

1 **Development of the Navigational System in Homing Pigeons:**
2 **Increase in Complexity of the Navigational Map**

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12
13 **Abstract:**

14 The present study analyzes GPS-recorded tracks from pigeons of different age from 11 sites
15 between 3.6 and 22.1 km from the home loft, which reveals changes in the navigational
16 system as the birds grew older and became more experienced. The efficiency of juveniles in
17 their 1st year of life, with only 0.27, was rather low, indicating that the young birds covered
18 more than three times the direct distance home. In the second year, after a standard training
19 program, the efficiency of the same birds increased up to 0.80 and was no longer different
20 from that of older pigeons. The short-term correlation dimension, a variable that reflects the
21 number of factors involved in the navigational process, also increased with age. In juveniles,
22 it is markedly lower than in the other two groups, but even in yearlings, it is still significantly
23 lower than that of old pigeons, indicating that the navigational map of the yearlings is
24 developing further. Our results indicate that the map system, although functional in the first
25 year of life, continues to become more complex: - older pigeons seem to either consider
26 more navigational factors than younger ones or at least weigh the same factors differently.

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28
29 **Introduction:**

30 Kramer's Map-and-Compass Model describes pigeon navigation as a two-step process:
31 pigeons first establish their position relative to their loft and determine the compass course
32 leading home, then they use their compass to locate this course (Kramer, 1957). The second
33 step, the compass step, is very well understood and so is its development. The magnetic
34 compass is innate; it is based on direct sensory input; the sun compass, in contrast, is

35 established by experience (for summary, see Wiltschko, 1983). The magnetic compass serves
36 as a directional reference when the sun compass is being established (Wiltschko and
37 Wiltschko, 1990). The sun compass becomes functional in the third month of life, but this
38 process can be accelerated by early flying experience (Wiltschko, 1983).

39

40 The map step, however, is not yet completely understood. When pigeons begin to fly, they
41 appear to apply a simple strategy to obtain their home direction, namely route reversal
42 (Schmidt-König, 1970) based on recording the direction of the outward journey with their
43 magnetic compass (Wiltschko and Wiltschko, 1978). Yet with increasing experience, pigeons
44 no longer rely on outward journey information alone, but increasingly base their navigation
45 on local information obtained at the release sites (Wiltschko and Wiltschko, 1985). They
46 establish a 'navigational map', a mental representation of the distribution of navigational
47 factors within their home range. This requires detailed knowledge of the surrounding area,
48 which the young pigeons presumably acquire by exploration.

49

50 It has been suggested (e.g. Graue, 1963; Wallraff, 1974; Wiltschko and Wiltschko, 1982) that
51 pigeons rely on two types of 'maps' that supplement each other. One of them, used for long
52 range navigation, is assumed to be based on at least two environmental gradients; it allows
53 pigeons to extrapolate information acquired in the home range and determine their home
54 course also at distant, unfamiliar sites. A multitude of factors have been proposed to be an
55 integral part of this so-called 'gradient map'; these include magnetic cues (Viguier, 1882;
56 Wagner, 1976; Walcott, 1978; Dennis et al., 2007; Wiltschko et al., 2010), Coriolis force
57 (Yeagley, 1947), olfactory cues (e.g. Papi et al., 1971; Papi, 1986; Gagliardo et al., 2009; but
58 see Jorge et al., 2009; Jorge et al. 2010 and also Gagliardo et al., 2011), infrasound (Quine,
59 1982; Hagstrum, 2000; Hagstrum, 2013), gravity (Lednor and Walcott, 1985), and landscape
60 features (Baker, 1984), but so far, only few are actually supported by experimental evidence.
61 A mathematical analysis of tracks from pigeons recorded with GPS-based flight recorders
62 suggests that at least four factors are involved in the navigational process, which means that,
63 aside from the compass, three or more factors are included in the pigeons' 'map' (Schiffner et
64 al., 2011a).

65

66 This 'gradient map' is supplemented by an additional map for short range navigation,
67 assumed to consist of a multitude of prominent landmarks in the area around the home loft
68 and their directional relationship to home (Graue, 1963; Wallraff, 1974; Biro et al., 2007).

69 The range of this so called ‘mosaic map’ would be theoretically limited by the amount of
70 detailed information it requires; the studies by Michener and Walcott and Braithwaite
71 (Michener and Walcott, 1967; Braithwaite, 1993) suggest an expansion of up to 10 km around
72 the loft. Both types of maps appear to overlap, with a gradual transition.

