoint (53.222395, -4.183856), Y Felinheli (53.181575, -4.202417), Anglesey halfway (53.250565, -4.255875), Llangefni (53.255997, -4.291744) and Lon ffynnon fair (53.163967, -4.233927) which allowed them to familiarise themselves with the local area as they had never before flown outside their loft before the experiment.

The release site chosen as the training site was located just outside of Pentraeth, Anglesey (53.272282, -4.211400). The release site is 6.7km away from the home loft in Treborth Botanical Gardens in Bangor (53.216827, -4.173168). The first off-route site (53.261251, -4.223857) is 1.49km left of the training release site. The second off-route site (53.267551, -4.189447) is 1.56km to the right of the training release site. These sites, unlike the off-route site at Y Felinheli, were not perpendicular to the training release site. This was due to a lack of access to suitable places perpendicular to the training site, with lots of inaccessible fields and a lack of roads. By using a different release site with a different cohort of birds, comparisons with the previous study (Griffiths *et al*., 2021) can be made to determine whether the birds again increase in efficiency as their experience with the area increases.

Releases

The birds being released from Y Felinheli had a total of 5 training releases from this site and all the birds were released individually with 5-minute intervals between each bird to reduce the chances of them following each other. All flights were recorded at 1-second intervals using either iGotU GPS trackers (releases 1-3 and 5) or more recently developed Bangor Biologgers (BBloggers, releases 4 and 5) attached to their backs with Velcro strips. Following this, half of the birds were displaced to the left off-route release site for one release and the same for the right off-route site. The first off-route site was just past Greenwood Forest Park (53.175200, -4.188700) which is 1.16km from the training site and the second off-route site was across the Menai Straights on Anglesey (53.1863886, -4.2183289) which is 1.19km away from the training site. The off-route release sites were 1.16km and 1.19km respectively perpendicular to the training release site.

The maximum wind speed for all the releases was 7mps as in previous homing experiments (Biro *et al*., 2004) to ensure the birds were not displaced by the wind and therefore all tracks recorded by the GPS loggers reflected the birds' decisions. The birds were fed after they had been released so they were more likely to fly straight back into the loft, where GPSs could be collected straight away. The experiment ended with 13 birds' successfully recorded tracks for all releases.

Release Number	*Time of 1st Release*	*Time of Final Release*	*Date*
1	12:30	15:25	27.5.2021
2	12:10	13:56	1.6.2021
3	12:20	12:55	5.6.2021
	12:35	13:45	12.6.2021
4	12:10	14:45	13.7.2021
Catch up 1	12:40	13:20	15.7.2021
Catch up 2	12:31	13:02	20.7.2021
Catch up 3	11:50	12:10	22.7.2021
5	12:00	12:37	3.8.2021
	11:30	12:30	4.8.2021
	12:05	12:35	16.8.2021
Off-route 1	11:20	12:20	23.8.2021
Off-route 2	11:33	12:35	24.8.2021

Table 1. The dates and times of all the releases at the Y Felinheli release sites. Some releases were over several days due to changing weather conditions, so these are split appropriately.

All 15 birds released at Pentraeth were again released individually with 5-minute intervals between each bird from the training release site. There was a total of 18 training releases from this site and all were recorded at 1-second intervals using iGotU GPS trackers attached to their backs with Velcro strips. Following this, 6 of the birds were displaced to the first off-route release site for one release and the same for the second off-route site. All of the off-route releases were completed on the same day to ensure weather conditions were approximately the same for both sites. The maximum wind speed for all the releases was 7mps as in previous homing experiments (Biro *et al*., 2004) to ensure the birds were not displaced by the wind and again they were fed after they had been released so they were more likely to fly straight back to the loft.

Release Number	*Time of 1st Release*	*Time of Final Release*	*Date*
1	11:25	12:35	26.8.2021
2	11:12	12:22	7.9.2021
3	11:00	12:05	10.9.2021
4	11:20	12:15	11.9.2021
5	11:15	12:20	14.9.2021
6	11:25	12:15	15.9.2021
7	11:30	12:30	16.9.2021

8	11:05	12:00	20.9.2021
9	11:50	12:50	21.9.2021
10	11:40	12:40	23.9.2021
11	11:45	12:45	6.10.2021
12	11:30	12:30	8.10.2021
13	11:10	12:10	10.10.2021
14	11:30	12:30	11.10.2021
15	11:30	12:30	12.10.2021
16	11:05	12:05	14.10.2021
17	11:30	12:30	15.10.2021
18	11:45	12:45	22.10.2021
Off-route 1	12:20	12:50	2.11.2021
Off route 2	13:10	13:35	2.11.2021

Table 2. The dates and times of all the releases at the Pentraeth release sites.

Comparisons of the off-route releases with the previous Bangor work and the work carried out in Oxford can be made. It is predicted that the birds from Y Felinheli will repeat the behaviour previously seen from this release site and not be attracted back to their established route, and instead will either parallel it or follow the coast home. The hypothesis that the birds from Pentraeth will also follow this behaviour is made, based upon the geographical location. Although the behaviour may differ from Y Felinheli as coast-following is not really an option from Pentraeth as it is inland and adjacen to the Menai Straits.

Figure 4. Map showing the locations of all the release sites for Y Felinheli and Pentraeth and the home loft in Treborth botanic gardens.

Data Analysis

All the data were analysed in R (Rx64 4.1.1) and GPS tracks were imported using the package 'PlotKML' (data was analysed by the release site). Calculations were completed using the R packages 'geosphere' and 'circular'. The distance from the release site, distance from home loft, home direction, current direction and cumulative distance were all calculated for each bird and each release. The circling behaviour around the home loft and the release site were cut out, with a 500m radius. Vincenty calculations were used to calculate the distances rather than using the 'Great Circle' method as it is a more accurate calculation.

Vincenty calculates the distance from one location to another on a spheroid, in this case, therefore, considering the curvature of the earth (Vincenty, 1975; Kifana and Abdurohman, 2012).

Efficiency was calculated with the shortest possible distance from the release site to the loft divided by the actual distance the bird had flown (Biro *et al*., 2004; Griffiths *et al.,* 2021). A mean efficiency for each release was then calculated and a linear model was applied to analyse the difference in the efficiency against the release number. Following this, a post hoc Tukey test was used for the Efficiencies at Pentraeth to investigate further the differences in efficiencies and which ones were significantly different.

