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

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Abstract:

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

Introduction:

Kramer's Map-and-Compass Model describes pigeon navigation as a two-step process: pigeons first establish their position relative to their loft and determine the compass course leading home, then they use their compass to locate this course (Kramer, 1957). The second step, the compass step, is very well understood and so is its development. The magnetic compass is innate; it is based on direct sensory input; the sun compass, in contrast, is established by experience (for summary, see Wiltschko, 1983). The magnetic compass serves as a directional reference when the sun compass is being established (Wiltschko and Wiltschko, 1990). The sun compass becomes functional in the third month of life, but this process can be accelerated by early flying experience (Wiltschko, 1983).

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

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

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

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

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

Material and Methods:

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

Experimental pigeons

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

Release sites

Release were performed at 11 sites in distances ranging from 3.2 km to 23.5 km (distance and home directions are included in Table 1), that is, all sites lay within an area that can be considered generally familiar to the pigeons. The juveniles were released from the four sites CP, EB, GT and HO for the first time; the data analysed here are the same that have been analysed in a different way in a previous paper (Schiffner et al., 2011b). The yearlings were also new to the release sites, except for the four sites mentioned above, from which they had homed as juveniles. The older pigeons were released at all sites for the first time except for EB, from which they had homed once before in flocks of 5 pigeons.

Experimental procedure

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

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

Mathematical and statistical analysis of tracks

The tracks of the pigeons were analysed to determine:

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

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

For the efficiency, we calculated the medians and compared the data of the yearlings and old birds in a second order analysis using the Wilcoxon signed rank test for paired samples; the Mann-Whitney U-test was used to compare variables of yearlings at familiar and unfamiliar sites. The short-term correlation dimensions of the tracks were compared on the first order level for each site individually by a two way ANOVA with repeated measurements using a factorial design, with the independent factors being the distance from the release site at which the short-term correlation estimates were taken and the age groups of the pigeons released at a given site. When the ANOVA indicated significance, we used the Tuckey HSD test to look for a difference between yearlings and old pigeons. Additionally we compared the data of the two older groups of pigeons on a second order level using a median short-term correlation dimension over 5 km segments from home using the Wilcoxon signed Rank test. The data of yearlings released at familiar sites and those from unfamiliar sites were compared with the Mann Whitney U-test.

Results

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

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

The short-term correlation dimensions are given in Figure 2, their medians are listed in Table 2 and a more detailed representation of the medians over 5 km distance intervals are given in Table 3. Those from the younger birds are mostly lower than those of the older birds. This is most pronounced in the juveniles, where the correlation dimensions, never exceeding 2.51, are significantly lower than those of the two older groups. Yet, as the pooled data from all sites in Figure 2 show, the average short-term correlation dimension estimate for yearlings is still mostly lower than for the old pigeons. This difference is most pronounced at distances of 10 to 15 km from the loft; at the two sites at greater distances, there are no significant differences (see Table 3). While there appears to be a general trend for higher short-term correlation dimensions in the old birds, there are at least indications that this may not hold for releases in the south. From the two release sites, GT and NI, it is actually higher in yearlings, although this difference is only significant in the release from NI.

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

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

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

Discussion

Our data reveal a marked development in the navigational system between the first and second year of life, reflected by a considerable increase in efficiency and in short-term correlation dimension. In our previous study on the routes chosen by young pigeons during the period when they establish their map system (Schiffner et al., 2011b), we interpreted the long, seemingly inefficient homing flights as representing exploratory behaviour. At the age of 6 months, the developing map had probably become functional, but was still rather crude and inexact. The lower short-term correlation dimensions indicate that the juveniles rely on fewer navigational factors than the other two groups. The young pigeons continued to explore in order to become more familiar with distribution of navigational factors within their home range. Interestingly, their behaviour appears to include strategies to avoid getting lost, like e.g. limiting the flights to a semicircle and not going farther away from the release point than the direct distance, using the release site as an anchor point etc. (see Schiffner et al., 2011b for details). With 0.41, the efficiency of the last flight as juveniles was already more efficient than the three previous flights, probably as a result of increasing experience from spontaneous exploration.

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

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

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

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

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

Our findings suggest that the formation of the navigational map system is a longer lasting process. The experience during the first year of life may form a framework for the map system, including obvious landmarks near the loft and the directions of the most prominent gradients. Pigeons continue to improve their maps by including new information like more landmarks and maybe additional local factors in order to develop their map system into a realistic representation of all suitable navigational factors in their home region. Even for an area within a 15 km radius around the loft, the map proved not yet complete in the second year of life - new factors and/or better interpretations of factor already included are still added, as indicated by the mostly higher short-term correlation dimension of the older pigeons. Old, experienced pigeon are still able to learn the navigational factors and update their idea on the distribution of the 'map' factors in distant regions later in life (Grüter and Wiltschko, 1990). Improving of the navigational 'map' appears to continue as long as the pigeons live.

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To the figures:

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

Figure 2. Average short-term correlation dimension for all releases for juvenile (green). yearlings (red) and old pigeons (blue). The thin lines indicate the means of the single 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.

			Juveniles		Yearlings		Old pigeons	
Site	**Dist.(km)**	**Home direction**	**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.