73

74 It is long known that increasing experience, e.g. by training flights, improves the homing
75 performance of pigeons considerably; here, general knowledge of the region appears to play a
76 much more important role than local familiarity with a specific site (e.g. Schiffner et al.,
77 2011a; Wallraff, 1959). However, it is not yet clear how experience affects the underlying
78 navigational process. The navigational processes in pigeons of different ages, corresponding
79 with increasing general experience, have never been investigated in detail. In the present
80 study, we apply the method of time lag embedding (Schiffner et al., 2011a) and determine the
81 correlation dimension, an indicator of the complexity of the system and the number of factors
82 involved, to find out whether there are systematic differences in the navigational process and
83 long term changes in the homing behaviour as pigeons become older and more experienced.

84

85 **Material and Methods:**

86 The experiments were conducted in the years 2005, 2006 and 2007 in sunny weather with no
87 or little wind.

88

89 *Experimental pigeons*

90 The experimental birds were homing pigeons, *Columba livia domestica*, from our Frankfurt
91 loft (50°08'N, 8°40'E). The juvenile pigeons in their first year of life were between 6 and 7
92 months old and had little flying experience aside from a few training flights with GPS-
93 recorders. The majority of releases involved yearling pigeons, the same pigeons in their
94 second year of life, and older pigeons that had completed at least their second year. These
95 birds had participated in a training program up to 40 km in the cardinal compass directions in
96 their first year of life. They had similar experience flying with a GPS recorder, the older
97 pigeons because they had homed as adult birds in previous experiments and the yearlings
98 because they had participated in the study as juveniles.

99

100 *Release sites*

101 Release were performed at 11 sites in distances ranging from 3.2 km to 23.5 km (distance and
102 home directions are included in Table 1), that is, all sites lay within an area that can be

103 considered generally familiar to the pigeons. The juveniles were released from the four sites
104 CP, EB, GT and HO for the first time; the data analysed here are the same that have been
105 analysed in a different way in a previous paper (Schiffner et al., 2011b). The yearlings were
106 also new to the release sites, except for the four sites mentioned above, from which they had
107 homed as juveniles. The older pigeons were released at all sites for the first time except for
108 EB, from which they had homed once before in flocks of 5 pigeons.

109

110 *Experimental procedure*

111 We used the same GPS recorders as in previous studies (Schiffner et al., 2011a; Schiffner et
112 al., 2011b) with a weight of ca. 23 g including the battery. They were set to take a positional
113 fix every second and had an operation limit of 3 hours. The GPS recorder was wrapped in
114 plastic foil and was attached to the pigeon's back by means of a harness made of Teflon tape.
115 Once equipped, the bird was released singly by hand. In order to assure pigeons had left the
116 release site pigeons were released in 5 minute intervals (for details, see Schiffner et al., 2011a;
117 Schiffner et al., 2011b).

118

119 The releases at a specific site took place over several days to minimize any potential influence
120 of variability in the availability of navigational factors on any given day. With the exception
121 of the site HO, yearlings and old pigeons were released on the same days in alternating order.

122

123 *Mathematical and statistical analysis of tracks*

124 The tracks of the pigeons were analysed to determine:

125 (1) the overall efficiency, which is the beeline distance divided by the actual length of the
126 track; it was calculated only for complete tracks with less than 10% signal loss (for a further
127 traditional analysis of the tracks, see Supplemental Material, Part 1 and 2).

128 (2) the short-term correlation dimension by means of time lag embedding (see Supplemental
129 Material, Part 3, for a brief summary and Schiffner et al., 2011a for details). In contrast to the
130 true correlation dimension of a track based on all data points, it was calculated as sliding
131 mean over only 180 seconds and averaged for each 500 m step the from the home loft. As a
132 consequence, it is lower than the true correlation dimension, but can be used for comparisons.

133

134 For the efficiency, we calculated the medians and compared the data of the yearlings and old
135 birds in a second order analysis using the Wilcoxon signed rank test for paired samples; the
136 Mann-Whitney U-test was used to compare variables of yearlings at familiar and unfamiliar

137 sites. The short-term correlation dimensions of the tracks were compared on the first order
138 level for each site individually by a two way ANOVA with repeated measurements using a
139 factorial design, with the independent factors being the distance from the release site at which
140 the short-term correlation estimates were taken and the age groups of the pigeons released at a
141 given site. When the ANOVA indicated significance, we used the Tuckey HSD test to look
142 for a difference between yearlings and old pigeons. Additionally we compared the data of the
143 two older groups of pigeons on a second order level using a median short-term correlation
144 dimension over 5 km segments from home using the Wilcoxon signed Rank test. The data of
145 yearlings released at familiar sites and those from unfamiliar sites were compared with the
146 Mann Whitney U-test.