To compare the idiosyncratic nature of individual birds, using nearest neighbour distance calculations; releases 1, 2 and 3 were used for Y Felinheli and releases 10, 13 and 17 were used for Pentraeth. The mean efficiency for each of these releases was calculated and compared to release 5 for Y Felinheli and release 18 for Pentraeth. These releases were chosen as all birds had these successfully tracked, allowing a fair comparison. Nearest neighbour distances are used to see how similar a track is compared to another track, for example, with 'self' nearest neighbour distances, the similarity between a birds own tracks can be identified, based on how near or far two points are from one another along the track. Similarly, with 'other' nearest neighbour distances, the similarity between tracks of the two different birds can be compared in the same way. Using nearest neighbour calculations for each birds' own tracks the 'self' nearest neighbour distance was calculated. This was then compared to the calculated 'other' nearest neighbour distance. To calculate the 'other' nearest neighbour distance, the same methods as 'self' was repeated but rather than the tracks being compared to themselves, the tracks were compared to another random birds' track. For these calculations, every second point was taken out of the dataset, so the measurements were every two seconds for the whole track. This was repeated for each of the three tracks for each bird and then repeated for each of another random bird's tracks with the distance between them measured. A mean distance was subsequently calculated. The nearest neighbour distances for 'self' and 'other' at Y Felinheli and then Pentraeth were then compared using a paired Wilcoxon signed-rank test. The nearest neighbour distances can then be used to see whether any of the birds' own previous track have any influence on their later tracks of if other birds' tracks are influencing others.

In order to investigate the influence, the birds' established routes have when displaced to another release site analysis of the off-route release tracks was done by plotting the final training flight for each bird along with the individual's off-route flight track. Visual analysis of the off-route tracks combined with calculated ID (Instantaneous Deflection) values allows the overall directions the birds flew in to be observed. Instantaneous deflection is described as the difference between the current heading and the direction of home (Griffiths *et al*., 2021).

Ethics

Handling of the birds was kept to a minimum to reduce stress. The GPS devices were fitted with Velcro glued to their backs using a non-toxic adhesive. This method was chosen as it reduces handling time compared to other methods such as using harnesses, which in turn reduces the birds'

stress and the GPS' weighed no more than 5% of the birds' body mass. All releases were carried out after 11:00 am as earlier than this increases the risk of predation by Sparrowhawks and Peregrines which was assessed via an AWERB (Animal Welfare Ethical Review Body) review. The methods were also approved by the University ethics committee.

2.3 Results

Y Felinheli

Efficiency: The efficiencies were calculated for each bird with circling behaviour both at the release site and the loft excluded from the calculations. The efficiencies for all the birds were then taken to calculate the mean efficiency for all birds in each release (mean efficiencies for releases 1-5 respectively 0.777, 0.784, 0.814, 0.835, 0.735). A linear model was applied to the mean efficiencies where p = 0.4757 with no significant difference between them and all highly efficient routes from the start. This result does not back the findings from previous studies as in these, there was a significant increase in efficiency across the first 5 training releases (Griffiths *et al*., 2021).

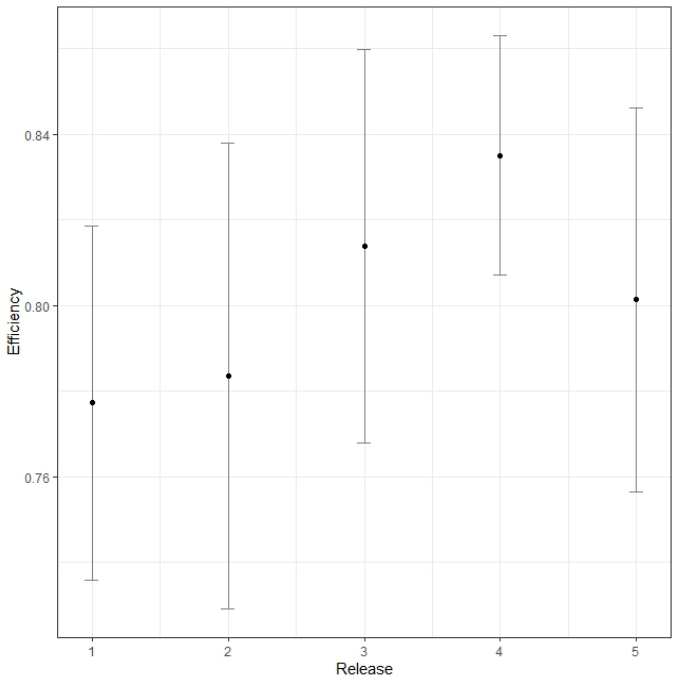

Figure 5. Mean efficiencies for each release plotted for Y Felinheli with error bars displayed.

Idiosyncrasy: The tracks for releases 1, 2 and 3 were used to calculate the nearest neighbour distances (nnd) for 'self' and 'other'. For the 'other' nearest neighbour distances, the final track (track 5) was compared to another random birds' track that wasn't itself, whereas the 'self' nnd was a comparison of its final track (track 5) and its own three tracks. Nearest neighbour distance calculates the distance between the two tracks at each point along the whole length of the track. *Figure 6* displays the nearest neighbour distances for 'self' and 'other' comparisons. Using a Paired Wilcoxon signed-rank test (v=13, P=0.9375) there was no significant difference found between the 'self' and 'other' comparisons of nearest neighbour distance, with the mean being approximately just over 400m for 'other' and just under 400m for 'self'. This means that each bird was flying a route home that was no more similar to its own tracks than it was to another bird's route home, therefore providing evidence against idiosyncratic routes home.

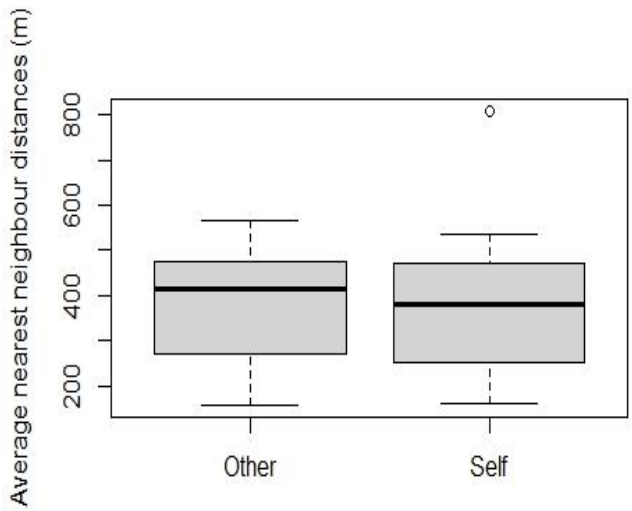

Figure 6. Average nearest neighbour distance comparison for 'self' and 'other' at Y Felinheli release site.

