

Animal Cognition

Individual strategies and release site features determine the extent of deviation in clock-shifted pigeons at familiar sites

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Abstract:	<p>When homing from familiar areas homing pigeons are able to exploit previously acquired topographical information, but the mechanisms behind this ability are still poorly understood. One possibility is that they recall the familiar release site topographical features in association with the home direction (site specific compass orientation strategy), another that the spatial relationships among landmarks guide their route home (piloting strategy), without relying on the compass mechanism. The two strategies can be put in conflict by releasing clock-shifted birds at familiar locations, in order to highlight which is preferred. We analysed GPS tracks of clock-shifted pigeons, with familiarity controlled at each of three different release sites, and we observed that pigeons can display individual preferences for one of the two orientation strategies, and that some characteristic features of the release site have an important role in determining the level of landmark-based homeward orientation.</p>
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Individual strategies and release site features determine the extent of deviation in clock-shifted pigeons at familiar sites.

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Abstract

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24 landmark-based homeward orientation.
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Introduction

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4 Homing pigeons can orient homewards when they have been displaced to unfamiliar locations using
5 a navigational map and compass system, but when they become familiar with a site they show
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7 improved homing and unimpaired performance, even when made anosmic in order to disrupt their
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9 navigational abilities (e.g. (Benvenuti et al., 1973) review in (Wallraff 2005)). Indeed, there are
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11 now several lines of evidence indicating that during homing birds are learning to attend to the
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13 features of the landscape through which they fly, in some cases in sufficient detail to allow faithful
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15 recapitulation of individually distinctive homing routes (Meade et al. 2005). Nevertheless, many
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17 questions concerning the nature of familiar area orientation remain to be resolved. Whilst it seems
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19 intuitively likely that visual features are important, and there is now considerable evidence that this
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21 is the case (Braithwaite and Guilford 1991; Gagliardo et al. 2001; Holland 2003), pigeons appear
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23 still able to orient homewards from familiar sites without detailed form vision (Schmidt-Koenig and
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25 Schlichte 1972), and pigeons may continue to be deviated in initial orientation under clock shift,
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27 implying that familiar area orientation can continue to be dependent on the sun-compass rather than
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29 direct guidance by visual landmarks (Füller et al. 1983). The significance of these findings is
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31 confused by the fact that familiar landmarks may be involved in the control of orientation in
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33 different ways, for example through direct guidance from the landmarks themselves or through
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35 association with a compass bearing to home. Thus, by using a “*site specific compass orientation*”
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37 strategy (Holland 2003; Wallraff 1974) birds are able to recall the familiar site features in
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39 association with a specific compass direction, while the use of a “*piloting*” strategy (Holland 2003)
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41 implies that orientation using familiar landmarks may be achieved without using the compass.
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56 The extent to which orientation is dependent on a time-compensated sun compass can be
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58 investigated by manipulating the birds’ internal clock through phase-shifting. The deflection
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60 induced by the phase-shift is a consequence of an error in the estimation of time, which produces a
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predictable error in the estimation of the sun's azimuth. The use of a piloting strategy from a
familiar site that involves direct guidance from topographical cues should result in unaltered
homeward orientation, while use of site specific compass orientation predicts continued deviation
comparable to that expected. However, very often the extent of the deflection from the home
direction reveals a compromise between these two strategies.

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Several authors have investigated which factors might affect the size of deflection following
clock shift, but discrepant results have not yet allowed clear resolution of the mechanisms involved
(Foà and Albonetti 1980; Gagliardo et al. 2004; Gagliardo et al. 2005b; Wiltschko et al. 1994).
Previous experience of the release site seems to be important in many studies (Bingman and Ioalè
1989; Biro et al. 2007; Bonadonna et al. 2000; Gagliardo et al. 1999; Gagliardo et al. 2002;
Gagliardo et al. 2005b; Holland et al. 2000; Papi et al., 1991) and in other studies reviewed in
Wallraff et al. (1999), but apparently not all (Füller et al. 1983; Wiltschko et al. 2005). Even at
familiar sites, access to olfactory cues increases deviation under clock-shift compared to anosmic
birds (Bingman and Ioalè 1989; Gagliardo et al. 1999). Uncharacterised peculiarities of particular
release sites may also alter the response to clock-shift in site-experienced birds (Bonadonna et al.
2000; Gagliardo et al. 2005b). Finally, at unfamiliar sites magnetic disruption can increase deviation
under clock-shift, implying that birds are capable of a partial switch to the magnetic compass, but
these effects are small and not thought to be dependent on familiarity (Gagliardo et al. 2009b;
Wiltschko et al. 1994; Wiltschko and Wiltschko 2001).

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A central issue in this puzzle is the role of familiarity, yet this is rarely controlled or varied
systematically, and little is known about how individual orientation strategies respond to familiarity
or whether that response itself depends on the nature of the landscape. In this study we aimed to
explore how individuals responded to clock-shift at different sites when they had the same level of
familiarity, and thus to elucidate further the interplay between direct landscape guidance and
compass-dependent orientation. Furthermore, by training the same birds from multiple sites in

1 different geographic directions we were able to eliminate potential effects of directional training
2 bias, which may as a consequence increase dependence on compass orientation. Using precision-
3 tracking of the same clock-shifted birds we found significant differences in the degree of reduced
4 deviation between sites, with the more inland site generally favouring a higher level of continued
5 attention to the sun-compass, and we found significant differences amongst individuals in the
6 degree to which they became dependent on piloting via direct guidance from the landscape.
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17 **Materials and methods**