147

148 **Results**

149 The analysis is based on 117 tracks from juvenile birds, 68 tracks from yearlings and 130
150 tracks from old pigeons. Figure 1 gives, as examples, the tracks for the yearlings and old birds
151 from the sites EB and HO; for the tracks of the juvenile birds in their first year of life, see
152 (Schiffner et al., 2011b).

153

154 Table 1 lists efficiencies of the three age groups returning from the release sites. With a
155 median of 0.27, the juveniles are much less efficient than the two other groups, flying on
156 average more than 3 times the direct distance, while the yearlings and the older birds, with
157 median efficiencies of 0.80 and 0.85, respectively, do not differ significantly ($T = 20.5$, n.s.;
158 Wilcoxon signed Rank test). The other traditional variables are essentially the same for the
159 two older groups, except that the yearlings tend to fly at higher speeds and that they deviate
160 further from the home course during the final homing phase (see Supplemental Material,
161 Table S1).

162

163 The short-term correlation dimensions are given in Figure 2, their medians are listed in Table
164 2 and a more detailed representation of the medians over 5 km distance intervals are given in
165 Table 3. Those from the younger birds are mostly lower than those of the older birds. This is
166 most pronounced in the juveniles, where the correlation dimensions, never exceeding 2.51,
167 are significantly lower than those of the two older groups. Yet, as the pooled data from all
168 sites in Figure 2 show, the average short-term correlation dimension estimate for yearlings is
169 still mostly lower than for the old pigeons. This difference is most pronounced at distances of
170 10 to 15 km from the loft; at the two sites at greater distances, there are no significant

171 differences (see Table 3). While there appears to be a general trend for higher short-term
172 correlation dimensions in the old birds, there are at least indications that this may not hold for
173 releases in the south. From the two release sites, GT and NI, it is actually higher in yearlings,
174 although this difference is only significant in the release from NI.

175

176 Having homed from a site the year before did not affect the efficiency or the median
177 correlation dimension of the yearlings. (both $U = 5$, n.s, Mann Whitney U-test).

178

179 The short-term correlation dimensions show a typical trend: they are generally markedly
180 lower at the beginning of the flight, but soon reach a higher level of the normal homing flight.
181 At all sites, we observe a clear correlation with distance, with the short-term correlation
182 dimension increasing as the pigeons approach their loft (Table 3; see Table S2 in
183 Supplemental Material for the F-values of the ANOVA). This trend is significant for the
184 releases with yearlings and old birds, but it is not so pronounced in juveniles, where only
185 tracks from four sites are available - here we even find a certain decrease when the juveniles
186 return from the farther sites (see Figure 2).

187

188 In summary, we find these differences between the age groups: the efficiency increases
189 considerably as the pigeons completed a training program and reach their second year of life;
190 the short-term correlation dimension also increases, but it continues to increase as the birds
191 grow older and more experienced, at least in range between 10 and 15 km, reflecting that the
192 navigational system becomes increasingly complex.

193

194

195 **Discussion**

196 Our data reveal a marked development in the navigational system between the first and
197 second year of life, reflected by a considerable increase in efficiency and in short-term
198 correlation dimension. In our previous study on the routes chosen by young pigeons during
199 the period when they establish their map system (Schiffner et al., 2011b), we interpreted the
200 long, seemingly inefficient homing flights as representing exploratory behaviour. At the age
201 of 6 months, the developing map had probably become functional, but was still rather crude
202 and inexact. The lower short-term correlation dimensions indicate that the juveniles rely on
203 fewer navigational factors than the other two groups. The young pigeons continued to explore
204 in order to become more familiar with distribution of navigational factors within their home

205 range. Interestingly, their behaviour appears to include strategies to avoid getting lost, like
206 e.g. limiting the flights to a semicircle and not going farther away from the release point than
207 the direct distance, using the release site as an anchor point etc. (see Schiffner et al., 2011b for
208 details). With 0.41, the efficiency of the last flight as juveniles was already more efficient
209 than the three previous flights, probably as a result of increasing experience from spontaneous
210 exploration.