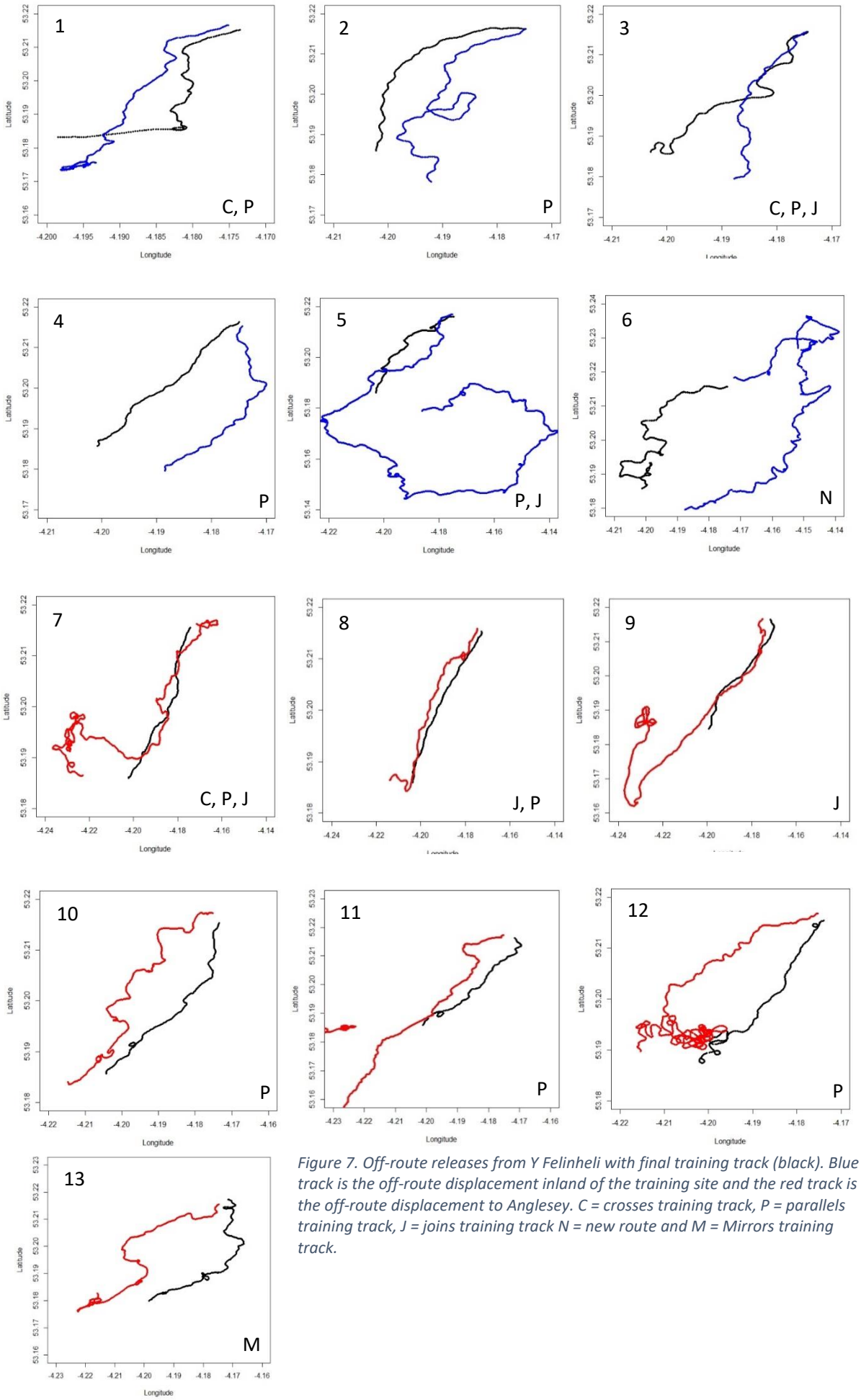

Figure 7. Off-route releases from Y Felinheli with final training track (black). Blue track is the off-route displacement inland of the training site and the red track is the off-route displacement to Anglesey. C = crosses training track, P = parallels training track, J = joins training track N = new route and M = Mirrors training track.

Off-route Releases: To establish the influence of the established route on the birds' navigational strategies, off-route release tracks were plotted against the final training release. Figure 7 shows the off-route releases in blue for the inland off-route release site to the right of the training site (1-6) and the off-route releases in red for the off-route releases from across the Menai Straights on Anglesey to the left of the training release site (7-13). The first 6 tracks, where the birds were displaced in a clockwise direction (to the right) of the training release site, all show a paralleling strategy to their established routes home. Two of the birds (tracks 1 and 3) cross their established routes with the bird from track 1 paralleling its established route all the way home, whilst the bird from track 3 tends to parallel and join repeatedly until it reaches home. Tracks 7-13, where the birds were displaced anticlockwise (to the left) of the training release site, demonstrate more of a recapitulating behaviour of their established route. The birds from tracks 7, 8 and 9 all join and follow (or parallel very closely) their established route from this point forwards. Birds from tracks 10, 11 and 12 all parallel their established routes again with the birds from track 13 showing more of a mirroring behaviour. Mirroring of the track is defined as a parallel method that appears more like a reflection of the established route than a true parallel of it. There does not appear to be any coast following behaviour in these birds from this release site, as can be seen in *figure 7,* only paralleling and joining the original route is shown in their behaviour. These results fall more in line with the results from the experiments carried out in Oxford (Biro *et al*., 2004), as there is more route recapitulation found here than in Griffiths *et al*. (2021), suggesting more pilotage than previously found at this site.

Figure 8. Circular diagrams showing the instantaneous deflection of the final release (release 5), off-route release 1 and off-route release 2. The positions of the diagrams displayed here corresponds to the geographical locations relative to the training release site in Y Felinheli with 0° being the home direction.

Circular diagrams displaying the instantaneous deflection for the birds in release 5, the final training release, and the two off-route releases are shown in *Figure 8*. The instantaneous deflection is shown by the green points, with each point representing the angular difference between the current heading and the home direction. The arrow shows the direction of the mean ID. For release 5, there is virtually no deflection clockwise or anticlockwise of the home direction (0°). For off-route release 1, there is a clockwise deflection of just over 90° from the home direction and for off-route release 2, there is a clockwise deflection of approximately 25° from home.

Pentraeth

Efficiency: The efficiencies for the releases from Pentraeth were calculated using the same methods as for Y Felinheli, however, there were 18 training releases from Pentraeth rather than 5 as in Y Felinheli. *Figure 9* shows there is an increase in mean efficiency for releases 1-5 followed by a general levelling off in efficiency from releases 5-17. Release 18 has the highest mean efficiency. (Mean efficiencies for releases 1-18 respectively 0.615, 0.562, 0.720, 0.793, 0.808, 0.772, 0.785, 0.796, 0.804, 0.823, 0.808, 0.768, 0.792, 0.834, 0.747, 0.767, 0.787, 0.851). A linear model was then applied to the mean efficiencies where p = 0.0002849 shows a significant increase in mean efficiency from release 1 to release 18, suggesting that release number is a significant predictor of efficiency P = 0.03906. This increase in efficiency supports previous studies' findings where the increase in experience at flying from a specific release site increases the birds' efficiency. *Post hoc* tests were performed to compare each mean efficiency with every other mean using an ANOVA (p = 0.000126) and a Tukey test for multiple comparisons of means. The results showed there were significant differences between releases 1 and 18 (p = 0.0254073), releases 2 and 4 (p = 0.0456245), releases 2 and 5 (p = 0.0164612), releases 2 and 9 (p = 0.0199514), releases 2 and 10 (p = 0.0067902), releases 2 and 11 (p = 0.0401826), releases 2 and 13 (p = 0.0375881), releases 2 and 14 (p = 0.0072175), releases 2 and 17 (p = 0.0481072) and releases 2 and 18 (p = 0.0002455). The post hoc tests suggest that the significance between the mean efficiencies for each release lies between release2 and releases 4, 5, 9, 10, 11, 13, 14, 17 and 18.

