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Animal Behaviour

Peer reviewed version

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):
Griffiths, C., Schiffner, I., Price, E., Charnell-Hughes, M., Kishkinev, D., & Holland, R. (2021).
Repeated training of homing pigeons reveals age dependent idiosyncrasy and visual landmark
use. *Animal Behaviour*, *177*, 159-170. https://doi.org/10.1016/j.anbehav.2021.05.004

18. Apr. 2024

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

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

18 Recent research into the navigational strategies of homing pigeons (*Columba livia*) in the familiar area

19 has highlighted the phenomenon of route fidelity – birds forming idiosyncratic flight paths to which

20 they are loyal over multiple releases from the same site, and even returning to this path when released

21 from a near-by unfamiliar location. Such results highlight the potential importance of visual landmark

22 cues in the homing process. However, not all birds have been shown to produce idiosyncratic routes

23 or show this route-joining behaviour. Here we use birds with and without flight experience to study

24 the formation of idiosyncratic routes when released repeatedly from a single location, followed by

25 two off-route releases with differing topography to see how flight experience and local landmark

26 features can influence navigational strategy in the familiar area. We found that, over the course of 20

27 sequential releases, birds with greater flight experience tended to form idiosyncratic routes whereas

28   less experienced birds did not show this tendency. When released from near-by sites (from which the

29   birds had not previously been released), a range of navigational strategies were seen, including flying

30   parallel to the learned route (suggestive of a learned compass direction), a direct flight path towards

31   home (again indicative of compass use), re-joining the learned route, and following the coastline.

32   These latter strategies are suggestive of landmark usage. Analysis using time lag embedding was also

33   used to assess the off-route releases, and the short-term correlation dimension values produced

34   (ranging from 1.5-2.5) were also indicative of strategies using one or two factors (landmarks, compass,

35   or a combination of these two). Individual birds often showed different strategies at different sites,

36   suggesting that the use of different navigational cues is highly flexible and situationally dependent.

37   KEYWORDS

38   Ageing, correlation dimension; familiar landmark; homing pigeon; idiosyncrasy; navigation, spatial

39   memory, route fidelity, time lag embedding.

40   HIGHLIGHTS

41   • Birds with greater flight experience form idiosyncratic routes more readily.

42   • Multiple homing strategies occur when released close to a familiar site.

43   • Age and site-specific biases occurred in which strategies were used.

44   • Flexibility within individuals was seen in terms of strategy choice and cue use.

45   The study of pigeon homing has for many years been focused on how the birds are able navigate from

46   an unfamiliar location for so-called "true navigation", usually framed in the paradigm of Kramer's

47   "map and compass" theory (Kramer, 1953). Here, navigation is broken down into a two-step process,

48   with a "map" providing a relative location from which the appropriate direction can be determined,

49   and the "compass" providing a real-world directional heading. The map stage of navigation theorises

50   a system of relatively stable gradients which vary predictable over a significant distance, such that

51   birds can learn the spatial relationships of these gradient concentrations to produce a mental

52   navigational map (Holland, 2014). A large body of evidence supports a role of olfactory cues in the

53   formation of a map (Wallraff 2005, Gagliardo, 2013 for review), although alternative roles for olfactory

54   cues have been proposed (Jorge et al. 2009, 2010, but see Gagliardo et al. 2011, 2018). Other cues

55   have also been proposed to play a role in the map, such as the magnetic field (Wiltschko and Wiltschko

56   2009), infrasound (Hagstrum, 2000, 2013), and gravity (Blaser et al. 2014). Both magnetic (Beason,

57   2005; Keeton, 1971; Walker, 1998; Wiltschko et al., 1981; Wiltschko and Wiltschko, 1972) and solar-

58   cues have been found to provide compass information (Guilford and Taylor, 2014; Schmidt-Koenig,

59   1990) in terms of magnetic declination and the time-compensated solar azimuth compass.

60   When navigating close to the loft in a familiar area, evidence suggests that both the sun compass and

61   magnetic compass still play significant roles. Birds subjected to clock-shift procedures to alter their

62   perception of time of day, and therefore their interpretation of the time-compensated sun compass,

63   show a relatively predictable deflection angle away from the home direction when navigating, and

64   this deflection can be seen even when navigating close to the loft (Armstrong et al., 2013; Chappell,

65   1997; Wiltschko et al., 1994). Experiments attaching magnets to the heads of navigating pigeons in

66   order to disrupt access to the magnetic compass (by producing a local strong magnetic field) show

67   that deflection under clock-shift increases, suggesting that there is some influence of the magnetic

68   compass on the chosen direction also, and that the cues are being combined (Gagliardo et al., 2009;

69   Wiltschko and Wiltschko, 2007, 2001).

70   When navigating in the familiar area, however, the importance of familiar area cues, particularly visual

71   landscape features, has been highlighted (Braithwaite and Guilford, 1991; Burt et al., 1997), although

72   curiously, not always supported (Schmidt-Koenig and Schlichte, 1972; Schmidt-Koenig and Walcott,

73   1978). Early studies found that birds deprived of object vision via the use of frosted lenses were able

74   to home from significant distances (up to 130km) (Schmidt-Koenig and Schlichte, 1972), although

75   many birds with frosted lenses were only able to locate the vicinity of the loft (0.5-5km) (Schmidt-

76   Koenig and Walcott, 1978). Surprisingly, birds deprived of object vision and rendered anosmic were

77 still able to orient successfully from a familiar area, again suggesting that object vision is not necessary

78 for homing, and that at least one other cue was necessary to explain homing (Benvenuti and Fiaschi,

79 1983). However, a subsequent study did not support this and suggested a crucial role for vision if birds

80 were made anosmic (Streng and Wallraff 1992). Later investigations found that birds able to view the

81 landscape prior to release showed increased homing performance, suggesting that, when available,

82 visual access to the landscape can be important in homing (Braithwaite and Guilford, 1991; Burt et al.,

83 1997).

84 The introduction of a whole new series of possible cues, unique to the local landscape, means that

85 strategies of navigation in the familiar area may be highly variable dependent on individual location.

86 Studies have highlighted the importance of landscape features such as rivers, roads and hedgerows

87 which make up patterns of straight lines in the environment to determine flight path structure (Lipp

88 et al., 2004), as well as how the density of edges in the landscape influences how well routes are

89 learned (Mann et al., 2014). The importance of landscape features when learning to navigate in the

90 familiar area is evident and brings in to question how the cues used outside of the familiar area

91 (olfactory, magnetic, solar) are integrated with the visual landmark cues.

92 Familiarity with an area comes in two forms – general flight experience in the local area, and

93 experience flying from a particular release site. Previous studies have demonstrated that homing

94 efficiency is greater in birds generally familiar with an area in comparison with naïve individuals

95 (Meade et al., 2006), suggesting that familiarity influences the navigational strategy. Studies of birds

96 released repeatedly from the same location show that birds tend to show an increase in route

97 efficiency and fidelity (Biro et al., 2006, 2004; Meade et al., 2005). However, these birds do not

98 produce maximally efficient routes, instead developing individually stereotypical routes, with

99 efficiency reaching a plateau once the route has been established. Furthermore, birds released from

100 sites alongside the learned route have been shown to return to the established route, rather than

101 flying a direct route (Biro et al., 2006, 2004). This suggests that, instead of flying on a direct compass

102   heading towards home, birds use the local landscape cues to inform their routes. One study found

103   that bottlenecks in tracks from repeated releases occurred alongside salient landmark cues,

104   suggesting the learned routes are constrained by particular landmark features (Mann et al., 2011).

