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Repeated training of homing pigeons reveals age dependent idiosyncrasy and visual landmark use.

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Abstract:	Recent research into the navigational strategies of homing pigeons (Columba livia) in the familiar area has highlighted the phenomenon of route fidelity – birds forming idiosyncratic flight paths to which they are loyal over multiple releases from the same site, and even returning to this path when released from a near-by unfamiliar location. Such results highlight the potential importance of visual landmark cues in the homing process. However, not all birds have been shown to produce idiosyncratic routes or show this route-joining behaviour. Here we use birds with and without flight experience to study the formation of idiosyncratic routes when released repeatedly from a single location, followed by two off-route releases with differing topography to see how flight experience and local landmark features can influence navigational strategy in the familiar area. We found that, over the course of 20 sequential releases, birds with greater flight experience tended to form idiosyncratic routes whereas less experienced birds did not show this tendency. When released from near-by sites (from which the birds had not previously been released), a range of navigational strategies were seen, including flying parallel to the learned route (suggestive of a learned compass direction), a direct flight path towards home (again indicative of compass use), re-joining the learned route, and following the coastline. These latter strategies are suggestive of landmark usage. Analysis using time lag embedding was also used to assess the off-route releases, and the short-term correlation dimension values produced (ranging from 1.5-2.5) were also indicative of strategies using one or two factors (landmarks, compass, or a combination of these two). Individual birds often showed different strategies at different sites, suggesting that the use of different navigational cues is highly flexible and situationally dependent.

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Recent research into the navigational strategies of homing pigeons (*Columba livia*) in the familiar area has highlighted the phenomenon of route fidelity – birds forming idiosyncratic flight paths to which they are loyal over multiple releases from the same site, and even returning to this path when released from a near-by unfamiliar location. Such results highlight the potential importance of visual landmark cues in the homing process. However, not all birds have been shown to produce idiosyncratic routes or show this route-joining behaviour. Here we use birds with and without flight experience to study the formation of idiosyncratic routes when released repeatedly from a single location, followed by two off-route releases with differing topography to see how flight experience and local landmark features can influence navigational strategy in the familiar area. We found that, over the course of 20 sequential releases, birds with greater flight experience tended to form idiosyncratic routes whereas less experienced birds did not show this tendency. When released from near-by sites (from which the birds had not previously been released), a range of navigational strategies were seen, including flying parallel to the learned route (suggestive of a learned compass direction), a direct flight path towards home (again indicative of compass use), re-joining the learned route, and following the coastline. These latter strategies are suggestive of landmark usage. Analysis using time lag embedding was also used to assess the off-route releases, and the short-term correlation dimension values produced (ranging from 1.5-2.5) were also indicative of strategies using one or two factors (landmarks, compass, or a combination of these two). Individual birds often showed different strategies at different sites, suggesting that the use of different navigational cues is highly flexible and situationally dependent.

KEYWORDS

Ageing, correlation dimension; familiar landmark; homing pigeon; idiosyncrasy; navigation, spatial memory, route fidelity, time lag embedding.

HIGHLIGHTS

- Birds with greater flight experience form idiosyncratic routes more readily.
- Multiple homing strategies occur when released close to a familiar site.
- Age and site-specific biases occurred in which strategies were used.
- Flexibility within individuals was seen in terms of strategy choice and cue use.

The study of pigeon homing has for many years been focused on how the birds are able navigate from an unfamiliar location for so-called “true navigation”, usually framed in the paradigm of Kramer’s “map and compass” theory (Kramer, 1953). Here, navigation is broken down into a two-step process, with a “map” providing a relative location from which the appropriate direction can be determined, and the “compass” providing a real-world directional heading. The map stage of navigation theorises a system of relatively stable gradients which vary predictable over a significant distance, such that birds can learn the spatial relationships of these gradient concentrations to produce a mental navigational map (Holland, 2014). A large body of evidence supports a role of olfactory cues in the formation of a map (Wallraff 2005, Gagliardo, 2013 for review), although alternative roles for olfactory cues have been proposed (Jorge et al. 2009, 2010, but see Gagliardo et al. 2011, 2018). Other cues have also been proposed to play a role in the map, such as the magnetic field (Wiltschko and Wiltschko 2009), infrasound (Hagstrum, 2000, 2013), and gravity (Blaser et al. 2014). Both magnetic (Beason, 2005; Keeton, 1971; Walker, 1998; Wiltschko et al., 1981; Wiltschko and Wiltschko, 1972) and solar-cues have been found to provide compass information (Guilford and Taylor, 2014; Schmidt-Koenig, 1990) in terms of magnetic declination and the time-compensated solar azimuth compass.

When navigating close to the loft in a familiar area, evidence suggests that both the sun compass and magnetic compass still play significant roles. Birds subjected to clock-shift procedures to alter their perception of time of day, and therefore their interpretation of the time-compensated sun compass, show a relatively predictable deflection angle away from the home direction when navigating, and this deflection can be seen even when navigating close to the loft (Armstrong et al., 2013; Chappell, 1997; Wiltschko et al., 1994). Experiments attaching magnets to the heads of navigating pigeons in order to disrupt access to the magnetic compass (by producing a local strong magnetic field) show that deflection under clock-shift increases, suggesting that there is some influence of the magnetic compass on the chosen direction also, and that the cues are being combined (Gagliardo et al., 2009; Wiltschko and Wiltschko, 2007, 2001).

When navigating in the familiar area, however, the importance of familiar area cues, particularly visual landscape features, has been highlighted (Braithwaite and Guilford, 1991; Burt et al., 1997), although curiously, not always supported (Schmidt-Koenig and Schlichte, 1972; Schmidt-Koenig and Walcott, 1978). Early studies found that birds deprived of object vision via the use of frosted lenses were able to home from significant distances (up to 130km) (Schmidt-Koenig and Schlichte, 1972), although many birds with frosted lenses were only able to locate the vicinity of the loft (0.5-5km) (Schmidt-Koenig and Walcott, 1978). Surprisingly, birds deprived of object vision and rendered anosmic were still able to orient successfully from a familiar area, again suggesting that object vision is not necessary for homing, and that at least one other cue was necessary to explain homing (Benvenuti and Fiaschi, 1983). However, a subsequent study did not support this and suggested a crucial role for vision if birds were made anosmic (Streng and Wallraff 1992). Later investigations found that birds able to view the landscape prior to release showed increased homing performance, suggesting that, when available, visual access to the landscape can be important in homing (Braithwaite and Guilford, 1991; Burt et al., 1997).

The introduction of a whole new series of possible cues, unique to the local landscape, means that strategies of navigation in the familiar area may be highly variable dependent on individual location. Studies have highlighted the importance of landscape features such as rivers, roads and hedgerows which make up patterns of straight lines in the environment to determine flight path structure (Lipp et al., 2004), as well as how the density of edges in the landscape influences how well routes are learned (Mann et al., 2014). The importance of landscape features when learning to navigate in the familiar area is evident and brings in to question how the cues used outside of the familiar area (olfactory, magnetic, solar) are integrated with the visual landmark cues.

Familiarity with an area comes in two forms – general flight experience in the local area, and experience flying from a particular release site. Previous studies have demonstrated that homing efficiency is greater in birds generally familiar with an area in comparison with naïve individuals (Meade et al., 2006), suggesting that familiarity influences the navigational strategy. Studies of birds released repeatedly from the same location show that birds tend to show an increase in route efficiency and fidelity (Biro et al., 2006, 2004; Meade et al., 2005). However, these birds do not produce maximally efficient routes, instead developing individually stereotypical routes, with efficiency reaching a plateau once the route has been established. Furthermore, birds released from sites alongside the learned route have been shown to return to the established route, rather than flying a direct route (Biro et al., 2006, 2004). This suggests that, instead of flying on a direct compass heading towards home, birds use the local landscape cues to inform their routes. One study found that bottlenecks in tracks from repeated releases occurred alongside salient landmark cues, suggesting the learned routes are constrained by particular landmark features (Mann et al., 2011).

However, the Frankfurt group failed to replicate these results (Wiltschko et al., 2007), with pigeons failing to show an increase in efficiency, or produce stereotyped routes. A later analysis found that birds unfamiliar to the area had a similar efficiency to familiar birds, but that birds released multiply from the same site did show a general increase in efficiency (Schiffner et al., 2013). Given the importance of individual landscape features unique to a particular area, it is possible that the ability to learn local routes varies between locations or landscape features (Mann et al., 2014). Therefore, we use a new location to test the hypotheses that birds develop stereotypical routes when navigating repeatedly from a known location, and that they will preferentially return to this learned route when released at a novel site nearby. Additionally, we classify our test groups as “old” and “young” birds, with over ten years or less than one year of experience respectively, to investigate how age and navigational experience affects navigational ability in the familiar area.