18 **General procedure**

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24 Subjects were 32 first-year pigeons (*Columba livia*) hatched and kept at the Arnino field station
25 (43°39'26"N, 10°18'14"E; Pisa, Italy). The experiment took place over three years (the number of
26 pigeons used were 7, 5, 20 in the 2009, 2010 and 2011, respectively). All the experimental
27 releases took place under sunny conditions, in nil or light winds. The pigeons were allowed to
28 perform spontaneous flights around the loft and were kept and manipulated according to Italian
29 law on animal welfare. About one month before the beginning of the experiments, the birds were
30 equipped with PVC dummies, having the same size and weight as the GPS data loggers (20 g), in
31 order to accustom them to carrying the load. The dummy was attached dorsally by means of a
32 Velcro® strip glued to the feathers, which had been previously shortened. During the experimental
33 releases the dummy was replaced with a miniature GPS data logger. The miniature GPS data
34 loggers allowed the recording of the flight path with an accuracy of about 4 m, and were of several
35 designs (TechnoSmart; Mobile Action IgotU). The position stored every second by the GPS data
36 logger included latitude, longitude, speed and time of recording. The tracks recorded were
37 visualized with Google Earth (Google Inc, US).
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58 The pigeons were subjected to 7 or 8 training releases in groups from each of the three sites chosen
59 for the experimental tests (Arnaccio, home direction and distance 269°, 13.5 km; Livorno 341°, 12
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1 km; La Sterpaia 194°, 9.5 km), followed by an additional solo release from each release site which
2 was recorded with GPS.
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4 After the last training release, the pigeons were captured and placed and in a light tight
5 room, where they were kept for at least 6 days in order to subject them to a 6 hours fast phase-shift.
6 The light-tight room was ventilated by an aspirator, and was provided with perches, *ad libitum* food
7 and water. The clock-shifted pigeons were then released singly, with at least 10 min between birds.
8 For the birds released on the 2009 (#c813, #cCNC, #cV) the sequence of the clock-shift test was
9 Arnaccio (08/08/2009), Livorno (10/08/2009), La Sterpaia (11/08/2009). For all the other birds
10 released both in the 2010 and 2011 the sequence of releases was Livorno (20/07/2010,
11 21/07/2011.), La Sterpaia (26/07/2010, 22/07/2011), and Arnaccio (28/07/2010, 23/07/2011 except
12 for the bird #766 released on the 28/07/2011). The homed birds were caught and put in the clock-
13 shift room in order to keep them phase-shifted for the whole period of the experiment.
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31 **Quantitative analyses and statistical procedures**

32 For the statistical analysis we have considered the tracks recorded during the last release in the
33 unshifted condition and the tracks recorded during the test release after clock-shift. Subjects were
34 excluded from the analysis if they joined during a homing flight, or failed to provide at least
35 substantially complete tracks for both shifted and unshifted conditions from all three sites, leaving
36 18 subjects for the analysis.
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48 For each track collected both during the last training release and during the clock-shift experiment,
49 we considered the bird's position every 500 m at increasing distance from the release site up to 9
50 km which was about the distance from the closest release site to Arnino. With the assistance of a
51 database available online (Astronomical Application Department Of the U.S. Naval Observatory),
52 we downloaded the sun azimuth for each point of the track recorded at the clock-shifted release and
53 we calculated the sun azimuth at the subjective time. On the basis of the sun azimuth at the time of
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1 release of each single bird, we calculated the expected deviation (i.e. the difference between the real
2 and the subjective sun azimuth). We applied the Two Way RM ANOVA to the following
3 parameters considered every 500 meters distance from the release site: a) the distance between the
4 position as the bird crossed for the first time each 500 m contour in the last training release and in
5 the clock-shift release; b) the deviation (expressed as percentage of the expected deviation) from the
6 track recorded during the last training release. Both analyses were also repeated with subject as
7 factor, to identify possible similarities and differences at the individual level. Finally, we attributed
8 to each pigeon a score equal to the distance from the release site at which the bird turned out to be
9 re-oriented, by assuming as the re-orientation criterion a deviation lower than 25% of that expected.
10 The differences among the distance at which reorientation occurred at the three release sites were
11 tested with the RM ANOVA on Ranks. Post hoc comparisons were performed with Tuckey tests.
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28 **Results**