105   However, the Frankfurt group failed to replicate these results (Wiltschko et al., 2007), with pigeons

106   failing to show an increase in efficiency, or produce stereotyped routes. A later analysis found that

107   birds unfamiliar to the area had a similar efficiency to familiar birds, but that birds released multiply

108   from the same site did show a general increase in efficiency (Schiffner et al., 2013). Given the

109   importance of individual landscape features unique to a particular area, it is possible that the ability

110   to learn local routes varies between locations or landscape features (Mann et al., 2014). Therefore,

111   we use a new location to test the hypotheses that birds develop stereotypical routes when navigating

112   repeatedly from a known location, and that they will preferentially return to this learned route when

113   released at a novel site nearby. Additionally, we classify our test groups as "old" and "young" birds,

114   with over ten years or less than one year of experience respectively, to investigate how age and

115   navigational experience affects navigational ability in the familiar area.

116   According to the predictions of earlier studies, birds forming idiosyncratic routes should show a

117   general increase in efficiency over early releases, but plateau below maximum efficiency (Flack et al,

118   2012; Guilford and Biro, 2014; Meade et al., 2005). Birds should show an increase in route fidelity,

119   with a bird's later releases more similar to each other than earlier releases. Once an idiosyncratic route

120   has been formed, it should be relatively distinct compared to the routes of others. Off-route releases

121   may produce a variety of strategies, with an expectation of either a) a direct route home, based on a

122   compass heading; b) a return to the learned route which is then followed home, presumably more

123   reliant on visual landmark cues (Biro et al., 2004); or c) possible offset of the learned route from the

124   novel release site, similar to the offset routes seen when clock-shifting birds from a learned route (Biro

125   et al., 2007).

126   METHODS

127 *Subjects, Training and Releases*

128 A total of 21 birds in two age categories (ten young birds, only one year old and eleven old birds,

129 nine/ten years old) were trained to fly repeatedly from a single release site at Y Felinheli (within 5km)

130 over the course of two months, from the 19/09/2017 – 14/11/2017, with a total of twenty releases

131 from the site. All of the birds had flight experience in the local area but had not participated in previous

132 homing experiments. The birds were kept indoors usually during the day and did not have

133 independent free access to the outdoors. Old and young birds had a greatly different flight experience

134 prior to the tracked releases from Felinheli (table 1).

135 During the experimental releases, birds were released individually. The majority of releases took place

136 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

137 day (morning and afternoon releases). All 21 birds completed the 20 training flights from Y Felinheli,

138 although a few flights were not successfully recorded. Any incomplete tracks were removed from the

139 analysis. All of the experimental flights were tracked using a GPS recorder (i-gotU USB GPS Travel and

140 Sports Loggers, 15.5g with outer casing removed), with position fixes every second and an accuracy of

141 ±5m. Trackers weighed less than 5% of the birds' bodyweight, and all birds had experience carrying

142 the trackers before the experimental releases. The trackers were attached to the back between the

143 wings using a Velcro strip glued to trimmed feathers. Following the repeated releases from Y Felinheli,

144 two off-route releases were performed, one from just across the Menai Strait on Anglesey, and one

145 further inland (see Figure 1 for a map of the release sites and home loft location). Off-route release 1

146 was 1.64km from the Y Felinheli release site, and off-route release 2 was 1.16km. Both off-route

147 releases were conducted once on separate days. All birds were housed at the Bangor University

148 Treborth Botanic Gardens loft, under natural daylight. Birds had free access to water and grit, and 25g

149 of food per bird per day.

150 *Data Analysis*

151 *Processing*

152 All tracks were processed and analysed using RStudio. Firstly, a low-pass filter was applied to the

153 latitude and longitude values to remove noise at the frequency of data collection. Following this,

154 calculations were applied to produce continuous flight bearings (CFBs, the bearing of each point from

155 the release site) for each point, distance travelled between each point, current heading, and

156 instantaneous deflection (ID, the difference between the current heading and the home direction) at

157 each point (Agostinelli and Lund, 2017, 2018; Hijmans, 2019). Point of decision analysis was then used

158 to remove early circling behaviour from the tracks (Schiffner and Wiltschko, 2009). The mean vector

159 length of current bearings was calculated across each set of ten consecutive points, and a cut-off for

160 navigational behaviour chosen when three of these consecutive mean vector lengths were all greater

161 than 0.85, implying relatively consistent direction of flight. This cut-off of 0.85 was chosen after testing

162 multiple values, as providing the best balance between removing circling behaviour without excluding

163 too much of the track. As well as this, a radius of 200m around the home loft was removed from the

164 tracks to discount the circling behaviour around the loft, as this distorts calculations of efficiency.

165 Following this processing, various calculations were performed to analyse the tracks.

166 *Efficiency*

167 Efficiency of a tracks is calculated as the shortest beeline distance divided by the actual distance flown

168 between the start and end points, ranging between zero and one. Efficiency was then compared

169 between young and old birds using the Mann-Whitney U test, and a linear mixed model was used to

170 analyse the factors influencing change in efficiency, with release number and age as fixed effects, and

171 bird as a random effect (Bates et al., 2015). An ANOVA test was used to compare a full and reduced

172 model to identify the significant factors.

173 *Idiosyncrasy*

174   In order to investigate whether birds showed individually unique routes, a mean route was computed

175   for each bird, consisting of the three final successful tracks recorded from Y Felinheli. The mean track

176   was first created as a series of equally-spaced points from the start to the end of the track. For each

177   point along the mean track, the nearest time-independent point on each of the tracks to be averaged

178   was found, and the mean track point moved to the mean of the nearest neighbour points. Once this

179   had been applied to the entire track, points were moved to fill out any gaps and reduce bunching

180   along the mean route by moving any points more than a set distance apart to the half-way point

181   between them.

182   Once the mean route had been constructed, the nearest-neighbour distances were calculated to three

183   tracks from the same individual (tracks 13, 15 and 16 as these were available for all birds), and to

184   tracks from a different individual (individual chosen at random for each track, tracks 8, 9, 10 and 12).

185   The average nearest neighbour distance for "self" and "other" comparisons was calculated for each

186   bird and compared using a Wilcoxon signed-rank test.

187   *Off-route releases*

188   To investigate the directional choices made when released from the off-route locations, CFBs were

189   calculated for the mean tracks of each bird (as described above). As the CFBs describe the angle from

190   the release site at each point along the track, matching CFBs from two tracks suggest a copying of the

191   known route. ID was also calculated for the mean tracks and compared to the ID values from the off-

192   route releases. The mode of each of these measures was calculated to identify the predominant

193   direction of flight over the course of the tracks. These measures, alongside visual inspection of the

194   flight paths, were used to classify the off-route releases into different categories of navigational

195   behaviour.

196   *Time lag embedding*

197   We analyzed data by means of time lag embedding to determine the underlying characteristics of the

198   navigational process used by Homing Pigeons - *Columba livia f. domestica* (Schiffner et al., 2011). Time

199   lag embedding is a method derived from dynamic systems theory, an advanced area of mathematics

200   and physics focused on understanding and describing complex dynamic systems. Time lag embedding,

201   commonly used to characterise dynamic systems (i.e. systems that change over time) (Nehmzow,

202   2006; Small, 2005), allows the physical/data driven reconstruction of a system in phase space.