According to the predictions of earlier studies, birds forming idiosyncratic routes should show a general increase in efficiency over early releases, but plateau below maximum efficiency (Flack et al, 2012; Guilford and Biro, 2014; Meade et al., 2005). Birds should show an increase in route fidelity, with a bird's later releases more similar to each other than earlier releases. Once an idiosyncratic route has been formed, it should be relatively distinct compared to the routes of others. Off-route releases may produce a variety of strategies, with an expectation of either a) a direct route home, based on a compass heading; b) a return to the learned route which is then followed home, presumably more reliant on visual landmark cues (Biro et al., 2004); or c) possible offset of the learned route from the novel release site, similar to the offset routes seen when clock-shifting birds from a learned route (Biro et al., 2007).

METHODS

Subjects, Training and Releases

A total of 21 birds in two age categories (ten young birds, only one year old and eleven old birds, nine/ten years old) were trained to fly repeatedly from a single release site at Y Felinheli (within 5km) over the course of two months, from the 19/09/2017 – 14/11/2017, with a total of twenty releases from the site. All of the birds had flight experience in the local area but had not participated in previous homing experiments. The birds were kept indoors usually during the day and did not have independent free access to the outdoors. Old and young birds had a greatly different flight experience prior to the tracked releases from Felinheli (table 1).

During the experimental releases, birds were released individually. The majority of releases took place once per day, apart from pairs 2 and 3, 5 and 6, 10 and 11, and 13 and 14 which took place in the same day (morning and afternoon releases). All 21 birds completed the 20 training flights from Y Felinheli, although a few flights were not successfully recorded. Any incomplete tracks were removed from the analysis. All of the experimental flights were tracked using a GPS recorder (i-gotU USB GPS Travel and Sports Loggers, 15.5g with outer casing removed), with position fixes every second and an accuracy of ±5m. Trackers weighed less than 5% of the birds' bodyweight, and all birds had experience carrying the trackers before the experimental releases. The trackers were attached to the back between the wings using a Velcro strip glued to trimmed feathers. Following the repeated releases from Y Felinheli, two off-route releases were performed, one from just across the Menai Strait on Anglesey, and one further inland (see Figure 1 for a map of the release sites and home loft location). Off-route release 1 was 1.64km from the Y Felinheli release site, and off-route release 2 was 1.16km. Both off-route releases were conducted once on separate days. All birds were housed at the Bangor University Treborth Botanic Gardens loft, under natural daylight. Birds had free access to water and grit, and 25g of food per bird per day.

Data Analysis

Processing

All tracks were processed and analysed using RStudio. Firstly, a low-pass filter was applied to the latitude and longitude values to remove noise at the frequency of data collection. Following this, calculations were applied to produce continuous flight bearings (CFBs, the bearing of each point from the release site) for each point, distance travelled between each point, current heading, and instantaneous deflection (ID, the difference between the current heading and the home direction) at each point (Agostinelli and Lund, 2017, 2018; Hijmans, 2019). Point of decision analysis was then used to remove early circling behaviour from the tracks (Schiffner and Wiltschko, 2009). The mean vector length of current bearings was calculated across each set of ten consecutive points, and a cut-off for navigational behaviour chosen when three of these consecutive mean vector lengths were all greater than 0.85, implying relatively consistent direction of flight. This cut-off of 0.85 was chosen after testing multiple values, as providing the best balance between removing circling behaviour without excluding too much of the track. As well as this, a radius of 200m around the home loft was removed from the tracks to discount the circling behaviour around the loft, as this distorts calculations of efficiency. Following this processing, various calculations were performed to analyse the tracks.

Efficiency

Efficiency of a tracks is calculated as the shortest beeline distance divided by the actual distance flown between the start and end points, ranging between zero and one. Efficiency was then compared between young and old birds using the Mann-Whitney U test, and a linear mixed model was used to analyse the factors influencing change in efficiency, with release number and age as fixed effects, and bird as a random effect (Bates et al., 2015). An ANOVA test was used to compare a full and reduced model to identify the significant factors.

Idiosyncrasy

In order to investigate whether birds showed individually unique routes, a mean route was computed for each bird, consisting of the three final successful tracks recorded from Y Felinheli. The mean track was first created as a series of equally-spaced points from the start to the end of the track. For each point along the mean track, the nearest time-independent point on each of the tracks to be averaged was found, and the mean track point moved to the mean of the nearest neighbour points. Once this had been applied to the entire track, points were moved to fill out any gaps and reduce bunching along the mean route by moving any points more than a set distance apart to the half-way point between them.

Once the mean route had been constructed, the nearest-neighbour distances were calculated to three tracks from the same individual (tracks 13, 15 and 16 as these were available for all birds), and to tracks from a different individual (individual chosen at random for each track, tracks 8, 9, 10 and 12). The average nearest neighbour distance for “self” and “other” comparisons was calculated for each bird and compared using a Wilcoxon signed-rank test.

Off-route releases

To investigate the directional choices made when released from the off-route locations, CFBs were calculated for the mean tracks of each bird (as described above). As the CFBs describe the angle from the release site at each point along the track, matching CFBs from two tracks suggest a copying of the known route. ID was also calculated for the mean tracks and compared to the ID values from the off-route releases. The mode of each of these measures was calculated to identify the predominant direction of flight over the course of the tracks. These measures, alongside visual inspection of the flight paths, were used to classify the off-route releases into different categories of navigational behaviour.

Time lag embedding

We analyzed data by means of time lag embedding to determine the underlying characteristics of the navigational process used by Homing Pigeons - *Columba livia f. domestica* (Schiffner et al., 2011). Time lag embedding is a method derived from dynamic systems theory, an advanced area of mathematics and physics focused on understanding and describing complex dynamic systems. Time lag embedding, commonly used to characterise dynamic systems (i.e. systems that change over time) (Nehmzow, 2006; Small, 2005), allows the physical/data driven reconstruction of a system in phase space. Observations of a system can be used to construct a multi-dimensional phase space, where each axis in this space represents a parameter of the system (Takens, 1981). The number of parameters (or degrees of freedom) in this space, therefore, is the minimum number of independent variables necessary to describe the system. The proper embedding dimension was determined using a false nearest neighbour approach and the correct time lag was estimated using a non-parametric normalized mutual information algorithm to deal with the sensor noise.

Correlation dimension

In order to estimate the number of navigational factors used by the birds' navigational system we calculated the correlation dimension, a measure of the degrees of freedom of the system. The methods described here have been tested rigorously in mathematical systems where the exact number of degrees of freedom is known and have been applied successfully to tracks of homing pigeons, allowing unprecedented insight into their navigational system (Schiffner et al., 2016, 2014, 2011; Schiffner and Wiltschko, 2014, 2013).

The method used to determine the correlation dimension is identical to the original algorithm described by Grassberger and Procaccia (Grassberger and Procaccia, 1983). By estimating the correlation dimension we can determine the nature of the underlying process: deterministic systems have an integer dimension (e.g. 1.0, 2.0, etc.); random systems are dimensionless; chaotic deterministic systems have a fractal/non integer dimension (e.g. 1.3, 2.1, etc.). Here we specifically estimated the short-term correlation dimension, a lower bound rolling estimate of the actual correlation dimension over a fixed time window calculated over the entirety of the track to analyse the tracks and potential changes in the navigational process throughout the pigeon's journey to its home loft.

Theoretical considerations

When considering an animal's navigational process, the degrees of freedom, as represented by the correlation dimension, indicates the number of independent sensory modalities involved in the navigational process - where the same sensor could pick up several independent cues. Applied to tracks of an animal the correlation dimension thus, allows us to draw conclusions about the navigational strategy used; low correlation dimensions suggest simpler forms of navigation, like navigation based on point-like information, while higher correlation dimensions suggest navigation based on multiple environmental gradients (Schiffner et al., 2011).

The effects of the different releases and types of behaviours on the short-term correlation dimension were tested using the Aligned Rank Transformed ANOVA (ART-ANOVA), a non--parametric approach utilizing GLMM and Global ranking to ensure normal distribution of the data (Wobbrock et al., 2011). For post hoc comparison, we employed least squared means using the Tukey method for multiple comparisons. While this method can ensure that data is drawn from a normal distribution, it still requires testing for homogeneity of variances. The Leneve's test, used to test for homogeneity of variances, ensured homogeneity of variances in all tests. In each test we considered the effect of either the release number or the type of behaviour and the distance from home as fixed effects, and the bird's identity as a random effect.

Ethical Statement

All applicable animal welfare guidelines were followed including the ASAB/ABS Guidelines for the treatment of animals in research. The project was reviewed by Bangor University AWERB and received approval for work to be carried out (approval number: CNS2017EJP01).