211

212 The increase in efficiency from juveniles to yearlings appears to reflect a great step in the
213 maturation of the navigational system. The training program up to 40 km in the cardinal
214 compass directions at the end of the first year of life had familiarized them with a larger area
215 in their home region. With this additional knowledge, their homing flights became
216 considerably more efficient. On the one hand, their 'map' had become a more realistic
217 representation of the distribution of the navigational factors and their possible irregularities,
218 on the other hand, their tendency to explore during their homing flights probably decreases as
219 they become more and more familiar with their home region. Single long tracks as shown in
220 Figure 1, however, suggest that individual birds still explore.

221

222 While the efficiency of homing in yearling birds appears to have reached the level of older
223 pigeons, at least within a radius of about 25 km from the loft, where this study took place, the
224 short-term correlation dimension still generally increases as the birds grow older and more
225 experienced. Particularly in the range between 10 and 15 km, systematic differences in the
226 navigational maps of yearlings and older pigeons are indicated. This may mean that older
227 pigeons include more factors in their navigational process. However, as the differences are not
228 very large, it could also mean that while using the same navigational factors, older pigeons,
229 because of their more extensive experience, weigh these factors differently. This may
230 represent a parallel case to the use of the sun compass, where also slight difference in the
231 weighing of the sun and the magnetic field between young and older birds have been observed
232 (Wiltschko et al., 1994).

233

234 The changes of the short-term correlation dimension with distance are interesting. Homing
235 from the closest site CP, just 3.6 km from the loft, it is below 2.0 in all three groups,
236 suggesting a strategy based mainly on landmarks (Schiffner et al., 2011a). At the two farther
237 sites, about 20 km away, the observed differences in the short-term correlation dimension
238 between yearlings and old birds are not significant, while they are most pronounced between

239 7 and 15 km, that is, at distances where according to previous estimates (Michener and
240 Walcott, 1967; Braithwaite, 1993), navigation by the grid map changes into navigation by the
241 mosaic map of landmarks. The lower short-term correlation dimension of the yearlings may
242 thus reflect a still limited knowledge of landmarks in this range. Or it could mean certain
243 problems with detecting the differences between the local values of the environmental
244 gradients and the home values, which must be expected to become increasingly more difficult,
245 the closer the pigeons approach their home - older, more experienced pigeons are maybe
246 better able to cope with this situation. At greater distances, the environmental gradients are
247 probably easier to use – this is in agreement with the observation that the difference in short-
248 term correlation dimension between yearlings and older birds disappears at farther distances.

249

250 A pronounced gap in short-term correlation dimension, as the pigeons enter the 7 to 15 km
251 range around their loft, is not observed, suggesting a gradual transition between the two types
252 of ‘map’. The continuously high values near home, which have also been observed in another
253 study (Schiffner et al., 2011a) suggests that the environmental gradients are still involved in
254 the vicinity of the loft. This interpretation is in agreement with earlier observations by
255 Schlichte (Schlichte, 1973) that pigeon deprived of object vision managed to approach the
256 Frankfurt loft very closely. The tracks of pigeons very familiar with the area between the
257 release site and the loft (Schiffner et al., 2011a; Wiltschko et al. 2007) showed that these birds
258 chose slightly different routes from day to day, which speaks against merely following
259 familiar landmarks, as colleagues (e.g. Biro et al., 2004; Meade et al., 2005) proposed for
260 their pigeons in England. The increase in correlation dimension as the pigeons approach their
261 loft, observed here (see Table 3) and before (Schiffner et al., 2011a), however, points to an
262 additional use of familiar landmarks in the mosaic map near the home loft. While an increase
263 in experience would not lead to increased short term correlation dimension if navigation was
264 based solely on the mosaic map (Schiffner et al., 2011a), the range of the mosaic map may
265 have increased, allowing pigeons to use both maps in parallel over larger distances. Yet it is
266 also possible that the increase in short term correlation dimension observed with increasing
267 experience is mainly due to the integration of additional factors or a change in the weighting
268 of factors in the grid map.

269

270 Our findings suggest that the formation of the navigational map system is a longer lasting
271 process. The experience during the first year of life may form a framework for the map
272 system, including obvious landmarks near the loft and the directions of the most prominent

273 gradients. Pigeons continue to improve their maps by including new information like more
274 landmarks and maybe additional local factors in order to develop their map system into a
275 realistic representation of all suitable navigational factors in their home region. Even for an
276 area within a 15 km radius around the loft, the map proved not yet complete in the second
277 year of life - new factors and/or better interpretations of factor already included are still
278 added, as indicated by the mostly higher short-term correlation dimension of the older
279 pigeons. Old, experienced pigeon are still able to learn the navigational factors and update
280 their idea on the distribution of the 'map' factors in distant regions later in life (Grüter and
281 Wiltschko, 1990). Improving of the navigational 'map' appears to continue as long as the
282 pigeons live.