203   Observations of a system can be used to construct a multi-dimensional phase space, where each axis

204   in this space represents a parameter of the system (Takens, 1981). The number of parameters (or

205   degrees of freedom) in this space, therefore, is the minimum number of independent variables

206   necessary to describe the system. The proper embedding dimension was determined using a false

207   nearest neighbour approach and the correct time lag was estimated using a non-parametric

208   normalized mutual information algorithm to deal with the sensor noise.

209   *Correlation dimension*

210   In order to estimate the number of navigational factors used by the birds' navigational system we

211   calculated the correlation dimension, a measure of the degrees of freedom of the system. The

212   methods described here have been tested rigorously in mathematical systems where the exact

213   number of degrees of freedom is known and have been applied successfully to tracks of homing

214   pigeons, allowing unprecedented insight into their navigational system (Schiffner et al., 2016, 2014,

215   2011; Schiffner and Wiltschko, 2014, 2013).

216   The method used to determine the correlation dimension is identical to the original algorithm

217   described by Grassberger and Procaccia (Grassberger and Procaccia, 1983). By estimating the

218   correlation dimension we can determine the nature of the underlying process: deterministic systems

219   have an integer dimension (e.g. 1.0, 2.0, etc.); random systems are dimensionless; chaotic

220   deterministic systems have a fractal/non integer dimension (e.g. 1.3, 2.1, etc.). Here we specifically

221   estimated the short-term correlation dimension, a lower bound rolling estimate of the actual

222   correlation dimension over a fixed time window calculated over the entirety of the track to analyse

223   the tracks and potential changes in the navigational process throughout the pigeon's journey to its

224   home loft.

225   *Theoretical considerations*

226   When considering an animal's navigational process, the degrees of freedom, as represented by the

227   correlation dimension, indicates the number of independent sensory modalities involved in the

228   navigational process - where the same sensor could pick up several independent cues. Applied to

229   tracks of an animal the correlation dimension thus, allows us to draw conclusions about the

230   navigational strategy used; low correlation dimensions suggest simpler forms of navigation, like

231   navigation based on point-like information, while higher correlation dimensions suggest navigation

232   based on multiple environmental gradients (Schiffner et al., 2011).

233   The effects of the different releases and types of behaviours on the short-term correlation dimension

234   were tested using the Aligned Rank Transformed ANOVA (ART-ANOVA), a non--parametric approach

235   utilizing GLMM and Global ranking to ensure normal distribution of the data (Wobbrock et al., 2011).

236   For post hoc comparison, we employed least squared means using the Tukey method for multiple

237   comparisons. While this method can ensure that data is drawn from a normal distribution, it still

238   requires testing for homogeneity of variances. The Leneve's test, used to test for homogeneity of

239   variances, ensured homogeneity of variances in all tests. In each test we considered the effect of either

240   the release number or the type of behaviour and the distance from home as fixed effects, and the

241   bird's identity as a random effect.

242   *Ethical Statement*

243   All applicable animal welfare guidelines were followed including the ASAB/ABS Guidelines for the

244   treatment of animals in research. The project was reviewed by Bangor University AWERB and received

245   approval for work to be carried out (approval number: CNS2017EJP01).

246 RESULTS

247 *Efficiency*

248 Efficiency was calculated with the exclusion of early circling and circling around the loft, as described

249 in the methods. There was a general increase in efficiency over the first five releases, with young birds

250 showing a much lower efficiency in the first few releases (Figures 2 and 3a). Comparison of the groups

251 using the Mann-Whitney U test found a significant difference in efficiency between young and old

252 birds during the first 4 releases (Mann-Whitney U Test: W = 1129, P = 5.028x10^{-4}), but not during the

253 final 4 releases (Mann-Whitney U Test: W = 1053, P = 0.268), (figure 3a and 3b respectively). The mean

254 efficiency stabilises between 0.8-0.9, showing that the birds are not using maximally efficient routes,

255 even when removing circling behaviour.

256 A linear mixed model found that both Release and Age group were significant predictors of Efficiency,

257 with an ANOVA comparison of a full model including an interaction between Age and Release and a

258 reduced model without the interaction showing a significant difference (ANOVA: P = 5.519x10^{-5}).

259 *Idiosyncrasy*

260 Mean tracks were calculated from the final three releases from Y Felinheli for each bird. Figure 4 shows

261 these tracks, as well as the mean efficiency averaged across the last three tracks, and the mean area

262 between the tracks is also given in km^2. No significant difference was found in the area between the

263 final tracks between the old and young birds (Wilcoxon signed-rank test: W = 41, P = 0.349). No

264 correlation between mean efficiency and area between tracks was found when a linear regression was

265 applied (ANOVA: $F_{1,19}$ = 0.0125, P = 0.912). Comparison of the calculated mean tracks (Figure 4) to

266 "self" and "other" tracks produced a list of average nearest neighbour distances for each individual.

267 Using a Wilcoxon signed-rank test, we find a significant difference between the self-comparisons and

268 other-comparisons of mean nearest neighbour distance (Wilcoxon signed-rank Test: V = 218, P =

269   1.918x10^{-3}), with self-distances being lower on average than comparisons to the tracks of other birds

270   (Figure 6).

271   Figure 5 breaks down the above to compare the "self" and "other" distances between young and old

272   birds. There is a significant difference in the "self" distances between young and old birds (Mann-

273   Whitney U Test: U = 28, P = 0.034) with old birds showing lower nearest neighbour distances than

274   young birds. However, there is no significant difference in the "other" distances between young and

275   old birds (Mann-Whitney U Test: U = 61, P = 1). The significant difference between self and other

276   comparisons is maintained when looking at old birds alone (Wilcoxon signed-rank Test (paired): V =

277   65, P = 1.953x10^{-3}), but not young birds (V = 47, P = 0.240).

278   *Short-term Correlation Dimension Analysis*

279   Using time lag embedding to calculate the short-term correlation dimension for each track of repeated

280   releases we observe a highly significant effect of the release number on the correlation dimension

281   (ART ANOVA: $F_{16,2903}$ = 44.565, P < 2x10^{-16}), which is also confirmed by the post hoc comparisons. Figure

282   6 suggests that this transition is not instantaneous, but rather gradual. The majority of initial flights

283   have a higher correlation dimension (Green colours: 2-2.5) compared to the later flights (Red colours:

284   1-1.5). These final values are close to what we would expect if the birds would switch to following

285   landmarks to aid their navigation. Two caveats though, the short-term correlation dimension is

286   generally lower than the actual correlation dimension and there is a lot of variation in this data set.

287   However, because of the high variation and the fact that we are looking at averages it is evident that

288   at least some of the birds do occasionally follow landmarks.

289   *Off-route Releases*

290   Figure 7 shows the mean track and off-route releases for the young and old birds. From visual analysis

291   of these tracks and use of CFBs and ID, off-route return strategies have been classified (Table 2). Flight

292   strategies have been broken down into several classes: a coast-following (CF) strategy seen from the

293 first-off route release where the bird follows the Menai Strait coastline of the Anglesey side before

294 crossing the Strait close to home; a direct route (D) where the bird flies a relatively straight course

295 between the release site and home; parallel (P) where the bird flies parallel to the Y Felinheli route,

296 and corrects towards home later on; joining (J) behaviour, where the bird clearly flies to and then

297 along the established learned route; and finally cross (C) where the bird appears to cross but not join

298 the established route.