RESULTS

Efficiency

Efficiency was calculated with the exclusion of early circling and circling around the loft, as described in the methods. There was a general increase in efficiency over the first five releases, with young birds showing a much lower efficiency in the first few releases (Figures 2 and 3a). Comparison of the groups using the Mann-Whitney U test found a significant difference in efficiency between young and old birds during the first 4 releases (Mann-Whitney U Test: $W = 1129$, $P = 5.028\times10^{-4}$), but not during the final 4 releases (Mann-Whitney U Test: $W = 1053$, $P = 0.268$), (figure 3a and 3b respectively). The mean efficiency stabilises between 0.8-0.9, showing that the birds are not using maximally efficient routes, even when removing circling behaviour.

A linear mixed model found that both Release and Age group were significant predictors of Efficiency, with an ANOVA comparison of a full model including an interaction between Age and Release and a reduced model without the interaction showing a significant difference (ANOVA: $P = 5.519\text{x}10^{-5}$).

Idiosyncrasy

Mean tracks were calculated from the final three releases from Y Felinheli for each bird. Figure 4 shows these tracks, as well as the mean efficiency averaged across the last three tracks, and the mean area between the tracks is also given in km^2. No significant difference was found in the area between the final tracks between the old and young birds (Wilcoxon signed-rank test: $W = 41$, $P = 0.349$). No correlation between mean efficiency and area between tracks was found when a linear regression was applied (ANOVA: $F_{1,19} = 0.0125$, $P = 0.912$). Comparison of the calculated mean tracks (Figure 4) to "self" and "other" tracks produced a list of average nearest neighbour distances for each individual. Using a Wilcoxon signed-rank test, we find a significant difference between the self-comparisons and other-comparisons of mean nearest neighbour distance (Wilcoxon signed-rank Test: $V = 218$, $P = 1.918\text{x}10^{-3}$), with self-distances being lower on average than comparisons to the tracks of other birds (Figure 6).

Figure 5 breaks down the above to compare the "self" and "other" distances between young and old birds. There is a significant difference in the "self" distances between young and old birds (Mann-Whitney U Test: $U = 28$, $P = 0.034$) with old birds showing lower nearest neighbour distances than young birds. However, there is no significant difference in the "other" distances between young and old birds (Mann-Whitney U Test: $U = 61$, $P = 1$). The significant difference between self and other comparisons is maintained when looking at old birds alone (Wilcoxon signed-rank Test (paired): $V = 65$, $P = 1.953\text{x}10^{-3}$), but not young birds ($V = 47$, $P = 0.240$).

Short-term Correlation Dimension Analysis

Using time lag embedding to calculate the short-term correlation dimension for each track of repeated releases we observe a highly significant effect of the release number on the correlation dimension (ART ANOVA: $F_{16,2903} = 44.565$, $P < 2\times10^{-16}$), which is also confirmed by the post hoc comparisons. Figure 6 suggests that this transition is not instantaneous, but rather gradual. The majority of initial flights have a higher correlation dimension (Green colours: 2-2.5) compared to the later flights (Red colours: 1-1.5). These final values are close to what we would expect if the birds would switch to following landmarks to aid their navigation. Two caveats though, the short-term correlation dimension is generally lower than the actual correlation dimension and there is a lot of variation in this data set. However, because of the high variation and the fact that we are looking at averages it is evident that at least some of the birds do occasionally follow landmarks.

Off-route Releases

Figure 7 shows the mean track and off-route releases for the young and old birds. From visual analysis of these tracks and use of CFBs and ID, off-route return strategies have been classified (Table 2). Flight strategies have been broken down into several classes: a coast-following (CF) strategy seen from the first-off route release where the bird follows the Menai Strait coastline of the Anglesey side before crossing the Strait close to home; a direct route (D) where the bird flies a relatively straight course between the release site and home; parallel (P) where the bird flies parallel to the Y Felinheli route, and corrects towards home later on; joining (J) behaviour, where the bird clearly flies to and then along the established learned route; and finally cross (C) where the bird appears to cross but not join the established route.

CFB is a measure of the absolute bearing of a point from the release site. As the absolute bearing of the home loft from the first off-route release site is 47.8° and from the second off-route release 12.6° (Figure 1), a modal CFB near these values for each release suggests a relatively direct route. Similarly, an ID of 0° suggests direct homewards flight, e.g. bird 919 with a CFB of 43 and ID of -2 for off-route release 1 and a CFB of 9 and ID of 3 for off-route release 2, both suggesting a direct flight path. The homewards bearing from the Y Felinheli release site is 26.5°, therefore modal CFBs near this on the off-route releases suggest a parallel of the learned route, e.g. birds 158 and 262, with CFBs of 26 for off-route release 2. A chi-squared contingency table analysis of flight strategy for each location finds no association between age and flight strategy from the first off-route release site (Chi-squared test: $\chi^2_3 = 0.952$, $P = 0.813$), but an association close to significance at the second off-route release site with old birds favouring the parallel strategy (Chi-squared test: $\chi^2_2 = 5.45$, $P = 0.066$).

In terms of mean flight efficiency and short-term correlation dimension (STCD) of the off-route releases, there is a significant negative correlation (-1.012), with STCD decreasing as efficiency increases (ANOVA: $F_{1,40} = 4.447$, $P = 0.0413$). There was no significant correlation between efficiency of the first and second off-route releases (ANOVA: $F_{1,19} = 2.298$, $P = 0.146$), nor STCD (ANOVA: $F_{1,19} = 1.081$, $P = 0.312$).

Using time lag embedding to calculate the short-term correlation dimension for each track of offs-route releases and comparing the prevalent types of behaviours (direct, parallel and coast-following) reveals a significant difference between direct routes and parallel routes, as well as differences between those two types and the coast following type of behaviour. While there is variation in the correlation dimension estimates indicating that the visual categorisation is not exact, it was still sufficiently accurate to detect significant differences between the different types of routes (ART ANOVA: $F_{2,214} = 44.731$, $P < 2\text{x}10^{-16}$). These differences are also confirmed by the post hoc comparisons, showing again significant differences between the individual types of routes. Figure 8 shows that Coast following has the highest correlation dimension (CF≈2.5). The Direct flights have a slightly lower correlation dimension (DIR≈2.0) and the parallel flights have the lowest correlation dimension (PAR≈1.5).

DISCUSSION

Efficiency

Figure 2 shows that average efficiency per flight increases over the first five flights, stabilising between 0.8 and 0.9. This demonstrates an improvement in path efficiency with experience, but is still variable and plateaus before reaching maximal efficiency. Given that this measure of efficiency was calculated from tracks where circling behaviour had been removed, the numbers are a true representation of the efficiency of the navigational path. This initial increase in efficiency is in agreement with previous findings, where birds flew routes significantly longer than the beeline (Biro et al., 2004; Meade et al., 2005). Consistently inefficient routes suggest that the flight path is not based solely on a compass direction, which should produce a beeline home. However, it should also be noted that we would only expect highly efficient routes if birds were suitably motivated to return home. Within the small flight radius of the study this might not be the case.

When comparing young and old individuals (Figure 3) it becomes evident that the inexperienced birds have a much lower efficiency on the first four flights and show a much more significant increase in efficiency than the old birds. After ~5 flights, both young and old birds show similar efficiencies on their learned routes. The earlier success of the old birds suggests that general experience may be important in determining flight efficiency from novel locations. A linear mixed model of route efficiency against flight suggests that both bird age and flight number are significant predictors of efficiency, with a significant interaction between age and flight number. This supports the differing relationship between efficiency increase in young and old birds across the flights.

In contrast to previous work (Biro et al., 2006, 2004; Meade et al., 2005), the Frankfurt group failed to find an increase in efficiency when releasing birds from shorter distances, with only birds being released from 30km showing an increase in efficiency over multiple releases (Schiffner et al., 2013; 2018). These birds were all experienced adults with significant homing experience in the region with efficiencies between 0.77 and 0.92 found (Wiltschko et al., 2007), although no significant increase in efficiency was seen over the recorded flights. The range of efficiencies is similar to the range at which the pigeons here stabilise at after the initial learning phase, and agrees with the results shown in Figure

3, where the more experienced birds begin with a much greater efficiency. It is possible that greater general flight experience of the older birds here or the Frankfurt birds means that their flight efficiency is generally high, so no significant increase is seen. In contrast, the inexperienced birds show a significant increase in efficiency over the first few flights. Additionally, the combination of navigational factors unique to the different flight areas between the groups may contribute to which cues are preferentially used (Schiffner et al., 2013).