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34 The tracks of 18 subjects were used for the analysis (Figure 1a and b): two out of seven, two out of
35 five and fourteen out of twenty pigeons' tracks recorded in the 2009, 2010 and 2011, respectively.
36 Some of the GPS data loggers (n=4) did not record or produced incomplete tracks and were
37 therefore excluded from the analysis. Seven pigeons were excluded from the analysis because they
38 joined during the homing flight and three pigeons were lost.
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46 The mean deviation from both the home direction and the direction taken by the birds during
47 the last training release was smaller than expected at the three release sites, as shown in Figure 2. In
48 particular at 2 km from the release site, that correspond to the distance at which vanishing bearings
49 are recorded in traditional experiments, the mean deviation was 41% and 35% at La Sterpaia, 62%
50 and 48% at Livorno, and 74% and 53% at Arnaccio from the home direction and the direction
51 assumed during the last training release, respectively.
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1 The analysis on the distances between the last training tracks and the tracks after the clock-
2 shift treatment taking into account the position of the birds recorded every 500m from the release
3 site (see Figure 3), revealed that there is a statistically significant difference between the three
4 site (see Figure 3), revealed that there is a statistically significant difference between the three
5 release sites (Two way RM ANOVA, $F_{2,34}= 6.356$, $p<0.005$). In particular, the distances between
6 the pigeons' tracks were significantly greater at Arnaccio with respect to the other two sites
7 (Student-Newman-Keuls test; $p<0.05$ for both comparisons). A significant difference in the distance
8 between the last training and the test tracks emerged also at different radii from the release site
9 (Two way RM ANOVA, $F_{17,289}=139.598$, $p<0.001$). Finally there was a significant interaction
10 between the release site and the distance from the release site (Two way RM ANOVA,
11 $F_{34,578}=11.093$ $p<0.001$). In particular, Arnaccio was significantly different from La Sterpaia
12 starting from 5 km up to 9 km from the release site (Student-Newman-Keuls test, $p<0.05$ at 5 and
13 5.5 km and $p<0.001$ at further distances), and significantly different from Livorno starting from 6
14 km up to 9 km from the release site (Student-Newman-Keuls test, $p<0.001$). The analysis on the
15 distance conducted with subjects as a factor revealed a significant difference among individuals
16 (Two Way RM ANOVA, $F_{17,289}=35.606$, $p<0.001$). The results of a multiple comparison (Student-
17 Newman-Keuls test) are reported in Table 1 in the Supplementary Materials. A significant
18 interaction between individual and release site (Two Way RM ANOVA, $F_{34,578}=29.134$, $p<0.001$)
19 emerged and the multiple comparison allowed us to distinguish different groups of birds on the
20 basis of their level of behavioural consistency at the different release sites. Some individuals
21 displayed the same pattern in the distance, either small (birds #136, #548, in Figure 1a) or large
22 (birds #955, #812, #067, #108 in Figure 1a and bird #992 in Figure 1b), between the last training
23 and the clock-shift tracks regardless the release site, suggesting a consistent use of landmark-based
24 navigation or site specific compass orientation strategy, respectively. Most birds belonged to a
25 group that changed behaviour only at one site. In particular, some birds (#766, #181 in Figure 1a,
26 and #899, #953 and up to a certain location the bird #723, in Figure 1b) retraced the learned route in
27 the unshifted condition only at La Sterpaia, and displayed a clear deflection both at Livorno and
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Arnaccio, while other birds (#949, #588, #813, #cNCN, #cV, #140 in Figure 1b) displayed the tendency to re-orient of the basis of the familiar landmarks at the two release sites La Sterpaia and Livorno compared to Arnaccio.

Considering the individual deviation (as percentage of expected) from the direction taken by each bird during its last training release (Figure 4), the Two-Way RM ANOVA did not reveal a significant difference between release sites ($F_{17,2}=2.490$, $p=0.098$). A significant difference at various distances from the release site ($F_{17,289}=7.187$, $p<0.001$), and more importantly a significant interaction between release site and distance from the release site emerged ($F_{34,578}=3.635$, $p<0.001$). In particular, a significant difference ($p<0.05$ in all cases) was found between Arnaccio and La Sterpaia starting from 5.5 km up to 9 km and between Arnaccio and Livorno starting from 6 up to 9 km from the release site.

Both the analysis and the visual inspection of the tracks (Figure 1a and b) showed that the birds released from Livorno displayed the tendency to follow the route taken during the last training flight after four-five kilometres from the release site, while the birds released from La Sterpaia tended to retrace their last training flight path almost immediately after release. A different behaviour emerged at Arnaccio, where most of the birds soon diverged from the flight path recorded during the last training release, reorienting at least further than 9 km from the release site. The comparison between the reorientation score revealed that the birds re-oriented at different distances at the three release sites (RM ANOVA on Ranks, $p<0.001$). The distance at which the re-orientation (deviation lower than 25% of the expected, see also Figure 5) occurred was significantly greater at the site from the East (Arnaccio) than at the other two sites (Tukey test $p<0.05$, for both comparisons).

Through the use of Google Earth, it is possible to visualize the single tracks of birds and to observe the topography of the area at which the re-orientation occurred. When released from Livorno 6 pigeons headed home soon after release; 8 pigeons re-oriented towards home (4-5 km from the release site) when arriving near the sea, and 4 birds (#067, #812, #955 in Figure 1a, and

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2 #c723 in Figure 1b) displayed a tortuous flight path with an orientation highly variable, especially
3 in the first part of the flight. For example the pigeons #067 and #c723 were initially oriented
4 towards South, with a very tortuous flight path, following the coastline up to 10 km from the release
5 site. Then, after having inverted their direction and always following the coastline, headed home. A
6 very curious route is that followed by the bird #812, which headed home soon after release.
7 However, once at about 1.5 km from Arnino, instead of reaching the loft, this bird flew towards La
8 Sterpaia and Arnaccio before homing back. The bird #955 has flown for 6 Km over the sea to reach
9 a rock-cliff at the Meloria Shoals and then deflected back towards the coast and orienting towards
10 home. Interestingly this bird also displayed a pronounced deviation at the other two release sites.

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12 At La Sterpaia, the analysis of the distances between the tracks before and after clock-shift,
13 revealed that thirteen birds tended to re-orient soon after release, retracing the same route followed
14 during the last training flight. These birds seem to be affected in their flight path by the presence of
15 a paved road that runs along a wooded area and by the presence of agricultural areas. In this case a
16 strong chromatic contrast appears to lead the pigeons back home. Differently from these birds, five
17 pigeons showed a tendency to deviate toward Eastwards about 90 degrees (with respect to the home
18 direction), before heading back home with a circular detour. When released from Arnaccio, only 1
19 out of 18 pigeon (#548) effectively retraced the last training route. The other birds progressively
20 drifted away from the route followed during the last training release.

21 22 **Discussion**

23 24 *Discussion of overall findings*

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26 In almost all cases, and at all three sites, clock-shift induced deviation from the course of each
27 bird's previous solo track that was less than would be expected from full dependence on a time-
28 compensated sun-compass. Indeed, this reduction was in many cases very considerable (see Figure
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5) and indicates that familiarity with the sites provided birds with guidance information from the landscape that is independent of the sun compass. The exact nature of this guidance is not clear, but could in principle range from gross orientation effects of panoramic or distant landmarks, to local guidance by specific ground features. Nevertheless, an effect of clock-shift remained at all three sites, and this implies that an individual's orientation is controlled by a compromise between direct familiar landmark guidance, and compass guidance. This compass guidance could be a residual effect of attendance to the true navigational map, or an effect of learnt site-specific compass instructions, but this study does not provide the ability to discriminate between these hypotheses (for example, we did not attempt to manipulate the navigational map).