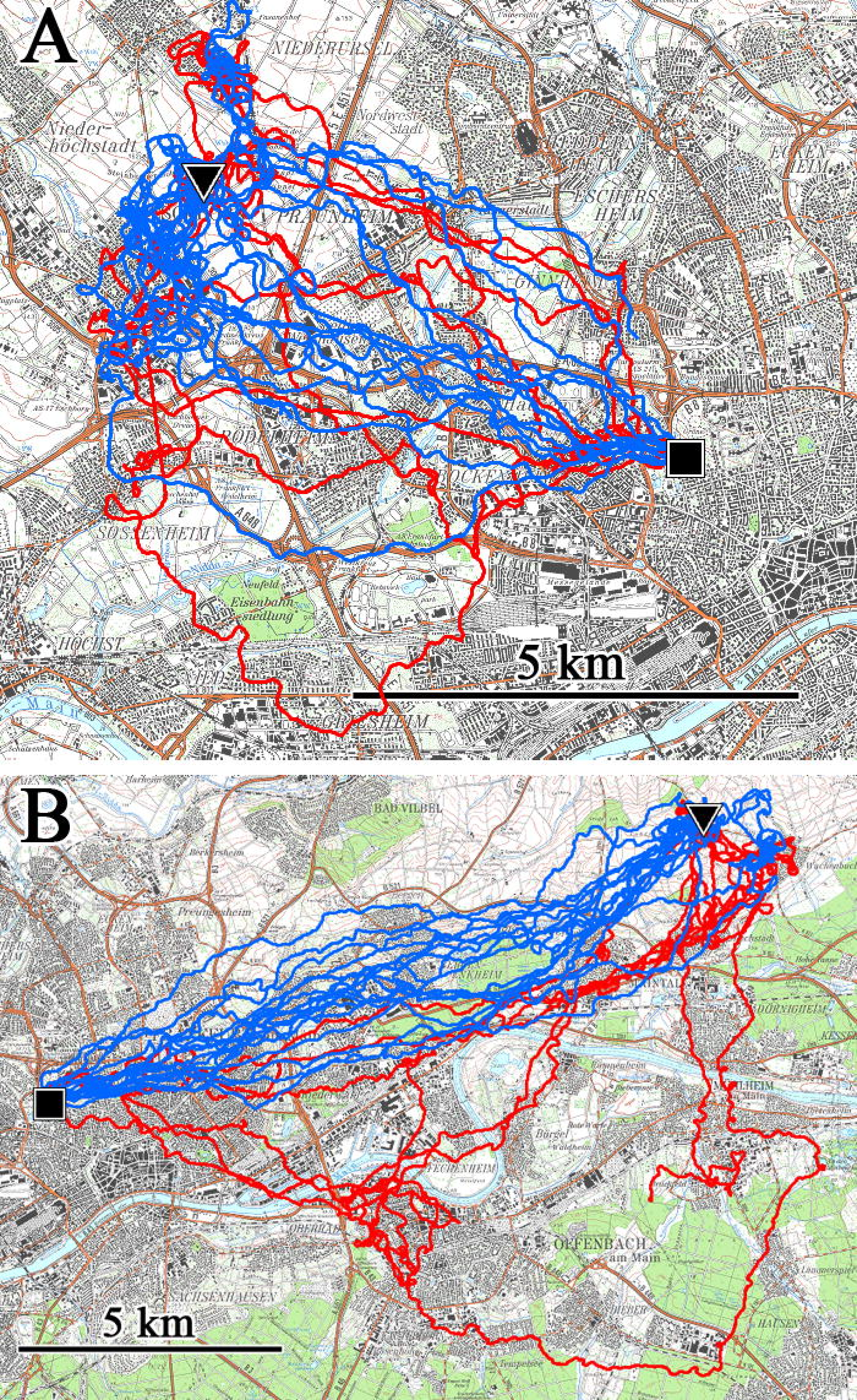
Site	Dist. (km)	Juveniles		Yearlings		Old pigeons		Difference yearlings/old significant?
		n	median	n	median	n	median	
CP	3.6	41	1.94	6	1.98	12	1.75	n.s.
GT	5.3	11	2.07	10	2.42	14	2.36	n.s.
EP	6.8	35	2.34	9	2.30	15	2.62	***
NI	9.0			5	3.09	11	2.75	***
MT	11.6			6	2.90	11	3.03	*
OB	12.5			5	2.73	12	3.03	***
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.

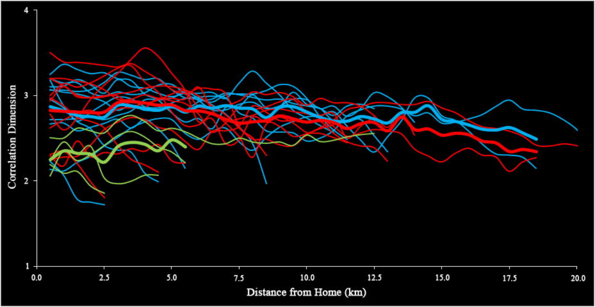
Table 3. Median short-term correlation dimension of the two older groups of pigeons at 5 km distance intervals

		< 5 km		5 – 10 km		10 – 15 km	
Site	**Dist. (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)**

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



A
NIEDERURSEL
Nieder-
höchstadt
PRAUNHEIM
ESCHERSHEIM
RÖDELHEIM
SOSSENHEIM
Eisenbahn-
siedlung
HÖCHST
GRIESHEIM
5 km
B
BAD VILBEL
FECHENHEIM
OFFENBACH
am Main
SACHSENHAUSEN
DÖRNIGHEIM
5 km



4
3
2
1
Correlation Dimension
0.0
2.5
5.0
7.5
10.0
12.5
15.0
17.5
20.0
Distance from Home (km)