299 CFB is a measure of the absolute bearing of a point from the release site. As the absolute bearing of

300 the home loft from the first off-route release site is 47.8° and from the second off-route release 12.6°

301 (Figure 1), a modal CFB near these values for each release suggests a relatively direct route. Similarly,

302 an ID of 0° suggests direct homewards flight, e.g. bird 919 with a CFB of 43 and ID of -2 for off-route

303 release 1 and a CFB of 9 and ID of 3 for off-route release 2, both suggesting a direct flight path. The

304 homewards bearing from the Y Felinheli release site is 26.5°, therefore modal CFBs near this on the

305 off-route releases suggest a parallel of the learned route, e.g. birds 158 and 262, with CFBs of 26 for

306 off-route release 2. A chi-squared contingency table analysis of flight strategy for each location finds

307 no association between age and flight strategy from the first off-route release site (Chi-squared test:

308 $\chi^2_3 = 0.952$, $P = 0.813$), but an association close to significance at the second off-route release site with

309 old birds favouring the parallel strategy (Chi-squared test: $\chi^2_2 = 5.45$, $P = 0.066$).

310 In terms of mean flight efficiency and short-term correlation dimension (STCD) of the off-route

311 releases, there is a significant negative correlation (-1.012), with STCD decreasing as efficiency

312 increases (ANOVA: $F_{1,40} = 4.447$, $P = 0.0413$). There was no significant correlation between efficiency

313 of the first and second off-route releases (ANOVA: $F_{1,19} = 2.298$, $P = 0.146$), nor STCD (ANOVA: $F_{1,19} =$

314 1.081, $P = 0.312$).

315 Using time lag embedding to calculate the short-term correlation dimension for each track of offs-

316 route releases and comparing the prevalent types of behaviours (direct, parallel and coast-following)

317 reveals a significant difference between direct routes and parallel routes, as well as differences

318 between those two types and the coast following type of behaviour. While there is variation in the

319 correlation dimension estimates indicating that the visual categorisation is not exact, it was still

320 sufficiently accurate to detect significant differences between the different types of routes (ART

321 ANOVA: $F_{2,214} = 44.731$, $P < 2\text{x}10^{-16}$). These differences are also confirmed by the post hoc comparisons,

322 showing again significant differences between the individual types of routes. Figure 8 shows that Coast

323 following has the highest correlation dimension (CF≈2.5). The Direct flights have a slightly lower

324 correlation dimension (DIR≈2.0) and the parallel flights have the lowest correlation dimension

325 (PAR≈1.5).

326 DISCUSSION

327 *Efficiency*

328 Figure 2 shows that average efficiency per flight increases over the first five flights, stabilising between

329 0.8 and 0.9. This demonstrates an improvement in path efficiency with experience, but is still variable

330 and plateaus before reaching maximal efficiency. Given that this measure of efficiency was calculated

331 from tracks where circling behaviour had been removed, the numbers are a true representation of

332 the efficiency of the navigational path. This initial increase in efficiency is in agreement with previous

333 findings, where birds flew routes significantly longer than the beeline (Biro et al., 2004; Meade et al.,

334 2005). Consistently inefficient routes suggest that the flight path is not based solely on a compass

335 direction, which should produce a beeline home. However, it should also be noted that we would only

336 expect highly efficient routes if birds were suitably motivated to return home. Within the small flight

337 radius of the study this might not be the case.

338 When comparing young and old individuals (Figure 3) it becomes evident that the inexperienced birds

339 have a much lower efficiency on the first four flights and show a much more significant increase in

340 efficiency than the old birds. After ~5 flights, both young and old birds show similar efficiencies on

341 their learned routes. The earlier success of the old birds suggests that general experience may be

342   important in determining flight efficiency from novel locations. A linear mixed model of route

343   efficiency against flight suggests that both bird age and flight number are significant predictors of

344   efficiency, with a significant interaction between age and flight number. This supports the differing

345   relationship between efficiency increase in young and old birds across the flights.

346   In contrast to previous work (Biro et al., 2006, 2004; Meade et al., 2005), the Frankfurt group failed to

347   find an increase in efficiency when releasing birds from shorter distances, with only birds being

348   released from 30km showing an increase in efficiency over multiple releases (Schiffner et al., 2013;

349   2018). These birds were all experienced adults with significant homing experience in the region with

350   efficiencies between 0.77 and 0.92 found (Wiltschko et al., 2007), although no significant increase in

351   efficiency was seen over the recorded flights. The range of efficiencies is similar to the range at which

352   the pigeons here stabilise at after the initial learning phase, and agrees with the results shown in Figure

353   3, where the more experienced birds begin with a much greater efficiency. It is possible that greater

354   general flight experience of the older birds here or the Frankfurt birds means that their flight efficiency

355   is generally high, so no significant increase is seen. In contrast, the inexperienced birds show a

356   significant increase in efficiency over the first few flights. Additionally, the combination of navigational

357   factors unique to the different flight areas between the groups may contribute to which cues are

358   preferentially used (Schiffner et al., 2013).

359   *Idiosyncrasy*

360   Despite the short distance of these flights, birds still show individually distinct paths. Calculation of a

361   mean route based upon the final three successful flights allowed nearest-neighbour distances to be

362   calculated against self and other tracks, giving a measure of similarity to a bird's own tracks and the

363   tracks of other birds. Figure 5 shows that "self" distances were significantly lower than "other"

364   distances, suggesting that individual birds fly routes which are more similar to their own other routes

365   than those flown by other birds. Additionally, we observe an overall reduction of the short-term

366   correlation dimension from the initial to the final releases, suggesting that with increased familiarity

367 birds rely on less cues supporting the formation of idiosyncratic routes based on visual cues (although

368 reliance of visual cues cannot be directly tested without removing object vision, e.g. via the use of

369 frosted lenses). This transition appears to be a rather gradual transition, rather than an abrupt switch

370 between two modes of navigation with individuals switching back and forth between both - which

371 would explain why this behaviour may sometimes to be hard to detect. However, splitting birds into

372 the two age categories (Figure 5) shows that this difference is primarily due to the old birds, with

373 young birds showing higher "self" distances. Only in old birds was the difference in nearest-neighbour

374 distances significant between "self" and "other" tracks, suggesting that the formation of idiosyncratic

375 routes may require more experience.

376 In previous studies where idiosyncratic routes were identified more experienced birds tended to be

377 used, e.g. all birds older than two years (Biro et al., 2007, 2004; Meade et al., 2006, 2005), or four

378 years (Biro et al., 2006). This suggests that greater flight experience may be an important factor in

379 determining the use of visual cues associated with higher idiosyncrasy. It is possible that the one-year-

380 old birds are more reliant on compass mechanisms to navigate, rather than using visual landmark

381 information, or that younger less experienced birds display more exploratory behaviour. Clock-shift

382 and magnetic treatments would be necessary to determine if compass mechanisms are being used;

383 Biro et al found that clock-shifting birds which had learned a route resulted in an off-set track which

384 paralleled the shape of the learned route, in the clock-shift direction (Biro et al., 2007). This

385 demonstrates that both landmark and compass information is being combined.

386 *Off-route releases*

387 Following the twenty training releases from Y Felinheli, two off-route releases (Figure 1) were

388 conducted to test whether birds would return to their learned route from a short distance away. Our

389 results identify several different navigational strategies, the most obvious being birds flying a relatively

390 direct route from the release site to home. This suggests use of a compass heading to navigate, and is

391 seen from both release sites, across young and old individuals (Table 2). Both of the off-route release

392   sites are relatively close to the Y Felinheli site, and birds have been trained in the general area, so it is

393   possible that the birds possess a familiar area map from which they can produce the correct headings.