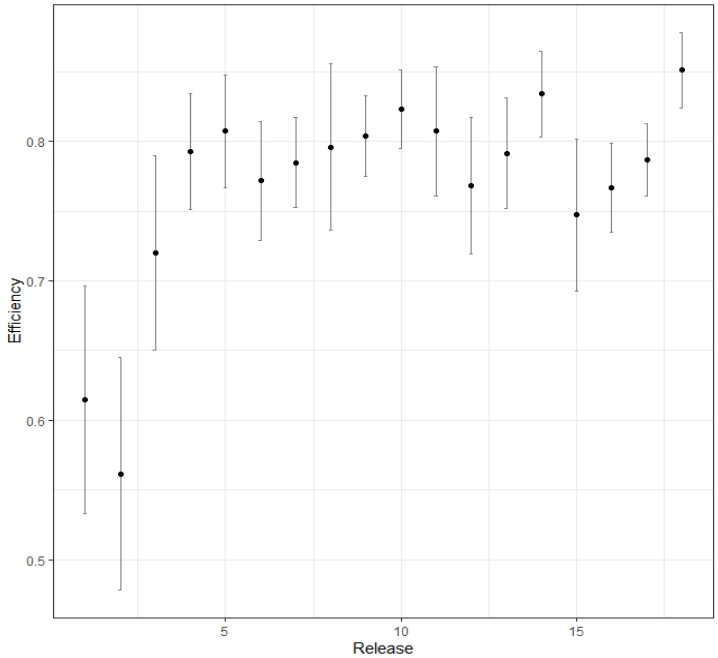

Figure 9. Mean efficiencies for each release plotted for Pentraeth with error bars displayed.

Idiosyncrasy: Releases 10, 13 and 17 were used to calculate the nearest neighbour distances (nnd) for ‘self’ and ‘other’. For the ‘other’ nearest neighbour distances, the final track was compared to another random birds’ track that wasn’t itself, whereas the ‘self’ nnd was a comparison of its final track and its own three tracks. *Figure 10* displays the nearest neighbour distances for ‘self’ and ‘other’ comparisons. Using a Paired Wilcoxon signed-rank test (v=69, P=0.1099) there was no significant difference found between the ‘self’ and ‘other’ comparisons of nearest neighbour distance, with the average distance for both ‘self’ and ‘other’ being approximately 400m. Again, this demonstrates a lack of idiosyncrasy found in other experiments with the birds flying routes home that are not more similar to themselves than any other bird.

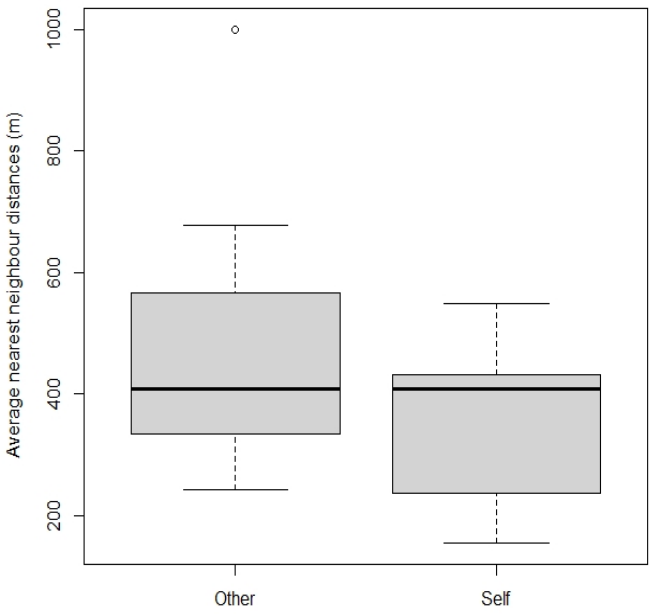

Figure 10. Average nearest neighbour distance comparison for 'self' and 'other'.

Off-route Releases: To analyse the off-route release tracks and identify the influence that the already learned route home has on their navigation; instantaneous deflection values were calculated. *Figure 11* shows the track of the final release 18, the black track, and the off-route release for each bird. Half of the birds were displaced to the left of the training release sight and the other half displaced to the right; each has two tracks. All the birds who were displaced to the left of the training site cross (c) their established route home and parallel (p) or find a new route (n) home on the right-hand side. Bird 2 is the only one that parallels the left side of the established route before crossing over just before reaching the loft. None of the birds fly back to their established route and follows it home from the point they intersect it. This is in conflict with results from Oxford studies but supports the previous findings from Griffiths *et al*. (2021)

When the track of the birds’ first release (black) and the off-route track for each bird are plotted (*Figure 12*) there again appears to be no pattern in flight similarity other than some vague mirroring in some of the flights and some coast following to correct the final leg of the journey.