Idiosyncrasy

Despite the short distance of these flights, birds still show individually distinct paths. Calculation of a mean route based upon the final three successful flights allowed nearest-neighbour distances to be calculated against self and other tracks, giving a measure of similarity to a bird's own tracks and the tracks of other birds. Figure 5 shows that "self" distances were significantly lower than "other" distances, suggesting that individual birds fly routes which are more similar to their own other routes than those flown by other birds. Additionally, we observe an overall reduction of the short-term correlation dimension from the initial to the final releases, suggesting that with increased familiarity birds rely on less cues supporting the formation of idiosyncratic routes based on visual cues (although reliance of visual cues cannot be directly tested without removing object vision, e.g. via the use of frosted lenses). This transition appears to be a rather gradual transition, rather than an abrupt switch between two modes of navigation with individuals switching back and forth between both - which would explain why this behaviour may sometimes to be hard to detect. However, splitting birds into the two age categories (Figure 5) shows that this difference is primarily due to the old birds, with young birds showing higher "self" distances. Only in old birds was the difference in nearest-neighbour distances significant between "self" and "other" tracks, suggesting that the formation of idiosyncratic routes may require more experience.

In previous studies where idiosyncratic routes were identified more experienced birds tended to be used, e.g. all birds older than two years (Biro et al., 2007, 2004; Meade et al., 2006, 2005), or four years (Biro et al., 2006). This suggests that greater flight experience may be an important factor in determining the use of visual cues associated with higher idiosyncrasy. It is possible that the one-year-old birds are more reliant on compass mechanisms to navigate, rather than using visual landmark information, or that younger less experienced birds display more exploratory behaviour. Clock-shift and magnetic treatments would be necessary to determine if compass mechanisms are being used; Biro et al found that clock-shifting birds which had learned a route resulted in an off-set track which paralleled the shape of the learned route, in the clock-shift direction (Biro et al., 2007). This demonstrates that both landmark and compass information is being combined.

Off-route releases

Following the twenty training releases from Y Felinheli, two off-route releases (Figure 1) were conducted to test whether birds would return to their learned route from a short distance away. Our results identify several different navigational strategies, the most obvious being birds flying a relatively direct route from the release site to home. This suggests use of a compass heading to navigate, and is seen from both release sites, across young and old individuals (Table 2). Both of the off-route release sites are relatively close to the Y Felinheli site, and birds have been trained in the general area, so it is possible that the birds possess a familiar area map from which they can produce the correct headings. Another strategy seen is taking a parallel track to the learned route. This is a relatively common strategy, identifiable as tracks with virtual vanishing bearings which match between the learned and off-route releases. In these cases, birds fly a parallel track to their learned route, usually correcting towards home once they have flown the correct distance. As with the direct route, this strategy suggests that the birds are relying on a compass heading, but this time a learned heading from their repeated releases, which they then copy when released at a nearby site.

A few birds showed the looked-for route joining behaviour, but in contrast with previous studies (Biro et al., 2006, 2004; Meade et al., 2005), this was not a common strategy. Re-joining the learned route suggests that the birds are at least partially relying upon visual cues, specifically the memory of cues associated with the repeated route, as the sites are in close enough proximity to each other that, from an aerial view, several landscape features should be visible from all sites, e.g. the coastline. It is possible that the short distance of the flights meant that joining the learned route was not necessary, with many birds simply taking the direct path. For the first off-route release site, the presence of the Menai Strait as an obstacle may have blocked birds from joining the original route, with uncertainties as to where to cross the body of water.

A final strategy was seen which demonstrated landscape following: when released from the first off-route site on Anglesey, several birds fly along the coast, and correct their route when reaching a particular landmark. For example, four of the old birds fly along the Menai Strait (160, 504, 552, 588), with 160 correcting towards the loft when Menai Bridge is reached, and 504/552 correcting after reaching Llanfairpwllgwyngyll. The same can be seen in many of the young birds. Following of landscape features has been previously documented (Lipp et al., 2004; Mann et al., 2014), and suggests that predominant features may override other navigational cues. However, the following of the coastline may simply be a temporary guide to help maintain the correct heading, as it roughly agrees with necessary heading, meaning that multiple navigational cues are combined, which is supported by the comparatively higher short term correlation dimension observed in birds that are using this strategy.

From the second release site there is far less evidence of following the landscape, with many parallel routes, most predominant in the old birds. The use of parallel routes is reminiscent of (Biro et al., 2007), where clock-shifted birds flew in parallel to the learned route. The authors took this as evidence of combining compass and landmark cues when navigating, which is supported by the variety of strategies demonstrated by these birds. The lack of distracting landscape features from the second off-route release site may be responsible for the reduced landmark following and predominance of parallel/direct flights.

Most birds did not show a fixed strategy at both of the off-route release sites, suggesting a flexibility of navigational strategy, responding to the particular local conditions of an unfamiliar release site. Many birds which showed a preference for landscape following from the first off-route release site flew either a direct or parallel route from the second site, demonstrating that both compass and visual landmark mechanisms could be used.

The coast following behaviour had the highest correlation dimension (2.5), suggesting that the birds following the coast were using the coastline as an additional cue instead of relying on it alone. The direct flights had a slightly lower correlation dimension (DIR: 2.0) and the parallel flights had the lowest correlation dimension (PAR: 1.5), with such a low correlation dimension suggesting reliance on the lowest number of factors. Given the idiosyncratic nature of the training routes, it is likely that an entrained compass heading may be responsible for the majority of the navigational information, with other factors being used more sparingly during the flight. From figure 6 we can see that the correlation dimension is not stable across the course of a flight, however, suggesting that the number of cues used may vary significantly across the course of a flight. Although this results in a single visually classified strategy, the actual information informing the flight path may be highly variable.

CONCLUSION

This study has demonstrated that pigeons can learn idiosyncratic routes when flying repeatedly from a nearby location, but this occurs more readily in birds with greater experience. These idiosyncratic routes were characterised by a low correlation dimension supporting the formation of idiosyncrasies in the routes, that most likely rely primarily or even exclusively on visual cues. We found a general increase in flight efficiency over the first few flights, although this was generally restricted to the young birds, which began with much more inefficient routes. Off-route releases demonstrated a variety of navigational strategies characterised by distinct differences in the short-term correlation dimension and therefore the number of cues involved in the underlying navigational process, although few birds returned to the learned route. Instead, birds used either additional landscape features (in this case the curve of the coastline) or compass directions (either a direct route home or paralleling the learned route) to navigate from the unfamiliar sites. These results suggest that multiple forms of navigational information are important when homing in a familiar area, and that the strategy used is flexible, depending on the particular local conditions.

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Table 1: Subject flight experience.

Release Location	**Bearing from loft (degrees, North=0)**	**Distance from loft (km)**
Young Birds		
Roman camp (53.233818, -4.127970)	58	3.6
Parc Menai (53.206992, -4.185048)	-144	1.4
Llanfairp.g. (53.220457, -4.194661)	-74	1.5
Llandygai roundabout (53.219084, -4.105247)	87	4.5
Old Birds		
Penmon (53.2950670, -4.0611793)	41	11.5
Caernarfon foreshore (53.1393739, -4.2825671)	-140	11.3
Waterloo port road (53.1526017, -4.2649993)	-139	9.4
Plas Menai (53.1698685, -4.2434940)	-138	7.0
Bush road (53.1815830, -4.2025464)	-153	4.4
Beach road (Felinheli 53.1838068, -4.2116039)	-145	4.5
Glan faenol (53.2045917, -4.1968571)	-131	2.1
Treborth sports fields (53.2148962, -4.1763044)	-135	0.3
Cadnant corner (53.2335445, -4.1568771)	30	2.2
Shore at chateau rhianfa (53.2376368, -4.1428572)	41	3.1
Lon ganol (53.2428050, -4.1420308)	36	3.6
Gazelle foreshore (53.2442042, -4.1286935)	44	4.3
Gallows point (53.2547081, -4.1052416)	47	6.2
Beaumaris foreshore (53.2628903, -4.0879517)	48	7.6

Friars bay (53.2764597, -4.0839630)	42	8.9
Traeth lleiniog (53.2907610, -4.0704235)	40	10.7

Table showing the release locations for the young and old birds demonstrating their range of flight experience. Both the distance and bearing of the release site from the loft is given. Release locations are given by name and coordinates.

Table 2: Individual tracks measurements for off route releases one and two.