394   Another strategy seen is taking a parallel track to the learned route. This is a relatively common

395   strategy, identifiable as tracks with virtual vanishing bearings which match between the learned and

396   off-route releases. In these cases, birds fly a parallel track to their learned route, usually correcting

397   towards home once they have flown the correct distance. As with the direct route, this strategy

398   suggests that the birds are relying on a compass heading, but this time a learned heading from their

399   repeated releases, which they then copy when released at a nearby site.

400   A few birds showed the looked-for route joining behaviour, but in contrast with previous studies (Biro

401   et al., 2006, 2004; Meade et al., 2005), this was not a common strategy. Re-joining the learned route

402   suggests that the birds are at least partially relying upon visual cues, specifically the memory of cues

403   associated with the repeated route, as the sites are in close enough proximity to each other that, from

404   an aerial view, several landscape features should be visible from all sites, e.g. the coastline. It is

405   possible that the short distance of the flights meant that joining the learned route was not necessary,

406   with many birds simply taking the direct path. For the first off-route release site, the presence of the

407   Menai Strait as an obstacle may have blocked birds from joining the original route, with uncertainties

408   as to where to cross the body of water.

409   A final strategy was seen which demonstrated landscape following: when released from the first off-

410   route site on Anglesey, several birds fly along the coast, and correct their route when reaching a

411   particular landmark. For example, four of the old birds fly along the Menai Strait (160, 504, 552, 588),

412   with 160 correcting towards the loft when Menai Bridge is reached, and 504/552 correcting after

413   reaching Llanfairpwllgwyngyll. The same can be seen in many of the young birds. Following of

414   landscape features has been previously documented (Lipp et al., 2004; Mann et al., 2014), and

415   suggests that predominant features may override other navigational cues. However, the following of

416   the coastline may simply be a temporary guide to help maintain the correct heading, as it roughly

417   agrees with necessary heading, meaning that multiple navigational cues are combined, which is

418   supported by the comparatively higher short term correlation dimension observed in birds that are

419   using this strategy.

420   From the second release site there is far less evidence of following the landscape, with many parallel

421   routes, most predominant in the old birds. The use of parallel routes is reminiscent of (Biro et al.,

422   2007), where clock-shifted birds flew in parallel to the learned route. The authors took this as evidence

423   of combining compass and landmark cues when navigating, which is supported by the variety of

424   strategies demonstrated by these birds. The lack of distracting landscape features from the second

425   off-route release site may be responsible for the reduced landmark following and predominance of

426   parallel/direct flights.

427   Most birds did not show a fixed strategy at both of the off-route release sites, suggesting a flexibility

428   of navigational strategy, responding to the particular local conditions of an unfamiliar release site.

429   Many birds which showed a preference for landscape following from the first off-route release site

430   flew either a direct or parallel route from the second site, demonstrating that both compass and visual

431   landmark mechanisms could be used.

432   The coast following behaviour had the highest correlation dimension (2.5), suggesting that the birds

433   following the coast were using the coastline as an additional cue instead of relying on it alone. The

434   direct flights had a slightly lower correlation dimension (DIR: 2.0) and the parallel flights had the lowest

435   correlation dimension (PAR: 1.5), with such a low correlation dimension suggesting reliance on the

436   lowest number of factors. Given the idiosyncratic nature of the training routes, it is likely that an

437   entrained compass heading may be responsible for the majority of the navigational information, with

438   other factors being used more sparingly during the flight. From figure 6 we can see that the correlation

439   dimension is not stable across the course of a flight, however, suggesting that the number of cues

440   used may vary significantly across the course of a flight. Although this results in a single visually

441   classified strategy, the actual information informing the flight path may be highly variable.

442   CONCLUSION

443   This study has demonstrated that pigeons can learn idiosyncratic routes when flying repeatedly from

444   a nearby location, but this occurs more readily in birds with greater experience. These idiosyncratic

445   routes were characterised by a low correlation dimension supporting the formation of idiosyncrasies

446   in the routes, that most likely rely primarily or even exclusively on visual cues. We found a general

447   increase in flight efficiency over the first few flights, although this was generally restricted to the young

448   birds, which began with much more inefficient routes. Off-route releases demonstrated a variety of

449   navigational strategies characterised by distinct differences in the short-term correlation dimension

450   and therefore the number of cues involved in the underlying navigational process, although few birds

451   returned to the learned route. Instead, birds used either additional landscape features (in this case

452   the curve of the coastline) or compass directions (either a direct route home or paralleling the learned

453   route) to navigate from the unfamiliar sites. These results suggest that multiple forms of navigational

454   information are important when homing in a familiar area, and that the strategy used is flexible,

455   depending on the particular local conditions.

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606   **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

607 Table showing the release locations for the young and old birds demonstrating their range of flight

608 experience. Both the distance and bearing of the release site from the loft is given. Release locations

609 are given by name and coordinates.

610 **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

611   For each of the 21 birds, mean continuous flight bearings (CFBs, degrees), mean instantaneous

612   deflection (ID, degrees), mean flight efficiency and median short term correlation dimension (STCD)

613   has been given.

614   **Figure 1:** Satellite map of the homing pigeon home and release sites, including the name of each site,

615   the latitude and longitude of each site in decimal degrees and the distance from the release site to

616   the loft in kilometres and the absolute bearing from the release site to the loft in degrees.

617   **Figure 2:** Mean efficiency of each release split into young (gold) and old (light blue) birds, with 95%

618   confidence intervals shown. Releases 1-20 are from Y Felinheli; 21 is the first off-route release from

619   Anglesey; 22 is the second off-route release (Figure 1).

620   **Figure 3:** Box and whisker plots of track efficiency split by age group (gold=young; light blue=old) for

621   (a) releases 1-4 and (b) releases 17-20. Centre line gives the median of the groups, the box edges the

622   first and third quartiles, and the whiskers the maximum and minimum of the groups. Circles represent

623   outliers.

624   **Figure 4:** Mean tracks (black) produced using nearest-neighbours to average the final three successful

625   recordings for each bird (orange) from the Y Felinheli release site, young birds (top) and old birds

626   (bottom). The mean area between the final three tracks has been given for each bird (km^2), as well as

627   the mean efficiency of the final three tracks.

628   **Figure 5:** Box and whisker plot comparing the average "self" and "other" nearest neighbour distances

629   for each bird, between young (gold) and old (light blue) individuals. Centre line gives the median of

630   the groups, the box edges the first and third quartiles, and the whiskers the maximum and minimum

631   of the groups.

632   **Figure 6:** Averages of the short-term correlation dimension for the individual releases, shown as a

633   gradient with earlier releases in green transitioning through brown to later releases in red. Release

634   number has been labelled at the end of each line, in the matching colour.