Two important additional results remain. First, the degree of direct familiar landmark guidance was not the same at all sites, despite the equivalent training. This shows that the switch towards landmark guidance, or the relative effectiveness of such guidance, is not just dependent on familiarity, but also on the nature of the site. We may speculate about what that might be, but these suggestions must remain hypotheses for future tests because they are not here systematically varied. The analysis of the deviation from both the home direction and the last training release revealed that birds re-oriented at different distances from the release point depending on the site. These results are consistent with previous vanishing bearing data and route recorder tracking data collected in the same region, which reported that the extent of the deviation at familiar locations is site-dependent (Bonadonna et al. 2000; Gagliardo et al. 2005a). In particular, the distance at which the re-orientation occurred was significantly greater at Arnaccio than at the two other sites suggesting that at this site the birds seemed to have more difficulty in using a landmark-based re-orientation strategy, and relied preferentially on compass orientation. Second, individuals varied in their relative dependence on direct landscape guidance versus sun-compass guidance, despite the fact that they had equivalent experience at the test sites. As with the site-dependence effects, this individual variation implies that guidance decisions are not solely a matter of familiarity, but also depend on currently unknown individual characteristics. It appears that some individuals

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2 consistently depend on direct landmark guidance, some are consistently deviated by clock-shift,
3 whilst others show pronounced clock-shift effects only at the inland site, Arnaccio.
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5 It is important to note that in general the reduced clock-shift effects we found cannot be
6 attributed to recalibration of the sun compass, which might happen with repeated release under
7 clock-shift according to (Wiltschko et al. 1984) because for most of the birds large reductions are
8 seen here in the first clock-shift releases, and because the largest effects of clock-shift are actually
9 seen at the last of the three sites tested (Arnaccio). Our data are consistent to what was reported by
10 (Foà and Albonetti 1980) that familiarity, rather than recalibration of the sun compass, may have
11 the primary role in reducing the deflection after clock shift.
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24 *Detailed speculations*

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29 Inspection of the tracks indicates that a major component of reduced deviation under clock shift is
30 caused by birds, for at least part of the flight, following close to the same detailed ground features
31 characteristic of their unshifted route home. Indeed, in a few cases clock-shifted birds even appear
32 to join sections of routes back from other release sites after they have apparently lost their way.
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39 In our experiment Arnaccio was apparently a place where the use of a piloting strategy seemed to
40 be less favoured. Looking at the topographic features of the three release sites, an important
41 difference is the distance from the sea: Livorno, 4.2 km, La Sterpaia, 4.5 km, Arnaccio, 14.0 km.
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46 Inspection of the tracks reveals that those birds released from Livorno that show obvious deviation
47 under clock shift markedly re-oriented when arriving at the coast. The coastline seemed to represent
48 a sort of topographical barrier perhaps informing birds of their erroneous flight direction.
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52 Interestingly, these results accord with those obtained during an experiment at the same familiar
53 release site with hippocampal lesioned pigeons, in which intact and HF-lesioned pigeons were
54 subjected to phase-shift (Gagliardo et al. 2009a). During that experiment, phase-shifted control
55 birds recognised the sea as a salient landscape boundary: the majority of the control birds that
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1 reached the coast subsequently re-oriented northwards towards home. In contrast, the HF-lesioned
2 pigeons were diminished in their capacity to use the coast for correction, and often flew out over the
3 sea. In fact, in the current experiment, several birds (two in particular: #812 and # 955) also flew
4 over the sea as if they were poorly able to recognise the orientational significance of this major
5 topographical feature, and these were also birds that showed the strongest clock-shift deviation at
6 all three sites.
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14 At La Sterpaia birds displayed the clearest landmark-based orientation, with some birds even
15 apparently flying close to the course of their previous, unshifted trajectory, a phenomenon
16 characteristic of habitual route following (Biro et al. 2007; Meade et al. 2005), even though the
17 expected direction after clock-shift was approximately East, away from the constraining effect of
18 the sea. Inspection of the tracks suggests two hypotheses to explain this behaviour. Birds might be
19 attending to specific, distinctive ground features which are obvious here: square-shaped dark green
20 wooded areas interspersed with cultivated yellow fields. Some birds appear to fly along these quasi-
21 linear boundaries. The second hypothesis is that that the pigeons are influenced by the panoramic
22 view of the sea that becomes unobstructed for a bird flying above tree level at an altitude of about
23 10m.
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39 It is worth noting that at Livorno the sea is as close as at La Sterpaia, but the behaviour
40 of the pigeons is not identical. From the diagram reporting the mean deviation at the three release
41 site, (Figure 3; see also Figure 5) we can see a tendency to rely on compass orientation for the first
42 4-5 km from the release point at Livorno, while at La Sterpaia the birds re-oriented soon after
43 release. A possible explanation for this different behaviour might be due to the brain hemisphere
44 engaged in processing spatially relevant visual features during the training flight. When released
45 from La Sterpaia, the birds oriented southward during their homing flight and therefore the sea was
46 seen with the right eye. As the fibres of the avian optic nerve cross over completely, visual input
47 through the right eye is mainly processed by the left brain hemisphere (Güntürkün 1997). Therefore,
48 it might be possible that the critical visual cues (such as the sea) contribute more efficiently to re-
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1 orientation when learned and processed by the left hemisphere. Previous studies have shown the
2 critical involvement of the hippocampal formation in landmark-based orientation after clock-shift
3 (Gagliardo et al. 1999; Gagliardo et al. 2009a). However homing experiments performed with
4 pigeons subjected to unilateral lesions of the hippocampal formation did not highlight any
5 functional asymmetry in relation to the spatial use of topographical features (Gagliardo et al. 2002),
6 as unilateral lesions turned out to impair the use of a pilotage strategy. Nevertheless
7 electrophysiological studies performed in freely moving pigeons in mazes have discovered peculiar
8 proprieties of some neurons of the left hippocampus (Hough and Bingman 2004). In fact, while in
9 both sides of the hippocampal formations there are cells sensitive to relevant and specific locations
10 in the maze (the so called “location cells”), neurons that increase their firing activity when the bird
11 is moving between two relevant locations inside the maze have been found only in the left
12 hippocampus (so called “path cells”). It has been proposed that path cells may be more sensitive to
13 the spatial relationship of the local visual cues than the overall spatial properties of a test
14 environment.
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34 The poorer ability of the pigeons to re-orient at Arnaccio might be due to the absence of
35 large chromatic contrasts, as this site is a largely cultivated area, lacking patches of woodland.
36 During the final training flight some pigeons seemed to be affected by the presence of linear
37 landmarks, such as the Arnaccio River, roads and short corridors delimited by aligned trees, but,
38 these linear features did not seem to be sufficient to determine re-orientation in clock-shifted
39 pigeons in many cases. In fact, all the pigeons except one, when released at Arnaccio, progressively
40 drifted away from the path followed during the last training release despite the presence of these
41 linear features. It is possible that birds are using these features without committing them strongly to
42 memory, since birds may also use linear features over unfamiliar terrain (Lipp et al. 2004), or that
43 they are only effective in guiding memorised orientation without a compass when in combination
44 with additional stabilising features such as a view of the sea.
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Acknowledgements