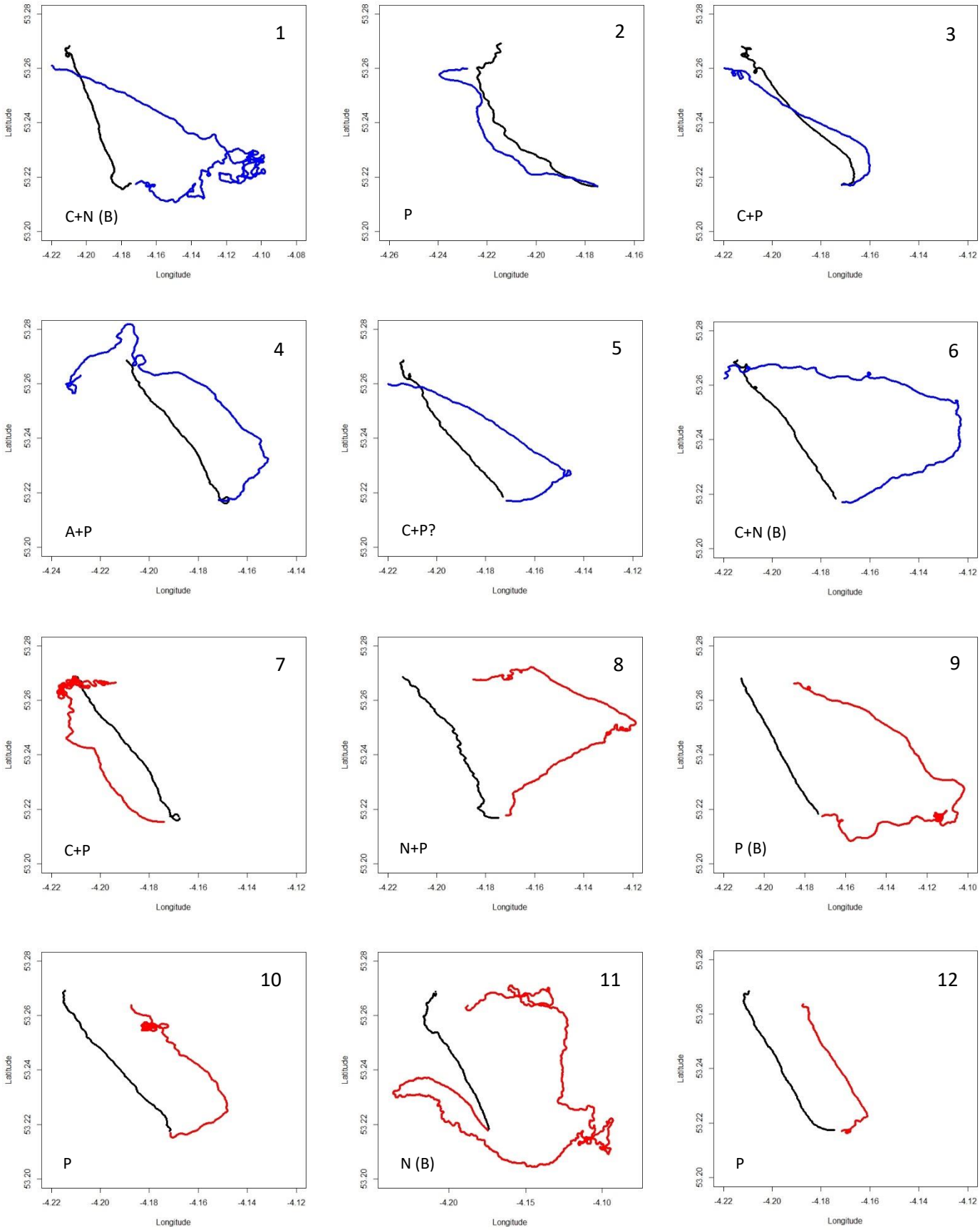

Figure 11. Off-route release foreach bird plotted against its final training release (release 18). Blue tracks (1-6) are the birds displaced to the left of the release site and red tracks (7-12) are birds displaced to the right of the release site. Behaviour abbreviations: C=crosses established route, P=parallels established route, N=new route, A=crosses around training release site and (B)=flies around Bangor.

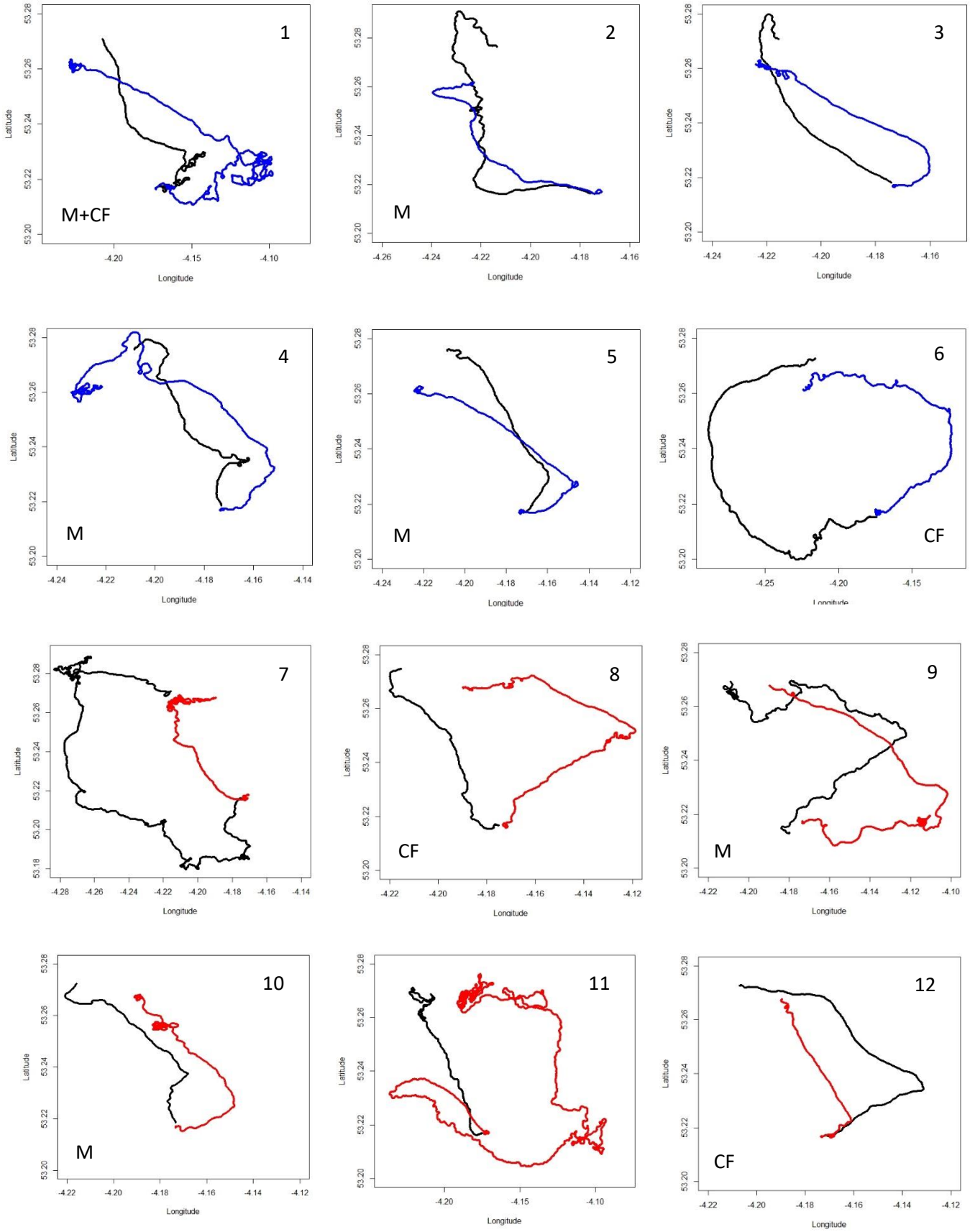

Figure 12. Off-route release for each bird plotted against its first training release. Blue tracks (1-6) are the birds displaced to the left of the release site and red tracks (7-12) are birds displaced to the right of the release site. M = mirroring CF = Coast Following.