	Off-route release 1					**Off-route release 2**				
Bird	**Strategy 1**	**CFB**	**ID**	**Efficiency**	**STCD**	**Strategy 2**	**CFB**	**ID**	**Efficiency**	**STCD**
					Young Birds					
176	CF	20	3	0.629	2.783	J	4	-6	0.529	1.733
187	D	48	13	0.885	2.633	P	30	63	0.614	1.567
283	CF	8	-64	0.370	2.183	J	3	-6	0.485	2.033
285	CF	21	-30	0.456	1.733	C	-9	-34	0.898	1.580
287	CF	9	-39	0.642	2.400	D	13	8	0.862	1.967
312	D	40	-36	0.641	2.267	D	15	2	0.978	0.550
418	C	67	-45	0.170	2.583	J	7	-10	0.265	1.980
422	P	6	-47	0.590	2.433	D	9	4	0.966	3.300
431	D	45	29	0.809	2.633	D	11	17	0.924	1.325
508	P	19	-69	0.259	1.900	D	10	7	0.937	1.950
					Old Birds					
158	D	41	-17	0.829	2.100	P	26	37	0.783	3.000
160	CF	44	-27	0.324	2.514	P	36	-81	0.300	1.467
262	D	43	-34	0.804	2.300	P	26	27	0.818	1.125
269	D	46	-10	0.848	2.800	P	23	21	0.726	1.125
504	CF	21	-40	0.345	2.067	D	5	-23	0.945	0.200

552	CF	29	-39	0.339	2.550	D	16	3	0.839	0.975
587	J	48	-7	0.535	2.150	P	42	26	0.625	2.500
588	CF	17	-60	0.731	2.250	J	7	-19	0.551	2.225
889	P	-2	-35	0.762	0.620	P	10	-3	0.837	1.220
900	D	23	-37	0.750	0.800	D	7	-7	0.969	0.450
919	D	43	-2	0.805	1.100	D	9	3	0.930	1.450

For each of the 21 birds, mean continuous flight bearings (CFBs, degrees), mean instantaneous deflection (ID, degrees), mean flight efficiency and median short term correlation dimension (STCD) has been given.

Figure 1: Satellite map of the homing pigeon home and release sites, including the name of each site, the latitude and longitude of each site in decimal degrees and the distance from the release site to the loft in kilometres and the absolute bearing from the release site to the loft in degrees.

Figure 2: Mean efficiency of each release split into young (gold) and old (light blue) birds, with 95% confidence intervals shown. Releases 1-20 are from Y Felinheli; 21 is the first off-route release from Anglesey; 22 is the second off-route release (Figure 1).

Figure 3: Box and whisker plots of track efficiency split by age group (gold=young; light blue=old) for (a) releases 1-4 and (b) releases 17-20. Centre line gives the median of the groups, the box edges the first and third quartiles, and the whiskers the maximum and minimum of the groups. Circles represent outliers.

Figure 4: Mean tracks (black) produced using nearest-neighbours to average the final three successful recordings for each bird (orange) from the Y Felinheli release site, young birds (top) and old birds (bottom). The mean area between the final three tracks has been given for each bird (km^2), as well as the mean efficiency of the final three tracks.

Figure 5: Box and whisker plot comparing the average “self” and “other” nearest neighbour distances for each bird, between young (gold) and old (light blue) individuals. Centre line gives the median of the groups, the box edges the first and third quartiles, and the whiskers the maximum and minimum of the groups.

Figure 6: Averages of the short-term correlation dimension for the individual releases, shown as a gradient with earlier releases in green transitioning through brown to later releases in red. Release number has been labelled at the end of each line, in the matching colour.

Figure 7: Tracks for each bird showing the calculated mean track from the last three successful recording from Y Felinheli (black), the first off-route release (red) and the second off-route release (green), (a) young birds; (b) old birds. Classification of the flight strategy of each off-route release is abbreviated in the matching colour for each bird at the top of the plot: CF = coast following; D = direct; P = parallel; C = cross; J = join.

Figure 8: Short-term correlation dimensions at 500m intervals for each bird classified by flight strategy for off-route release 1 (a) and off route release 2 (b). Green lines show the coast-following behaviour (CF), red a parallel route (P) and yellow a direct route (D), with unbroken lines representing old birds and dashed lines representing young birds.

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Figure 1

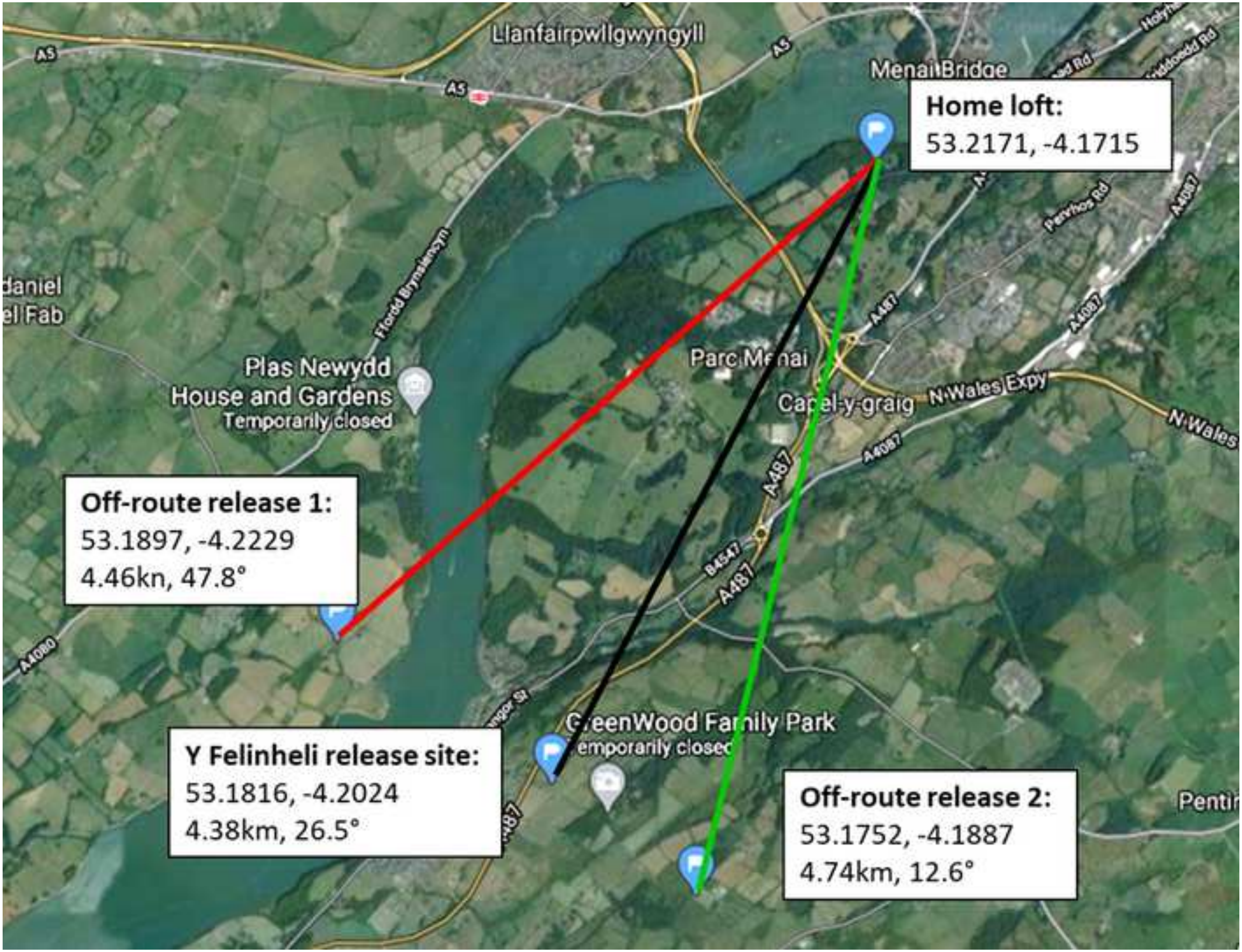
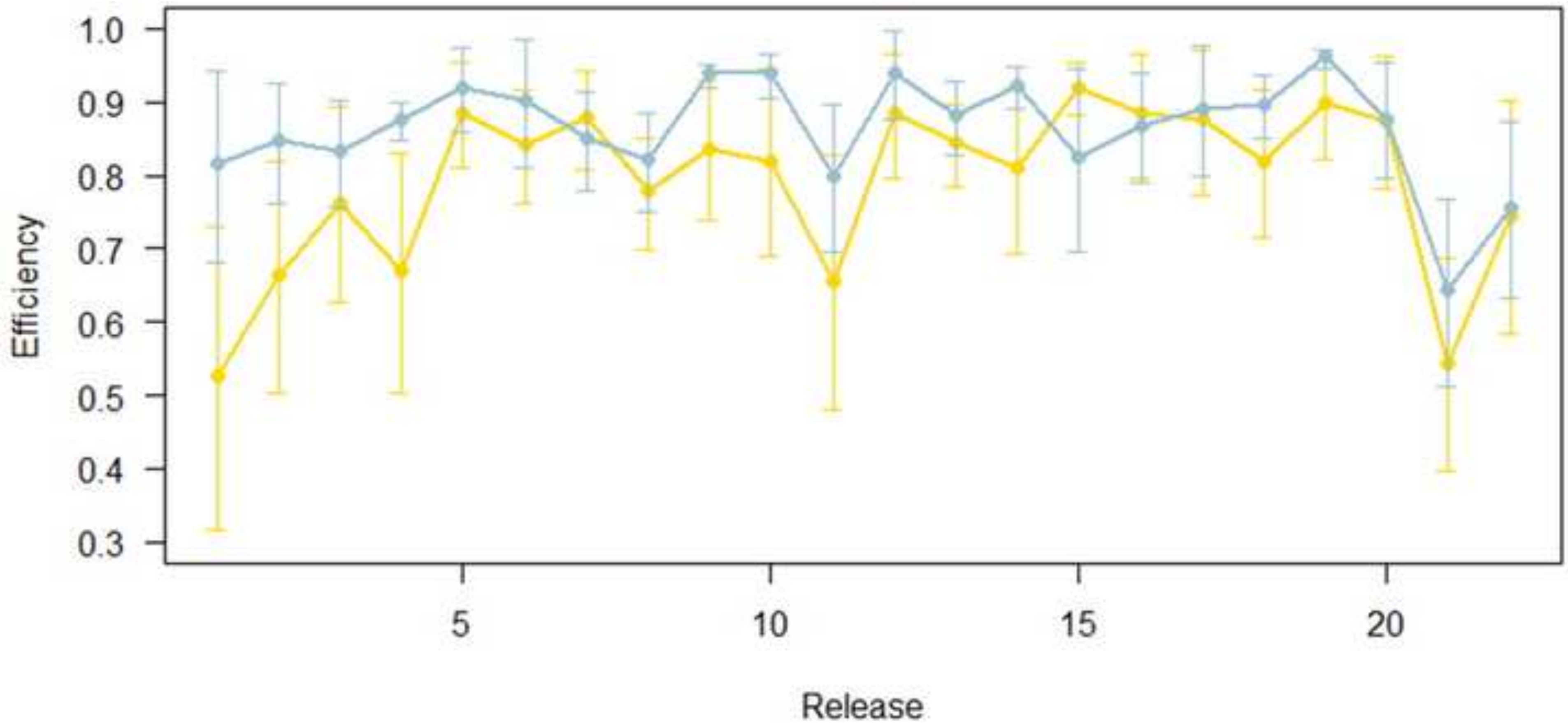