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Figure captions

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5 Figure 1 Observed mean and median deviation from the home direction and expected deviation of
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7 birds released under clock-shift at the three release sites every 500 meters from the release site.
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9 Deviation from home of the same birds released in the last training release is also reported. Error
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11 bars represent standard errors. Negative and positive values of the ordinate axis represent counter-
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13 clockwise and clockwise deflections, respectively.
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19 Figure 2 Mean distance between the track recorded in unshifted and clock-shifted condition every
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21 500 meters from the release site. Error bars represent standard errors
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26 Figure 3 Mean deviation from the direction taken by the birds in the unshifted condition every 500
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28 meters from the release site. The deviation is represented as percentage of the expected. Error bars
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30 represent standard errors.
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36 Figure 4 Each panel show the tracks of a single bird released at each of the three release sites in the
37
38 unshifted (light blue, blue and dark blue for La Sterpaia, Livorno and Arnaccio, respectively) and
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40 clock-shifted (yellow, red and orange for La Sterpaia, Livorno and Arnaccio, respectively)
41
42 conditions.
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48 Figure 5 Individual deviation from the direction taken by each bird in the unshifted condition every
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50 500 meters from the release site. The deviation is represented as percentage of the expected. Codes
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52 of the birds identify each line according to symbols and colours. The thick straight black line
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54 represent the 25% threshold. Other explanation in the text.
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Fig.1a

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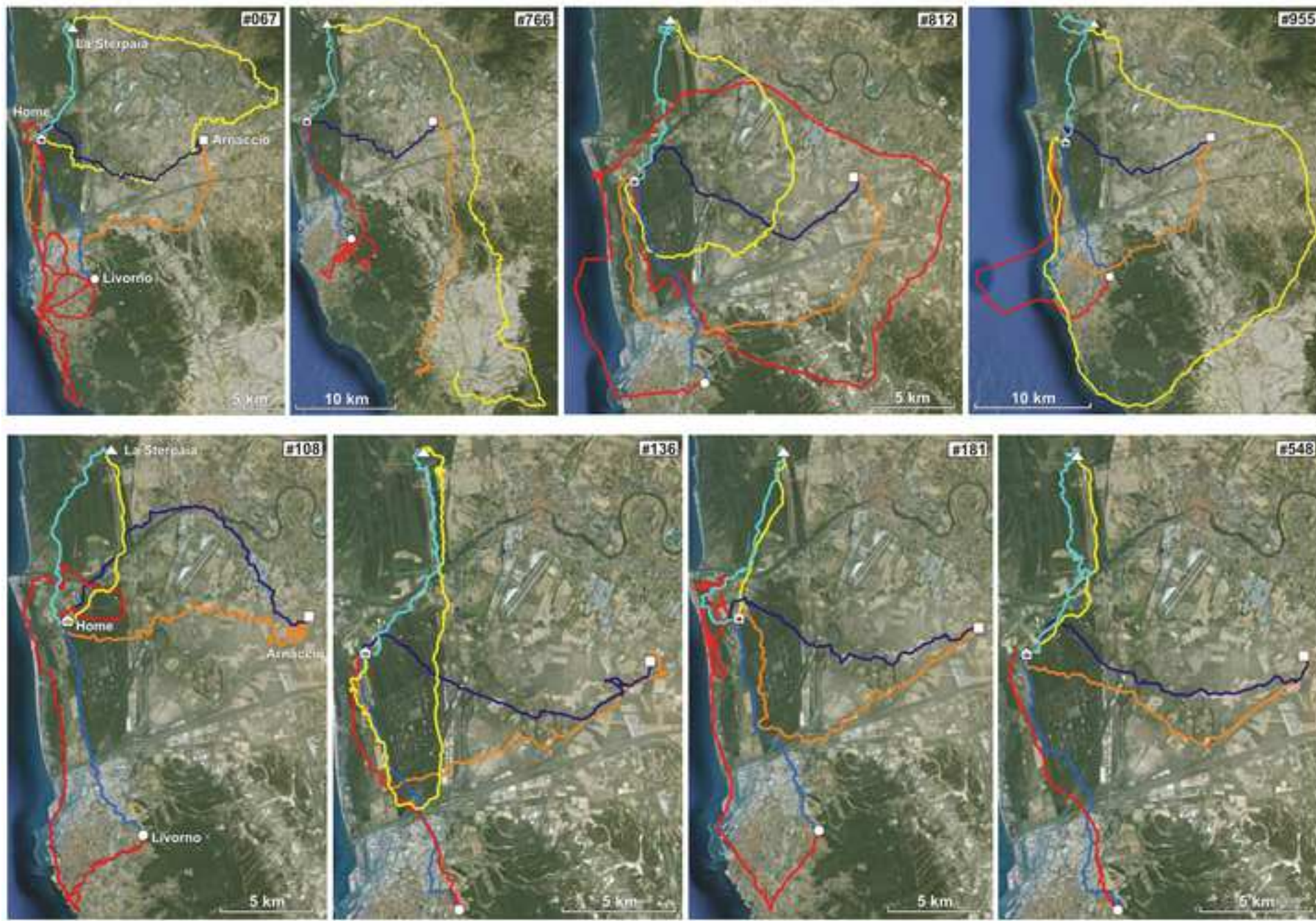