635   **Figure 7:** Tracks for each bird showing the calculated mean track from the last three successful

636   recording from Y Felinheli (black), the first off-route release (red) and the second off-route release

637 (green), (a) young birds; (b) old birds. Classification of the flight strategy of each off-route release is

638 abbreviated in the matching colour for each bird at the top of the plot: CF = coast following; D = direct;

639 P = parallel; C = cross; J = join.

640 **Figure 8:** Short-term correlation dimensions at 500m intervals for each bird classified by flight strategy

641 for off-route release 1 (a) and off route release 2 (b). Green lines show the coast-following behaviour

642 (CF), red a parallel route (P) and yellow a direct route (D), with unbroken lines representing old birds

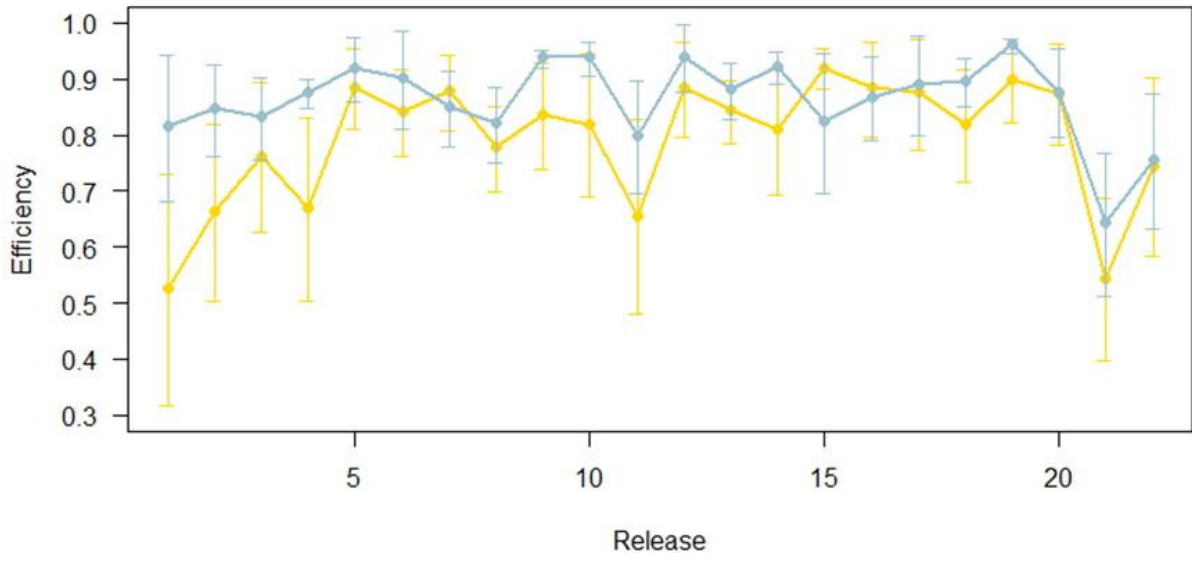643 and dashed lines representing young birds.