283

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293

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389 **To the figures:**

390 **Figure 1.** Tracks of yearlings (red) and older pigeons (blue) from (A) ES (6.8 km. home
391 direction 120°) and (B) HO (13.6 km. home direction 247°). The release sites are marked
392 with a black triangle and the home loft with a black square

393

394 **Figure 2.** Average short-term correlation dimension for all releases for juvenile (green).
395 yearlings (red) and old pigeons (blue). The thin lines indicate the means of the single
396 sites. the thick line gives the average.

Table 1. Names and location of the release sites with respect to the home loft and efficiencies of the three groups of birds.

Site	Dist.(km)	Home direction	Juveniles		Yearlings		Old pigeons	
			n	median	n	median	n	median
CP	3.6	261°	21	0.26	4	0.87	12	0.88
GT	5.3	313°	6	0.28	6	0.82	12	0.80
EB	6.8	120°	14	0.24	7	0.79	11	0.82
NI	9.0	336°			4	0.80	10	0.86
MT	11.6	263°			4	0.82	7	0.82
OB	12.5	297°			5	0.80	11	0.88
HO	13.6	247°	11	0.41	4	0.79	17	0.85
HOF	13.8	83°			3	0.89	10	0.81
AH	14.6	105°			5	0.87	8	0.89
RB	19.0	195°			2	0.90	5	0.92
RAV	22.1	251°			3	0.91	6	0.81
median				(0.27)		0.80		0.85

Dist., distance from the loft; ,Home dir., home direction; n, number of tracks

Table 2. Median short-term correlation dimension of the three groups of pigeons.

Site	Dist. (km)	Juveniles		Yearlings		Old pigeons		Difference yearlings/old significant?
		n	median	n	median	n	median	
CP	3.6	41	1.94	6	1.98	12	1.75	n.s.
GT	5.3	11	2.07	10	2.42	14	2.36	n.s.
EP	6.8	35	2.34	9	2.30	15	2.62	***
NI	9.0			5	3.09	11	2.75	***
MT	11.6			6	2.90	11	3.03	*
OB	12.5			5	2.73	12	3.03	***
HO	13.6	30	2.51	8	2.79	17	2.90	*
HOF	13.8			6	2.59	11	2.87	***
AH	14.6			6	2.93	10	2.95	***
RB	19.0			4	2.69	9	2.52	n.s.
RAV	22.1			3	2.72	8	2.80	n.s.
Median			2.21		2.71		2.80	

Abbreviations as in Table 1. The last column indicates the significance of the difference between yearlings and old pigeons by the Tuckey HSD test. Significance levels: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; n.s. not significant.

1 **Table 3.** Median short-term correlation dimension of the two older groups of pigeons at 5 km
 2 distance intervals

Site	Dist. (km)	< 5 km		5 – 10 km		10 – 15 km	
		Yearlings	Old Pigeons	Yearlings	Old Pigeons	Yearlings	Old Pigeons
CP	3.6	1.98	1.81	--	--	--	---
GT	5.3	2.50	2.43	2.05	2.06	--	--
EP	6.8	2.33	2.64	1.95	1.90	--	--
NI	9.0	3.33	2.81	2.59	2.48	--	--
MT	11.6	3.07	3.10	2.68	3.02	2.36	2.43
OB	12.5	3.10	3.13	2.63	3.00	2.11	2.37
HO	13.6	2.77	2.90	2.82	2.94	2.63	2.78
HOF	13.8	2.52	3.16	2.64	2.84	2.38	2.45
AH	14.6	2.98	3.08	2.96	2.91	2.65	2.78
RB	19.0	3.11	2.45	2.80	2.57	2.51	2.70
RAV	22.1	3.06	2.84	2.67	2.71	2.85	2.79
Median		2.98	2.84	2.66	2.77	2.51	2.70
Sign.?			n.s.(30)		n.s.(20)		*(1)

3 Last line indicates difference between yearlings and older pigeons by the Wilcoxon signed rank test, with the test
 4 statistic T in parentheses. Significance levels *, p<0.05; n.s. not significant