Fig.1b

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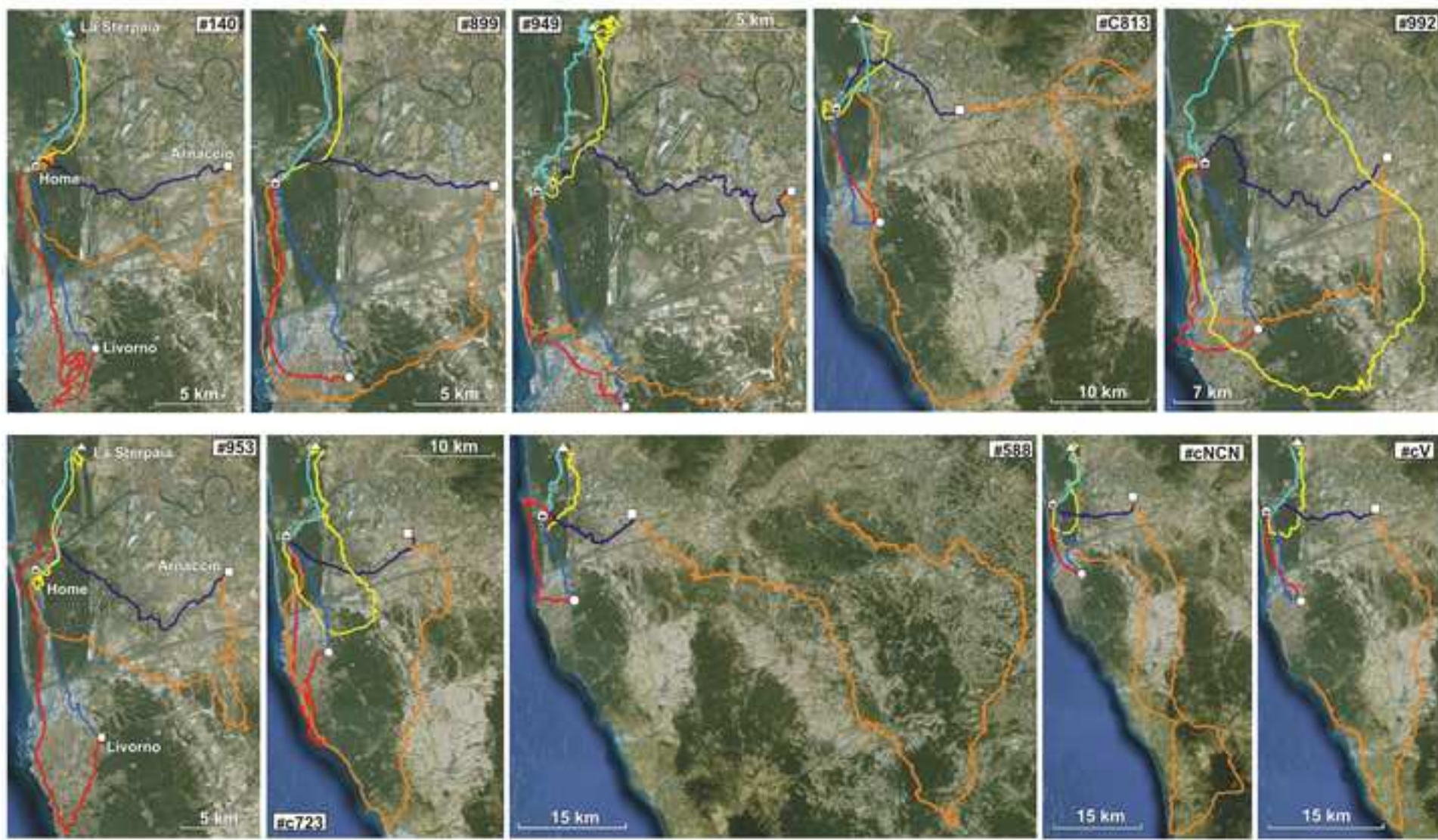