Llanfairpwllgwyngyll
A5
A5
A5
Menai Bridge
Home loft:
53.2171, -4.1715
Ffordd Brynsiencyn
Plas Newydd
House and Gardens
Temporarily closed
daniel
el Fab
Parc Menai
Capel-y-graig
N Wales Expy
N Wales
A487
A4087
Penrhos Rd
Off-route release 1:
53.1897, -4.2229
4.46kn, 47.8°
A4080
B4547
A487
GreenWood Family Park
Temporarily closed
Y Felinheli release site:
53.1816, -4.2024
4.38km, 26.5°
Off-route release 2:
53.1752, -4.1887
4.74km, 12.6°
Pentir

Figure 2



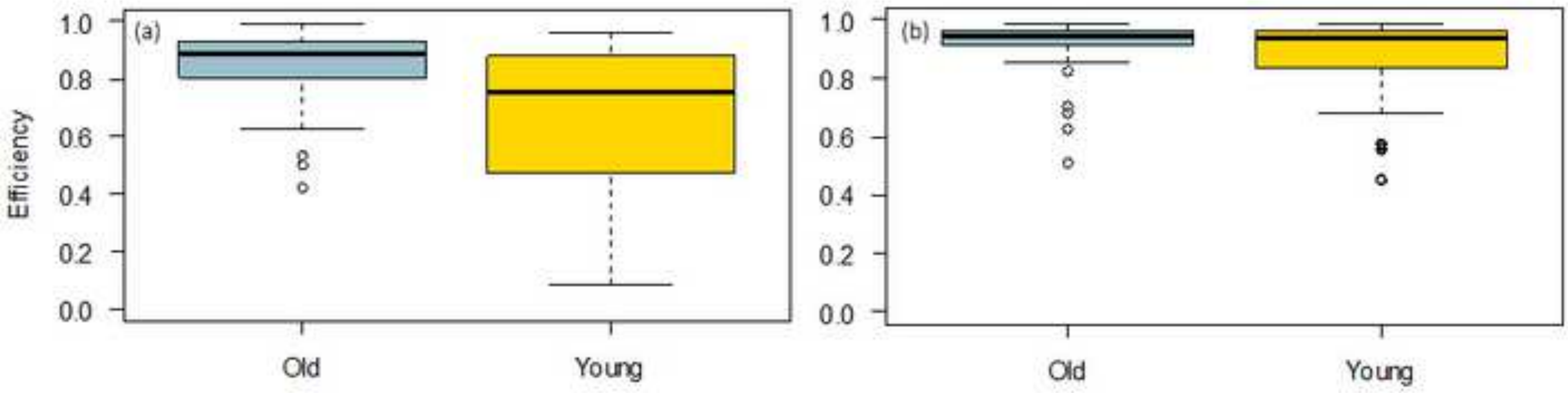

(a)
(b)
Efficiency
1.0
0.8
0.6
0.4
0.2
0.0
Old
Young

Figure 4

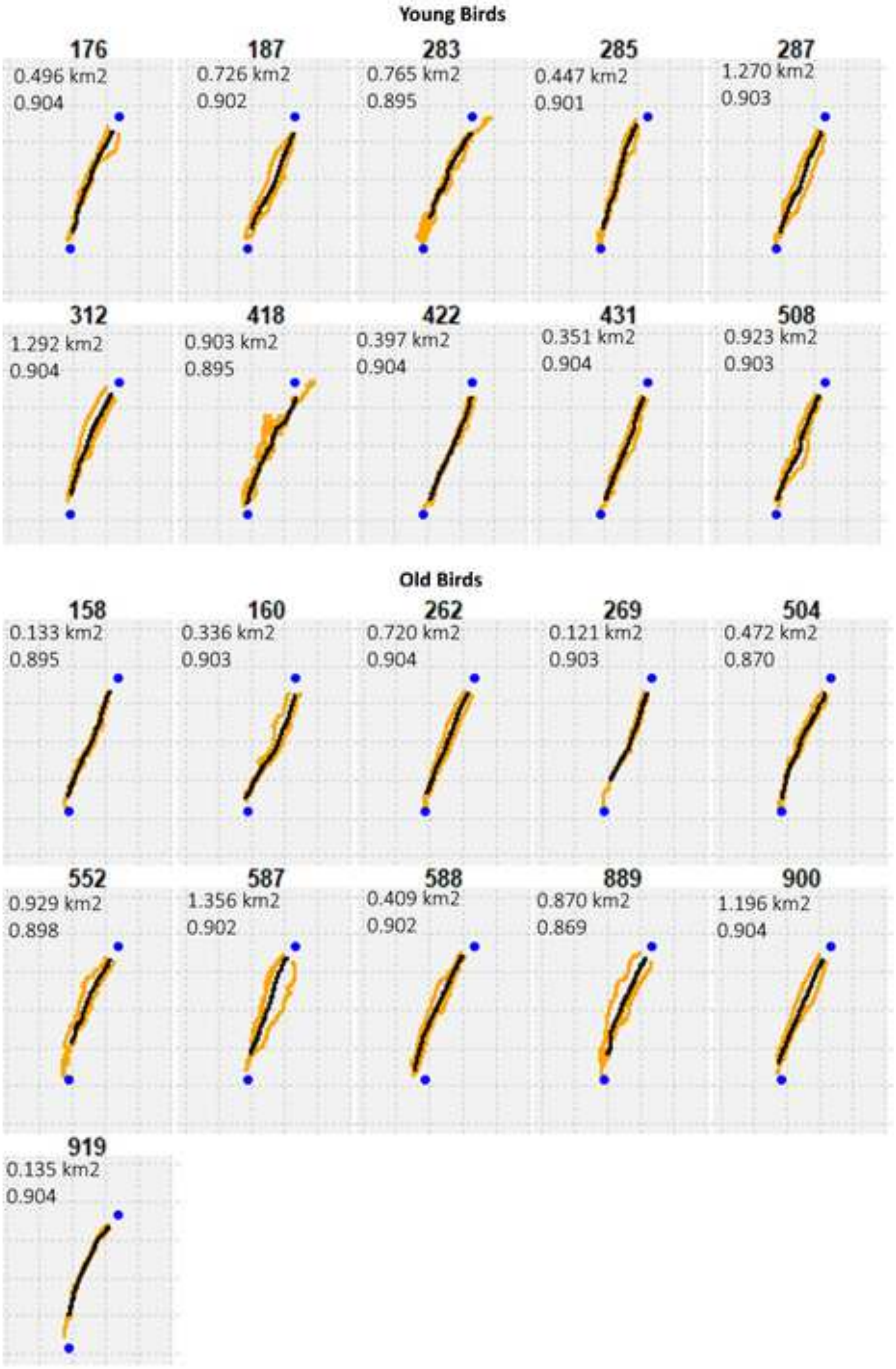
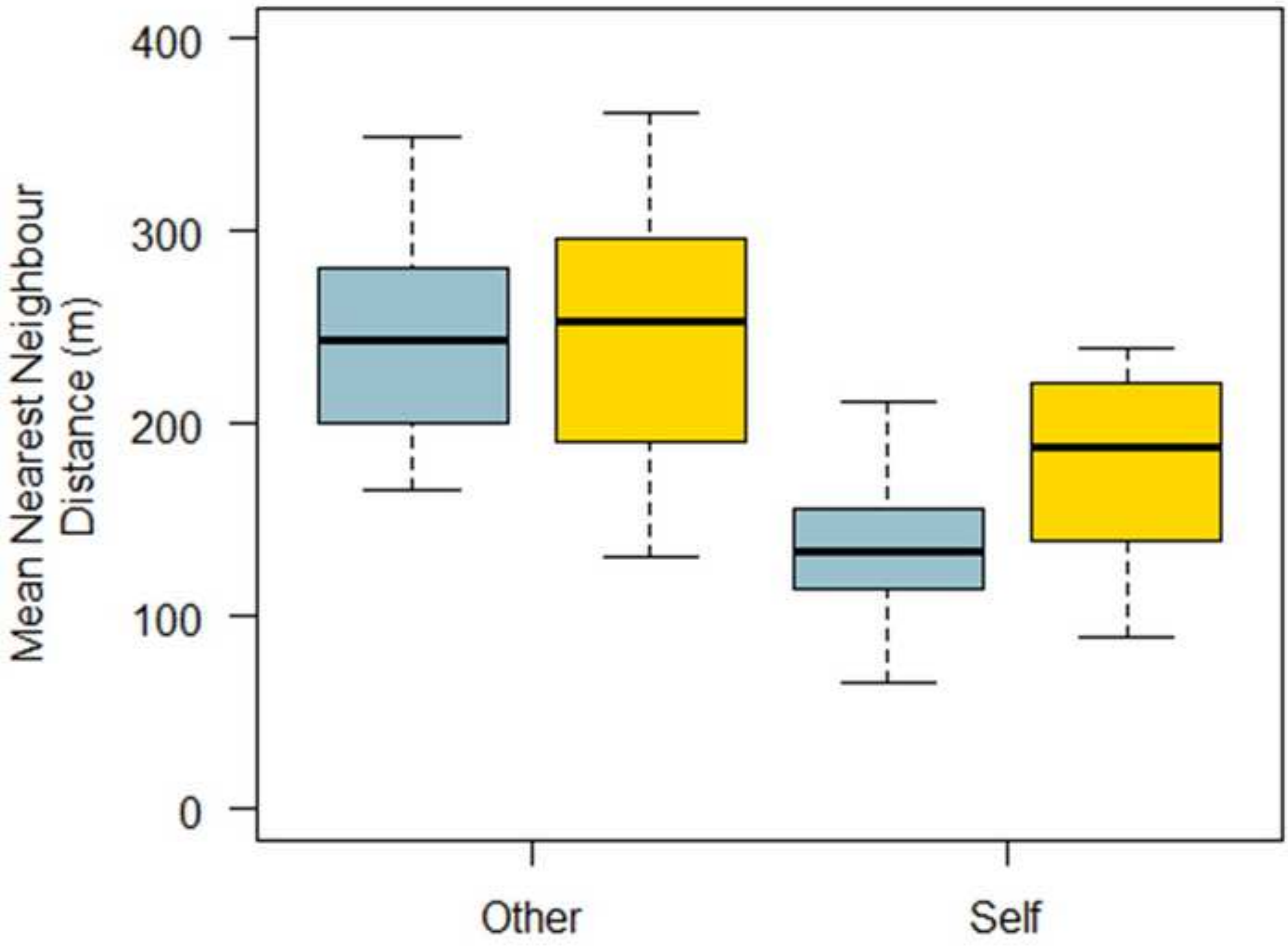

Young Birds
176
0.496 km2
0.904