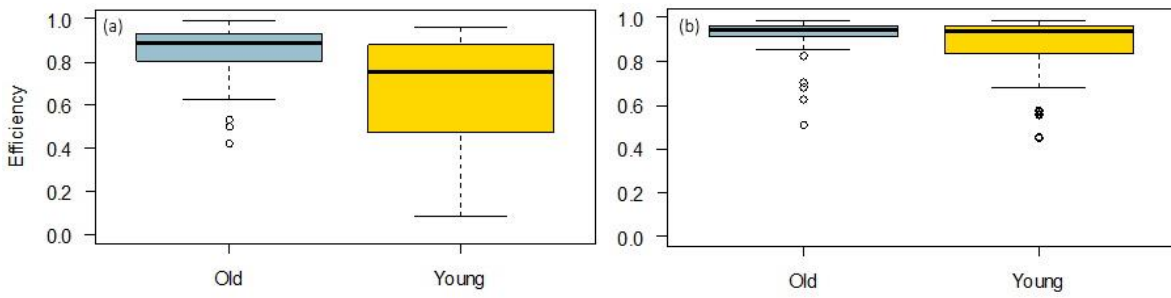644 Figure 1
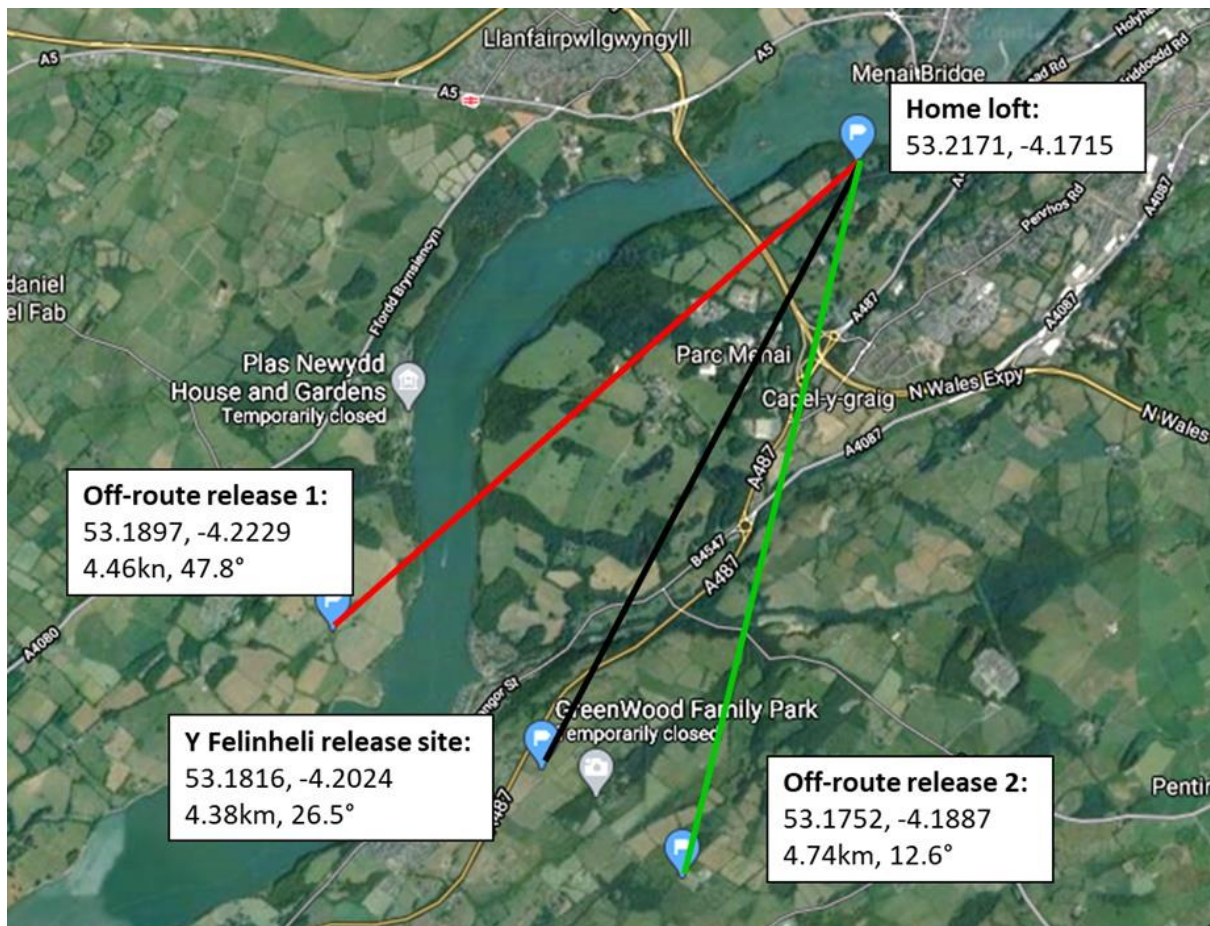
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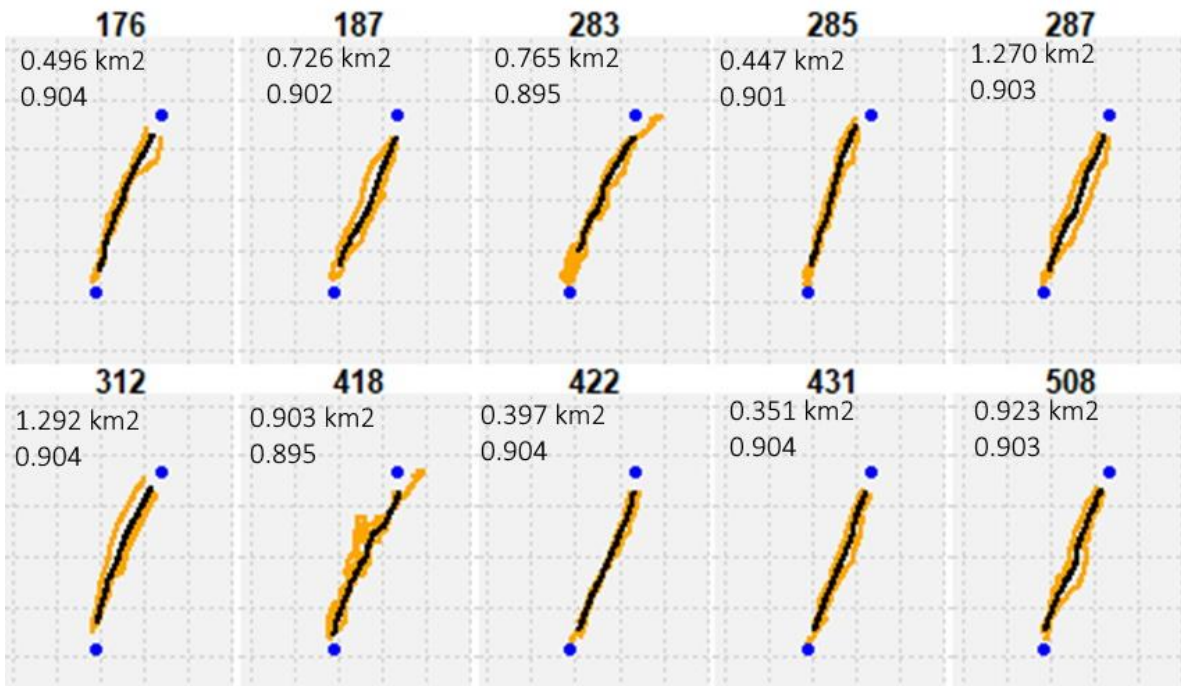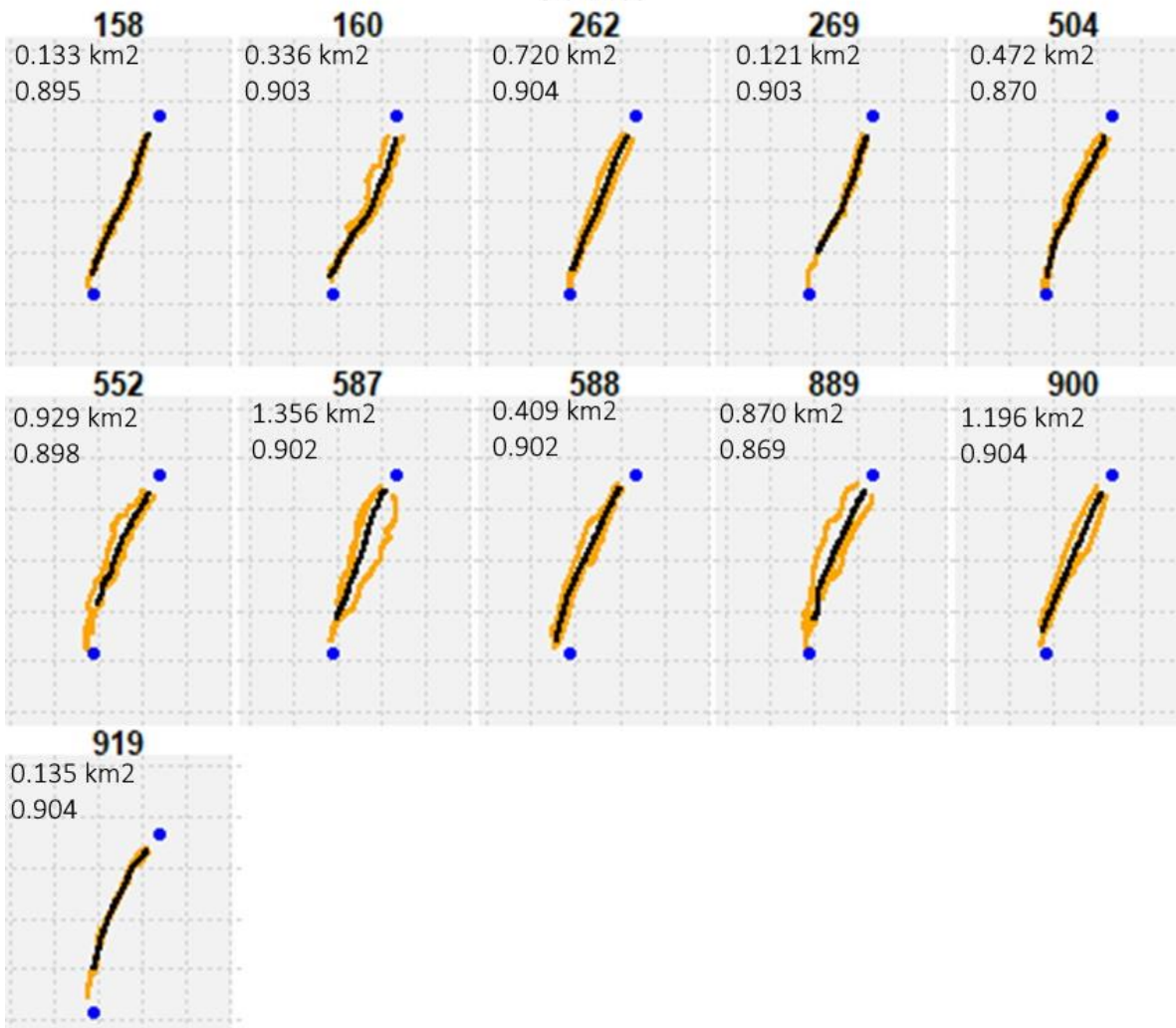648   Figure 2