Fig.2

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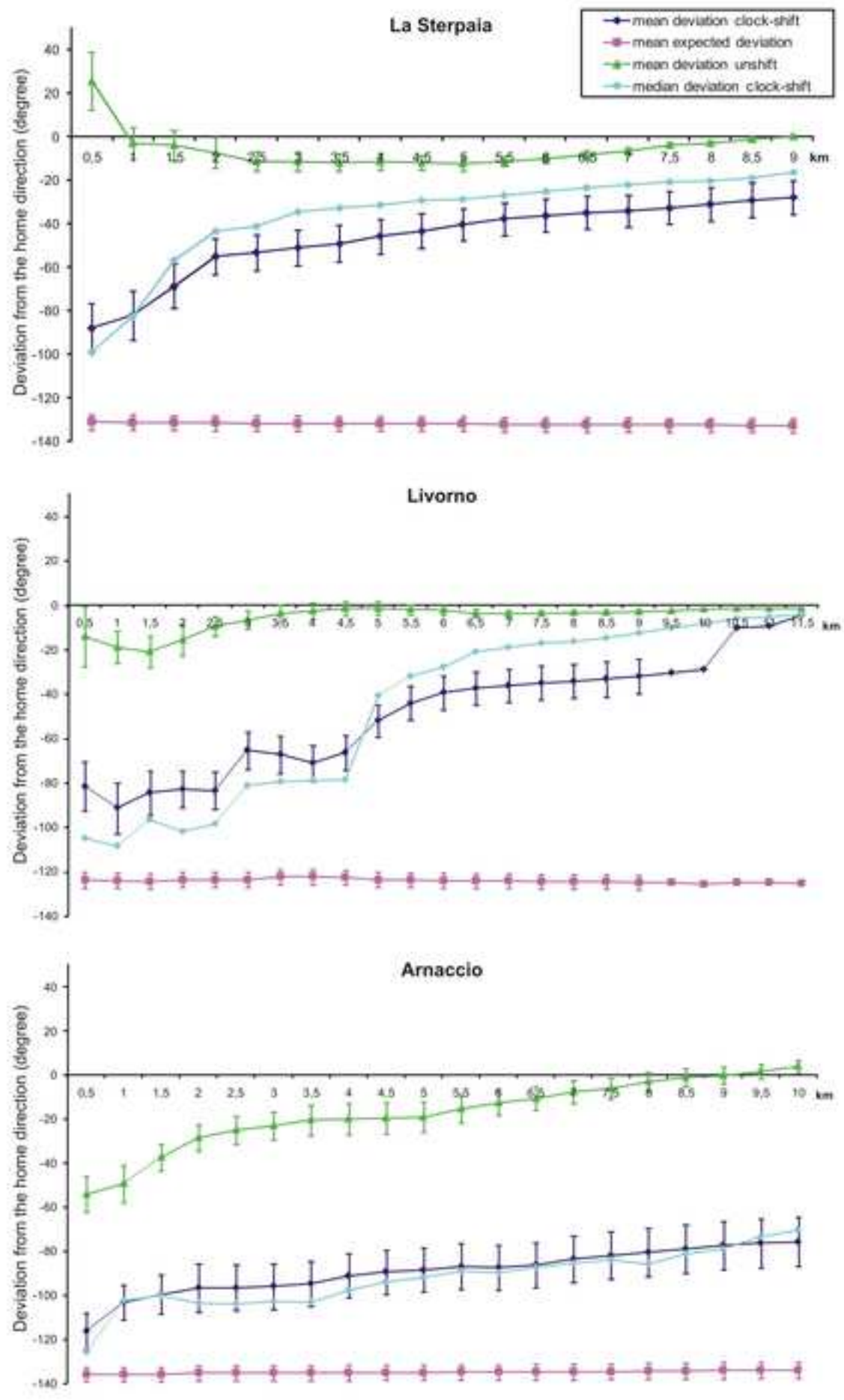