187
0.726 km2
0.902
283
0.765 km2
0.895
285
0.447 km2
0.901
287
1.270 km2
0.903
312
1.292 km2
0.904
418
0.903 km2
0.895
422
0.397 km2
0.904
431
0.351 km2
0.904
508
0.923 km2
0.903
Old Birds
158
0.133 km2
0.895
160
0.336 km2
0.903
262
0.720 km2
0.904
269
0.121 km2
0.903
504
0.472 km2
0.870
552
0.929 km2
0.898
587
1.356 km2
0.902
588
0.409 km2
0.902
889
0.870 km2
0.869
900
1.196 km2
0.904
919
0.135 km2
0.904

Figure 5


400
300
200
100
0
Mean Nearest Neighbour Distance (m)
Other
Self

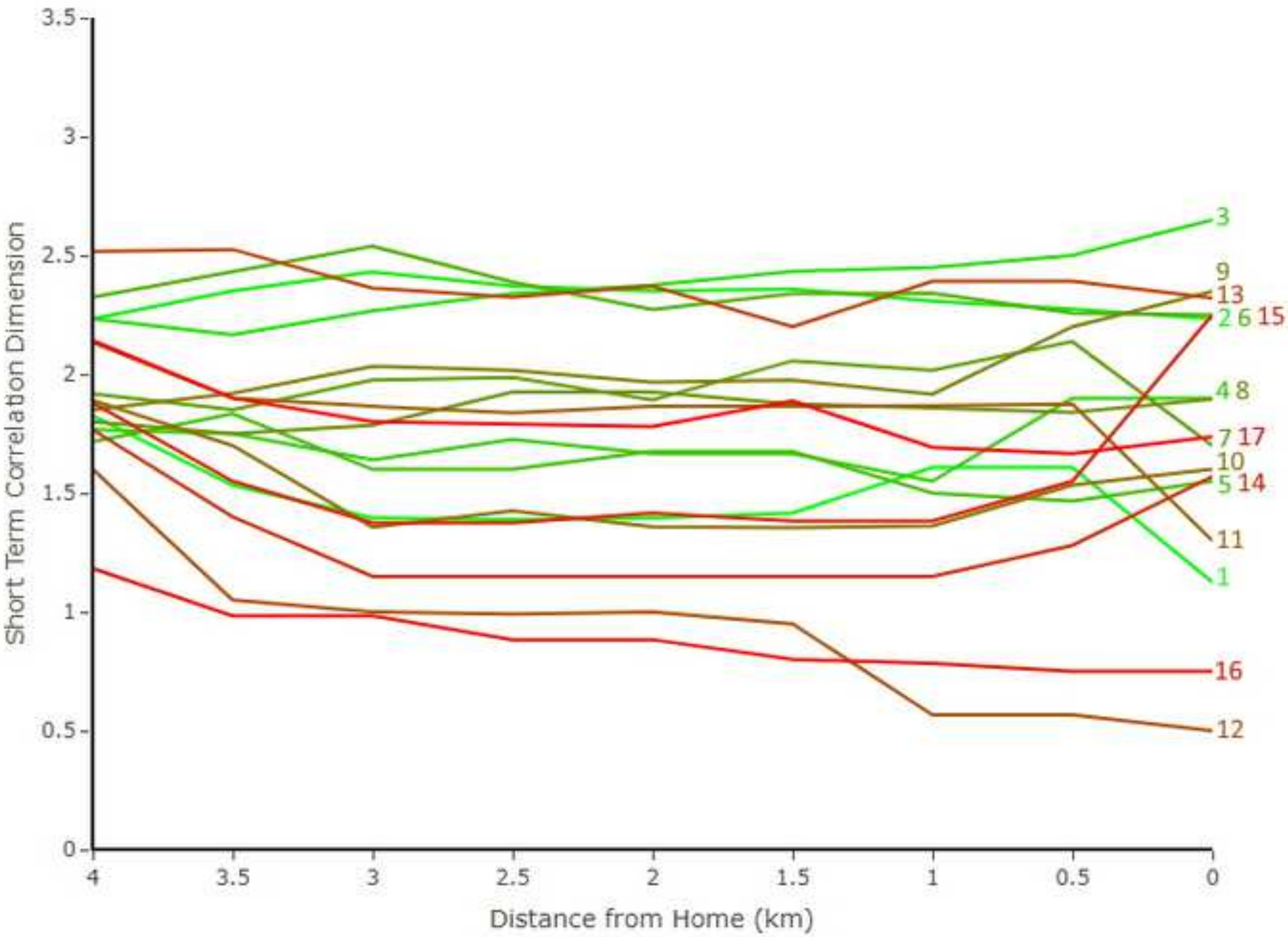

Short Term Correlation Dimension
3.5
3
2.5
2
1.5
1
0.5
0
4
3.5
3
2.5
2
1.5
1
0.5
0
Distance from Home (km)
3
9
13
2 6 15
4 8
7 17
10
5 14
11
1
16
12