When all the final tracks and all of the off-route tracks are plotted onto the same map, it becomes clear that there is no consistency throughout the off-route releases, especially when compared to the final tracks as shown in *Figure 13*. There seems to be some attraction to Bangor and some coast following to get back to the loft.

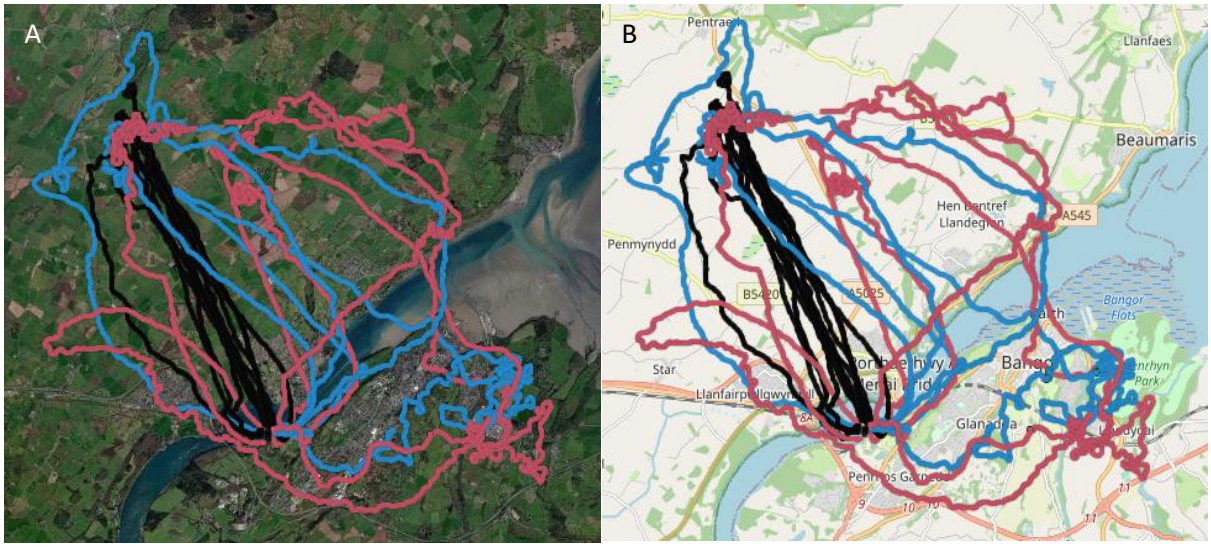

Figure 13. A displays all final flight tracks (black), and all displaced off-route tracks (left = blue, right = red) laid over satellite image of the area. B shows the same plots laid over a map of the area.

Circular diagrams displaying the instantaneous deflection for the birds in release 18, the final training release, and the two off-route releases are shown in *Figure 14*. The instantaneous deflection is again shown by the green points, with each point representing the angular difference between the current heading and the home direction. The arrow shows the direction of the mean ID. For release 18, there is an approximate deflection clockwise of the home direction (0°) of 20°. For off-route release 1, there is an anticlockwise deflection of approximately 50° from the home direction and for off route release 2, there is an anticlockwise deflection of 20° from home.

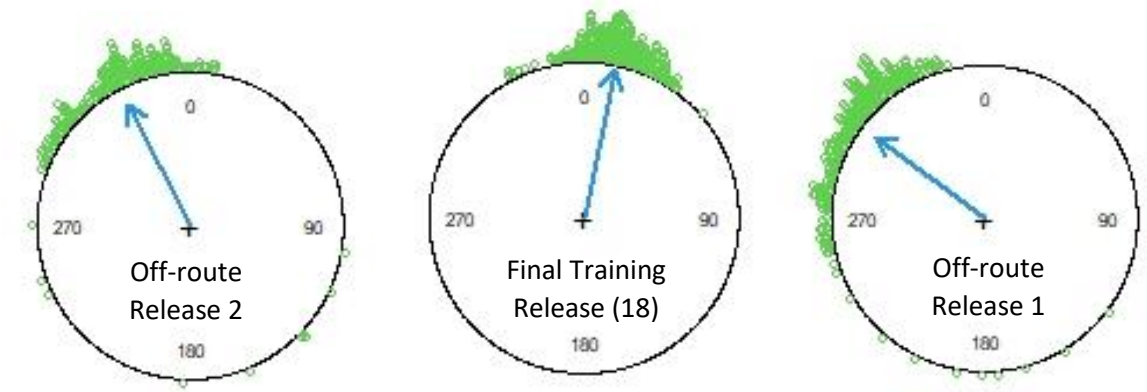

Figure 14. Circular diagrams showing the instantaneous deflection of the final release (release 18), off-route release 1 and off-route release 2. The positions of the diagrams displayed here corresponds to the geographical locations relative to the training release site in Pentraeth with 0° being the home direction.

2.4 Discussion

The overall findings are a mix of previously seen behaviour and new behaviour. The efficiencies for Y Felinheli are already very high and show no significant difference between the first training release and the final training release (release 5). On the other hand, in Pentraeth, the efficiencies increase with an increase in the number of training releases as expected (Biro *et al*.,2004, 2006; Guilford and Biro, 2014; Griffiths *et al*., 2021). For both Y Felinheli and Pentraeth, the birds showed no idiosyncrasy as the nearest neighbour distances (nnd) we not significantly different between 'self' and 'other'. This is conflicting with all previous studies, where the birds have shown some idiosyncrasy in their routes home. there is very little route recapitulation displayed in either cohort of birds, with only 3 of the Y Felinheli birds flying back to their established route and the rest paralleling their established route. None of the birds from the Pentraeth release sites showed any recapitulation, with half of the birds paralleling and the other half crossing their established routes and paralleling on the opposite side to where they were released. This builds a somewhat chaotic picture of the methods being used for these off-route navigational strategies, which don't fit the results of any of the previous studies. The fact that the distances of the release sites to the loft are relatively small, there may be no adaptive advantage to having an efficient route, which may explain why the off-route releases especially seem so inefficient and much more exploratory.