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650   Figure 3

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656

657   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

658

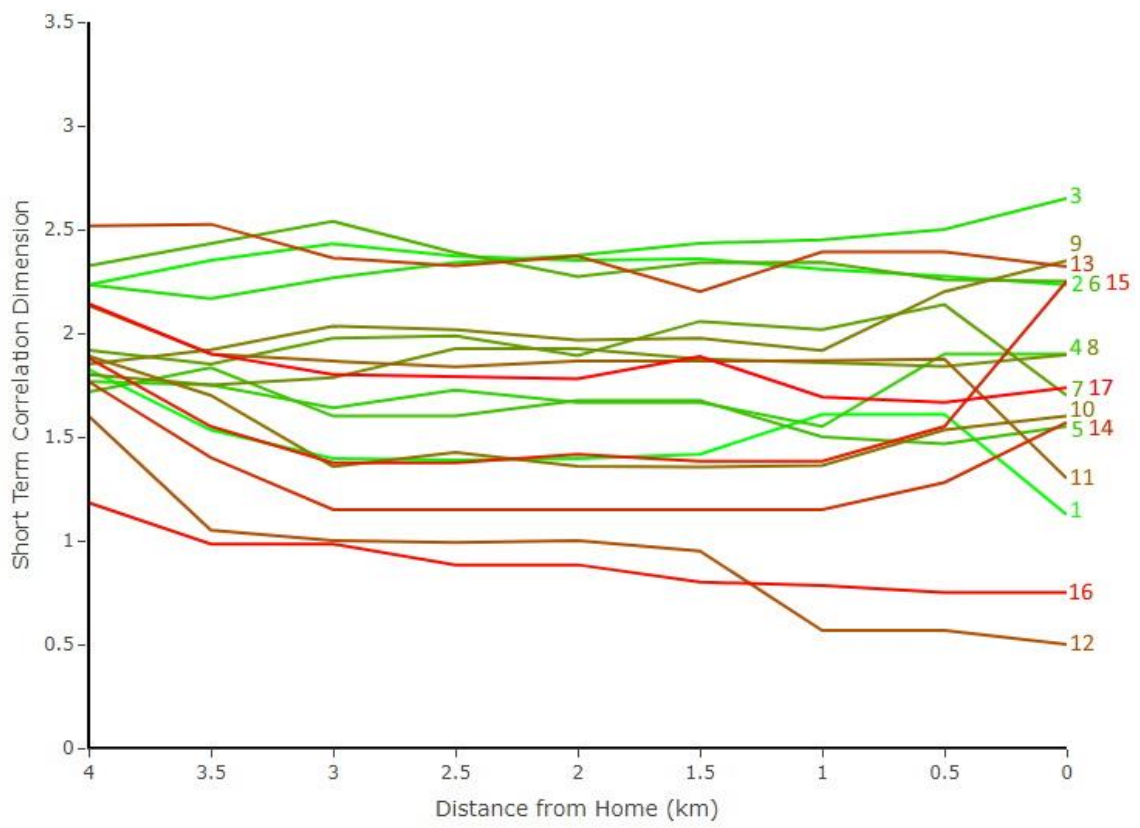659   Figure 5
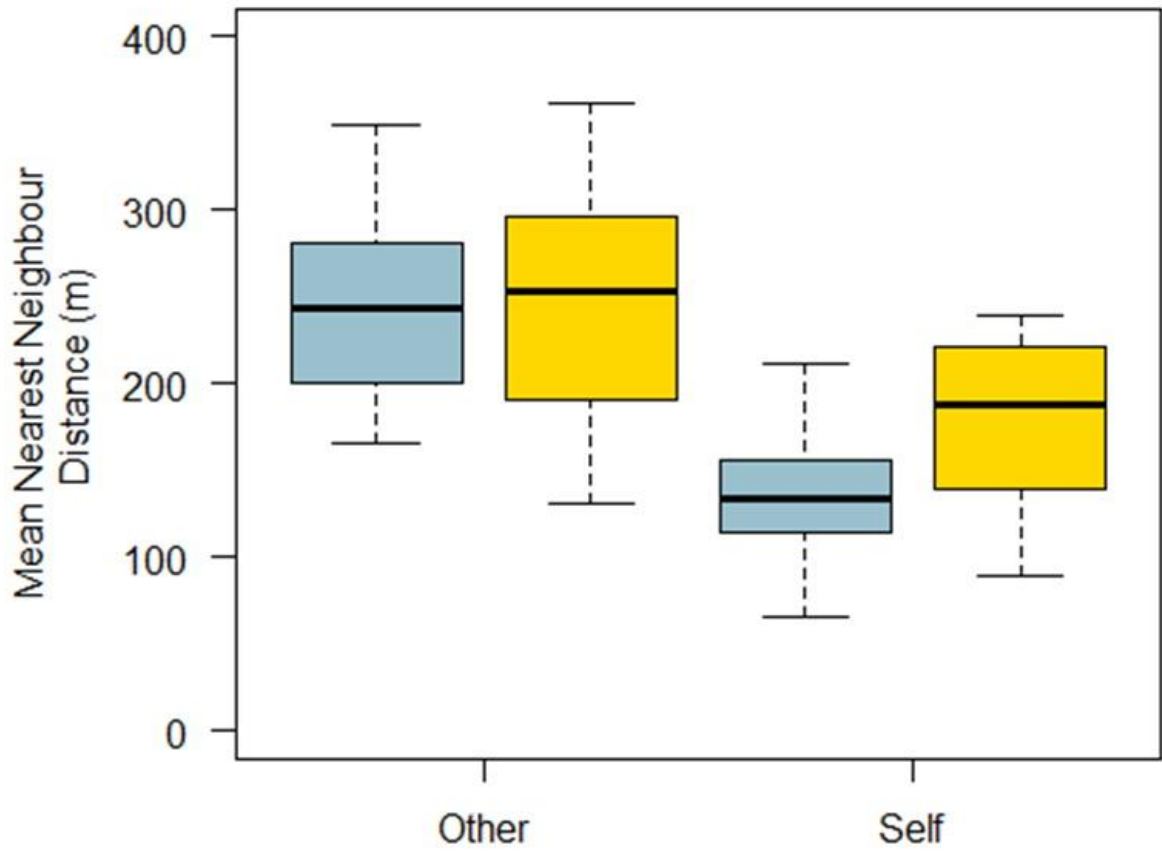
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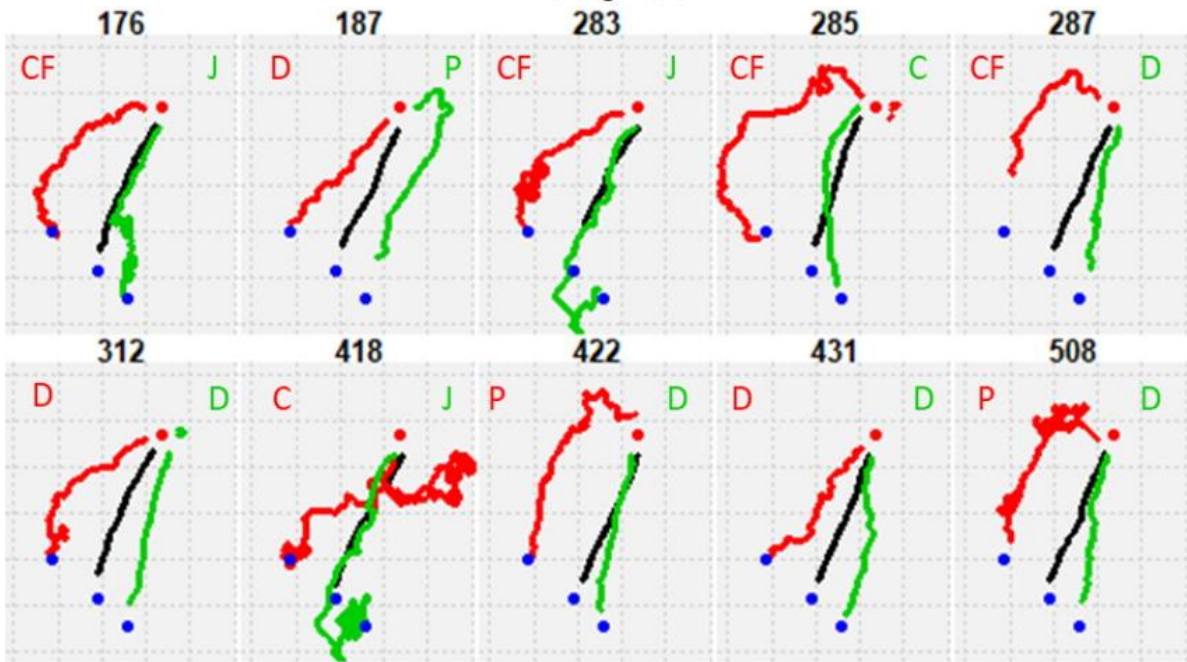661   Figure 6

662

663   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

665   Figure 8

666