Figure 7

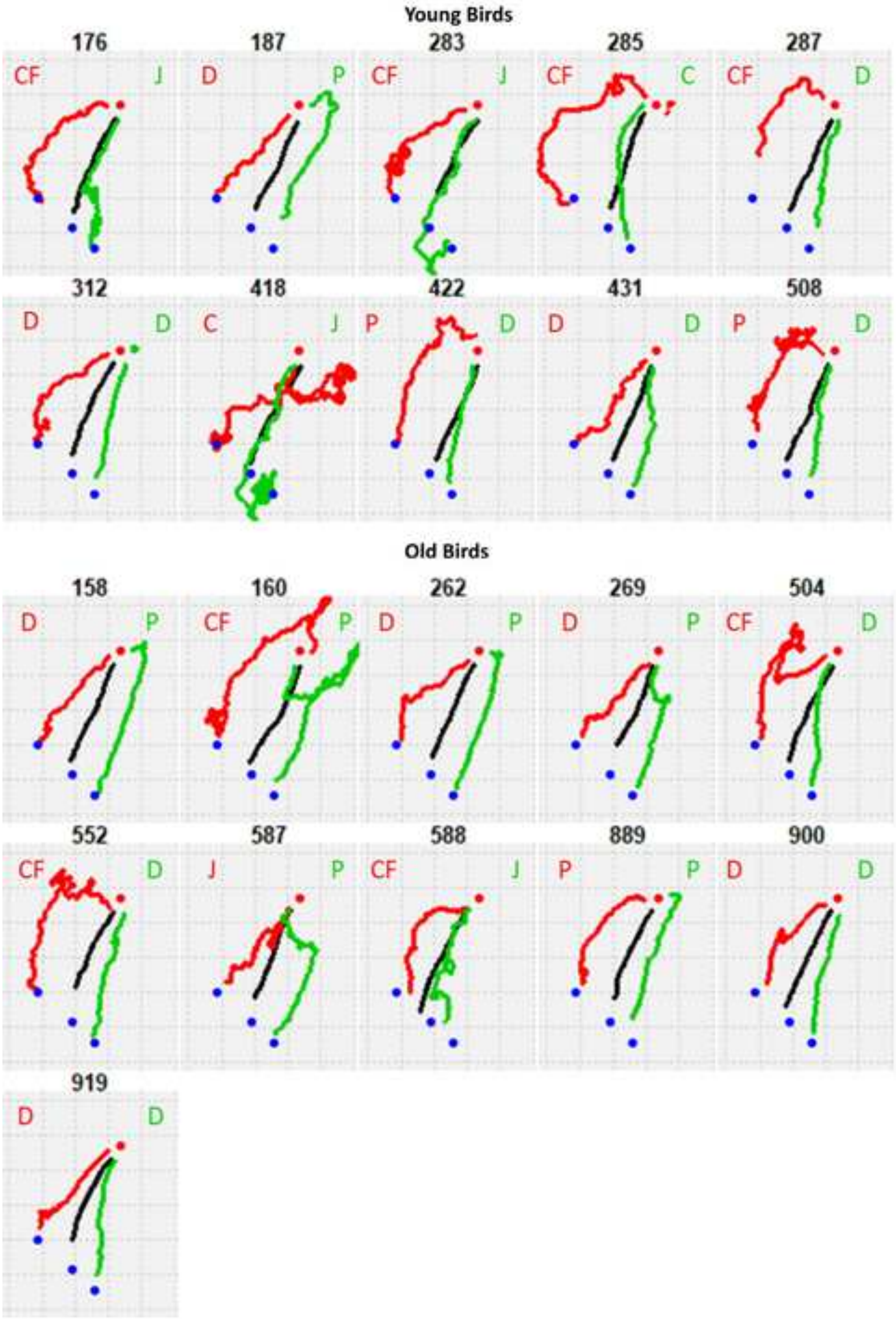
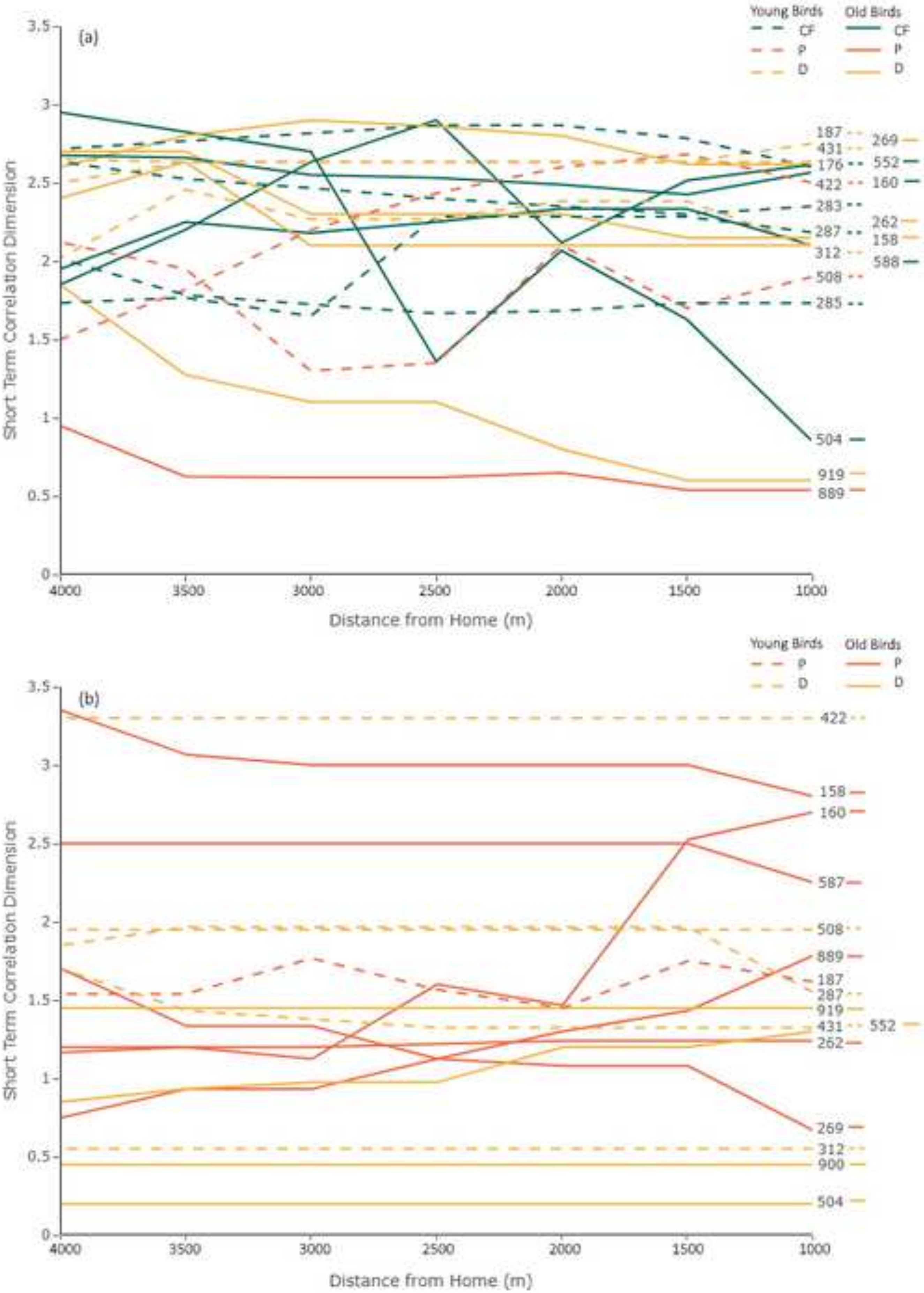

Young Birds
176
CF
J
187
D
P
283
CF
J
285
CF
C
287
CF
D
312
D
D
418
C
J
422
P
D
431
D
D
508
P
D
Old Birds
158
D
P
160
CF
P
262
D
P
269
D
P
504
CF
D
552
CF
D
587
J
P
588
CF
J
889
P
P
900
D
D
919
D
D

Figure 8


(a)
Young Birds
Old Birds
CF
P
D
Short Term Correlation Dimension
0
0.5
1
1.5
2
2.5
3
3.5
4000
3500
3000
2500
2000
1500
1000
Distance from Home (m)
187
431
176
422
283
287
312
508
285
504
919
889
269
552
160
262
158
588
(b)
Young Birds
Old Birds
P
D
Short Term Correlation Dimension
Distance from Home (m)
422
158
160
587
508
889
187
287
919
431
552
262
269
312
900
504