Y Felinheli

The Y Felinheli release site did not yield the same results as previous studies have shown (Griffiths *et al*., 2021). There was no significant difference between the efficiencies of the training releases, and all releases were highly efficient, to begin with. This could be because this cohort of birds was used in homing experiments the previous year, from a release site slightly further away but on the same direct route home. This suggests the birds likely remembered their most efficient routes home from the previous year (Collet *et al*., 2021). In Griffiths *et al*. (2021), using the same release site in Y Felinheli as used in this experiment, they found that the birds reached their peak efficiency at release 5 and then saw a levelling off after this. This part of the experiment aimed to decipher whether or not 5 releases were sufficient for peak efficiency to be reached, and therefore reduce the number of training releases required for similar homing experiments. The mean efficiency stabilised between 0.8 and 0.9 in Griffiths *et al*. (2021). In this experiment, the efficiency ranged from 0.78 to 0.84. Based solely on this release site and this cohort of birds, the answer to this question is inconclusive due to the already highly efficient routes selected by the birds. This evidence suggests that if a pigeon has been trained from a similar release site up to at least a year prior, then they may not need training releases at all, and one or two releases would be satisfactory for subsequent homing experiments (Collet *et al*., 2021).

Comparing the nearest neighbour distances (nnd) to 'self' and 'other', with the final release for each bird being the track the other three tracks are compared to, suggests that these birds fly routes home

that are no more similar to their own, than they are to other birds, with no significant differences between the nnd values for ‘self’ and ‘other’. This conflicts with previous studies (Meade et al., 2005; Griffiths et al., 2021) which have demonstrated that homing pigeons have their own individually unique routes home. However, Griffiths et al. (2021) provide some evidence that this idiosyncrasy may be age dependent as they found no significant difference between the ‘self’ and ‘other’ nnd of their young cohort, only their older cohort. This also suggests a difference in the navigational cues being used as a lack of individuality between the birds may indicate a heavier reliance on compass cues rather than visual cues in younger birds (Wiltschko and Wiltschko, 1981; Griffiths *et al*., 2021).

Analysis of the off-route tracks shows a mostly paralleling of their established routes, with only 3 birds flying back to their established route and recapitulating. Even with the birds that do fly back, it is not a continuous recapitulation back to the loft. These results reflect the results from Griffiths *et al*. (2021), but with no coast following identified. However, there is more of a similarity to the Oxford birds’ behaviour found here than in Griffiths *et al.* (2021). This paralleling behaviour is more akin to the behaviour expected as a result of clock-shift experiments, where the shape of the established route is replicated in parallel to the established route (Biro *et al*., 2006) however, clock-shift procedures were not carried out here.

This combined lack of idiosyncrasy and route recapitulation suggests strategies against pilotage and is in favour of the mosaic map hypothesis.

Pentraeth

The average efficiency of each release increased with an increasing number of releases. *Figure 9* shows the sharp increase in efficiency between releases 1 and 5 and then a much more levelling but slightly increasing efficiency between releases 6 and 18. The post hoc Tukey test for comparison of multiple means shows that all but one of the significant differences is between release 2 and subsequent releases (4, 5, 9, 10, 11, 13,14,17 and 18) with the other significant difference in efficiency being between releases 1 and 18. This suggests that in only two releases, the birds have learned a highly efficient route home and any other adjustments they make beyond this have no significant effect on the overall efficiency. The increase found here has also been previously found from the Y Felinheli release site (Griffiths, *et al*., 2021) and elsewhere in Oxford (Biro *et al*., 2004). From this release site, it is evident that the birds become more efficient at flying after repeated training flights. Although the birds are flying relatively direct and quite efficient routes, there is still some level of inefficiency which is suggestive that the birds are using landmark cues for pilotage (Biro *et al*., 2004) rather than compass cues.

The nearest neighbour distance comparisons again provided different results from previous studies in that the birds were no more similar to their own tracks than other birds’ tracks, as was found at the Y Felinheli site. Since the birds used for this release site were young birds, being first years with no prior flying experience outside their loft in previous years, the results presented here also support the hypothesis that young birds’ lack of idiosyncrasy may be age-dependent (Griffiths *et al*., 2021). Since young 1st-year birds were tested here, they may be using a route reversal strategy, where they learn

the cues on the outward journey and reverse them for the homeward journey (Wiltschko *et al*., 1985) for example reversing the outward compass direction either the sun compass or the magnetic compass (Wiltschko, 1983). As birds become more experienced with age or with even more training releases, the navigational methods used may shift more to visual landmark cues, which is a more reliable strategy than the route reversal method and therefore increase (Wiltschko *et al*., 1985).

As can be seen in *Figure 11,* route following, that is, flying back to their established route and following it from the intersection, is not observed here as in the Oxford studies (Biro *et al*., 2004, 2006, 2007). The birds who were displaced to the left of the training release site, show an overall behaviour of crossing their established route home and either paralleling it home or then flying a new route home. Many of them seem to be attracted to fly around Bangor before finally flying home via the coast. This behaviour is observed for all the left-hand displaced birds except one who paralleled his route home on the left side of the established route. The birds displaced to the right all paralleled their established routes or made a new route home. One bird crossed to the left and paralleled it from there. Again, a lot of the birds were attracted to fly around Bangor. From this, it appears that the birds' established route bears no influence on their navigation home from the off-route site, thus suggesting a more compass-based approach (Biro *et al*., 2004; Guilford and Biro, 2014). When comparing the off-route tracks to each of the birds first training release, again there isn't much of a pattern between them. Plots 1, 2, 5, 9 and 10 in *Figure 12* all appear to have some vague mirroring between the first and off-route, however, they also appear to be at a different angle. There is also an overall deflection anti-clockwise of the direct route home when looking at the vanishing bearings of the off-route releases on a circular diagram (*Figure 14*). This is the direction Bangor is from the training release site. There is a main road from Pentraeth to Beaumaris which two of the birds seem to follow in their off-route release but most of the tracks are between this road and Pentraeth road (which leads in the direction of the loft). It is therefore doubtful that the birds here are using the roads as directional cues, as has been suggested by Lipp *et al*. (2004). Even in this rather chaotic picture of the off-route releases, there is more evidence of coast following (Griffiths *et al*., 2021) rather than road following.

Although the efficiencies of the training releases suggest the use of landmarks for pilotage more than compass cues, when the birds are displaced off-route the primary mechanism seems to change. It appears from the off-route release sites that the birds ignore all landmarks than would be familiar to them from the training releases and a more compass-based approach seems to take priority.

This is interesting as none of the birds flew in the direction of Bangor on their final and most efficient release, which poses the question as to why a large number of them were attracted to Bangor or in the Bangor direction on this day. As previously mentioned, both off-route releases took place on the same day, so the weather was not a factor in this. The wind speed was less than 7mps and in a north-easterly direction so the birds couldn't have been displaced by the wind. Perhaps most interesting of all was the decision of all but one of the left off-route displaced birds to cross their established routes and fly out of their way in a very inefficient route home. When all the tracks are laid over one another as seen in *Figure 13*, it is clear that the birds are not following an efficient route home, nor are they in any way influenced by their established routes. These results again suggest a rather contradictory

conclusion from those of previous experiments, especially those found in Oxford where the birds were nearly always attracted back to their established route, demonstrating high route stereotypy and recapitulation (Meade *et al*., 2005). These off-route tracks produce a somewhat chaotic picture of the birds' navigational methods in North Wales.

The idea that the birds were attracted to their first route from the off-route release site rather than their established route is unlikely as there is no strong pattern in the tracks. However, it could be said that a few of the birds do show some vague mirroring of their first tracks in the off-route release, but again this is inconclusive. The fact that the Pentraeth cohort were 1st-year birds may mean that the displacement reset their navigational mechanisms and they were learning a new route again.

The results indicate that compass cues may have been used over landmarks as all the birds appear to have the same deflection angle, regardless of which off-route site they were released from. Perhaps on this particular day, there was some other factor involved that led them to behave in this chaotic manner.

Overall Discussion

One difference between the studies conducted in Oxford and here in Bangor is the topography of the landscape. Oxford is rather flat and not coastal, whereas Bangor is very close to the mountains of Snowdonia and the coast. The release sites at Y Felinheli are all parallel to the mountains and the coast when taking the direction of the loft. Therefore, there are potentially strong visual cues on both sides of the route home almost acting like a channel back to the loft for the birds to use, which may be constraining the birds to an already highly efficient route and masking any exploratory flying that may otherwise take place. From Pentraeth, the birds are flying towards the mountains in Snowdonia, no matter which route they take or bearing they follow, and they all need to cross the Menai Straights. When displaced the young birds may be overstimulated and their senses may become overwhelmed with the variety of different cues available, or the fact that there are so many cues may make each cue less prominent to the birds. Griffiths *et al*. (2021) found evidence that young birds may be more inclined to explore the local area than older birds. Since Pentraeth birds were not experienced with homing experiments, they may have used the off-route displacement release for exploration.

There is evidence that pigeons homing in urban and suburban areas have a reduced homing ability due to an increase in landscape complexity (Wiltschko *et al*., 2006; Mann *et al*., 2014). Perhaps the increase in landscape complexity found in urban areas producing a reduced homing ability applies also to more rural landscapes where complexity is also high with natural landmarks. In areas of low landscape complexity, or rather optimal landscape complexity (Mann *et al*., 2014) pigeons may rely on visual landmark cues for pilotage as is evident in the Oxford group (Biro *et al*., 2004; Meade *et al*., 2005; Biro *et al*., 2006, 2007). However, in areas of high landscape complexity, be that urban or rural, pigeons may be more likely to encompass visual landmark cues into the mosaic map model for navigation (Wiltschko *et al*., 2006). This combined with the fact that young birds are more likely to explore their surroundings may explain the more haphazard results found from Pentraeth. Landmarks may not be as prominent when the topography of the landscape is so varied as in North Wales. In

Oxford where the landscape is much flatter, roads, rivers and hedgerows for example may stand out more or act as better waypoints for pilotage. Weddell seals have been found to use pilotage to locate their breathing holes from under the Antarctic ice. By using the overhead landmarks such as different thicknesses of snow and ice for example, and taking short shallow dives to get their bearings, they can navigate back to their familiar breathing hole. Here the landscape is very sparse with few visual landmarks available to them, therefore in this situation, pilotage is likely an optimal strategy (Fuiman *et al*., 2020)., similar perhaps in complexity to that found in Oxford, for pigeons.

Different strategies of homing in a familiar area may also be age-dependent. The two cohorts of birds used in this study were all young birds, with the Y Felinheli group being a year old and in their second year of homing and the Pentraeth birds being in their first year and only a few months old. Griffiths *et al*. (2021) found that older birds with more flight experience produced the idiosyncratic flights seen in the homing pigeons experimented on in Oxford. The younger inexperienced birds, however, did not produce this typical idiosyncratic route, therefore strongly suggesting that the birds may use different strategies depending on their age and experience level.

It has been long known that vector orientation in naive migratory songbirds is innate and cannot correct for displacement. These birds, once already completed their first migration and are more experienced, can then correct for a displacement. This behaviour has not only been seen in long-distance migratory songbirds such as starlings (Perdeck, 1967) but also in long-lived seabirds such as the Manx Shearwater (Wynn *et al*., 2022). This then changes as age and experience increase and the birds are able to take cues from the landscape around them and develop their navigational migratory routes. Adult Streaked Shearwaters who migrate from Japan to New Zealand take one of two routes which avoid landmasses, however, the young birds on their first migration take a direct southward route which forces them to fly over mountainous regions, not the most efficient for a pelagic seabird (Yoda *et al*., 2017). Again, with Weddell seals, it has been observed that adults appear to change their diving behaviour when they have their pups with them, compared to when they are diving by themselves (Weitzner *et al*., 2021). This demonstrates that navigational mechanisms can change with age and experience. Evidence from this study and Griffiths *et al*. (2021) suggests that this may also be the case when homing over a short distance in a familiar area.

2.5 Conclusion

In conclusion, with the results from these experiments in combination with the results from other similar studies, it can be assumed that the more training flights homing pigeons receive from a particular release site, the more efficient their flight becomes. However, it only takes a few training releases before they are close to peak efficiency. Since none of the birds produces the most efficient routes home, it can be assumed that they are relying to some extent on visual landmark cues. The lack of idiosyncrasy found in the flights from both Y Felinheli and Pentraeth, is in stark contrast to studies by Biro *et* al. (2004), Meade *et al*. (2005), Griffiths *et al*. (2021), where the birds produced highly stereotyped routes.

The fact that the birds used in these experiments were young (1st and 2nd-year birds) and did not show any idiosyncrasy, may be evidence for potential changes in cognitive processes being age-dependent. With Griffiths *et al*. (2021) also providing evidence that young pigeons do not produce idiosyncratic routes, and the hypothesis that young birds rely more on route reversal rather than landmarks, the results presented here also back these theories up.

As can be seen from the difference between the results of the two release sites here, Y Felinheli, although still in a rather highly complex landscape, the coast, and the mountains, may override the complexity of the rest of the landscape. In Pentraeth however, with these two landscape features both being directly ahead, the landscape complexity may not be optimal for them to use pilotage as a navigational method. Given the evidence provided by Griffiths *et al*. (2021) for more exploration found in the younger birds, this combined with landscape complexity may be the reason for the different results gathered from the inexperienced young birds released from Pentraeth.

Further work needs to be done to assess different landscape complexities, and not just looking at urban areas, but also more rural areas such as North Wales, where there are mountains, coastal features, rivers, main roads and towns, and forests. There is also room for further exploration into the cognitive processes of young birds and how they change with age and experience. Given the evidence from Weddell seals changing their diving behaviour with age as well as the evidence from migratory songbirds and Manx shearwaters birds, it is likely that this phenomenon of navigational strategy changing with age and experience is present in homing pigeons and many other species of birds and mammals alike.

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