Fig.3

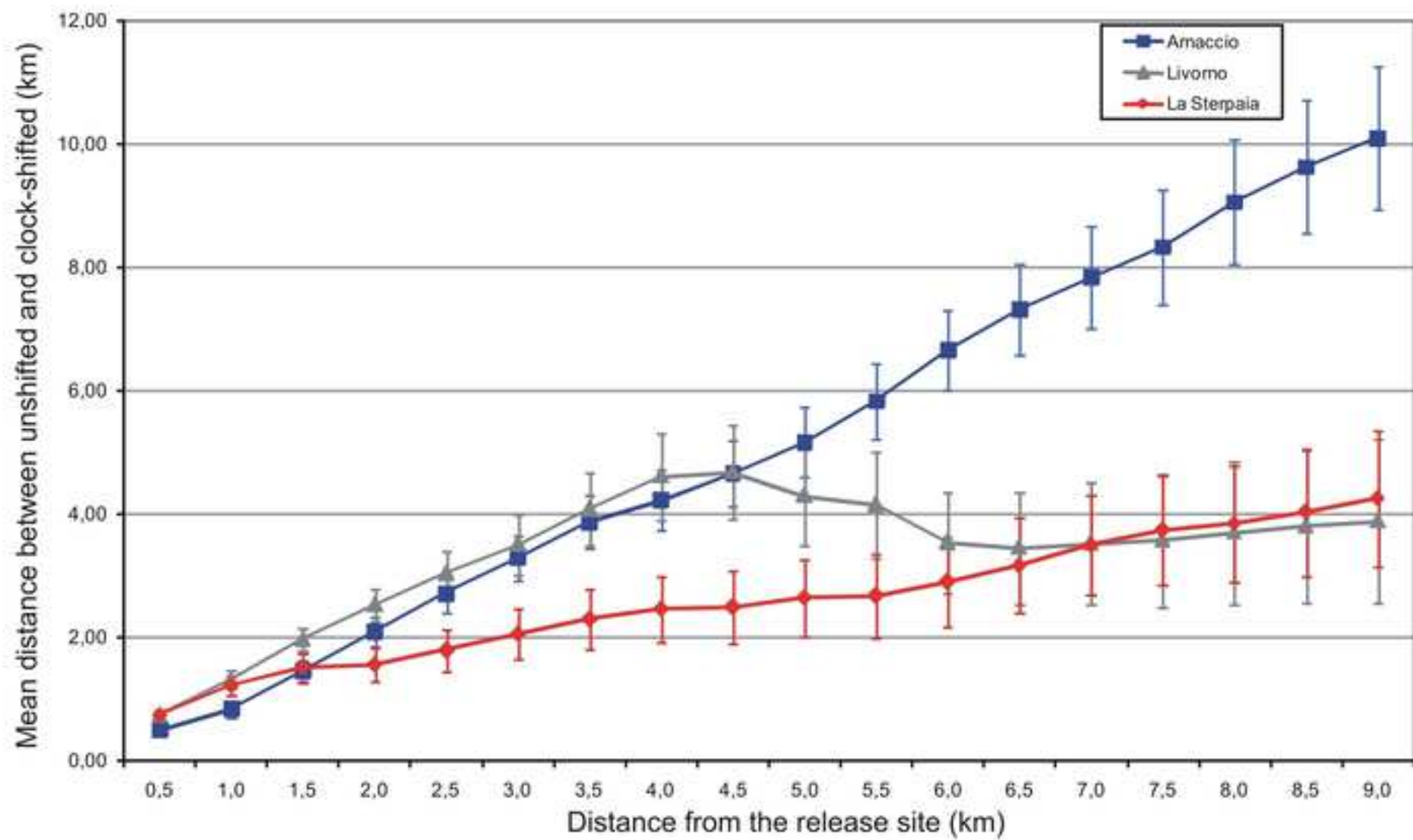
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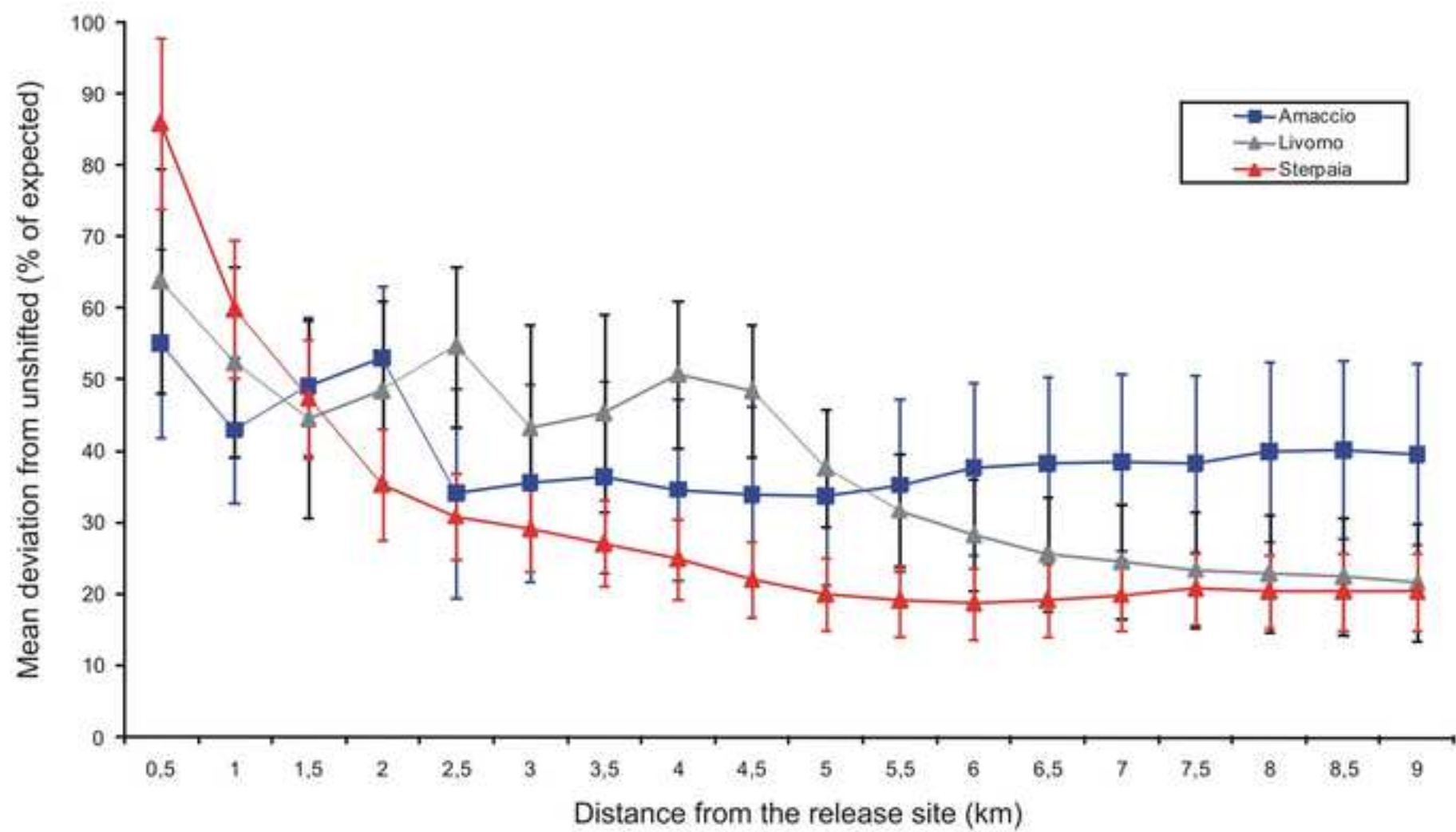
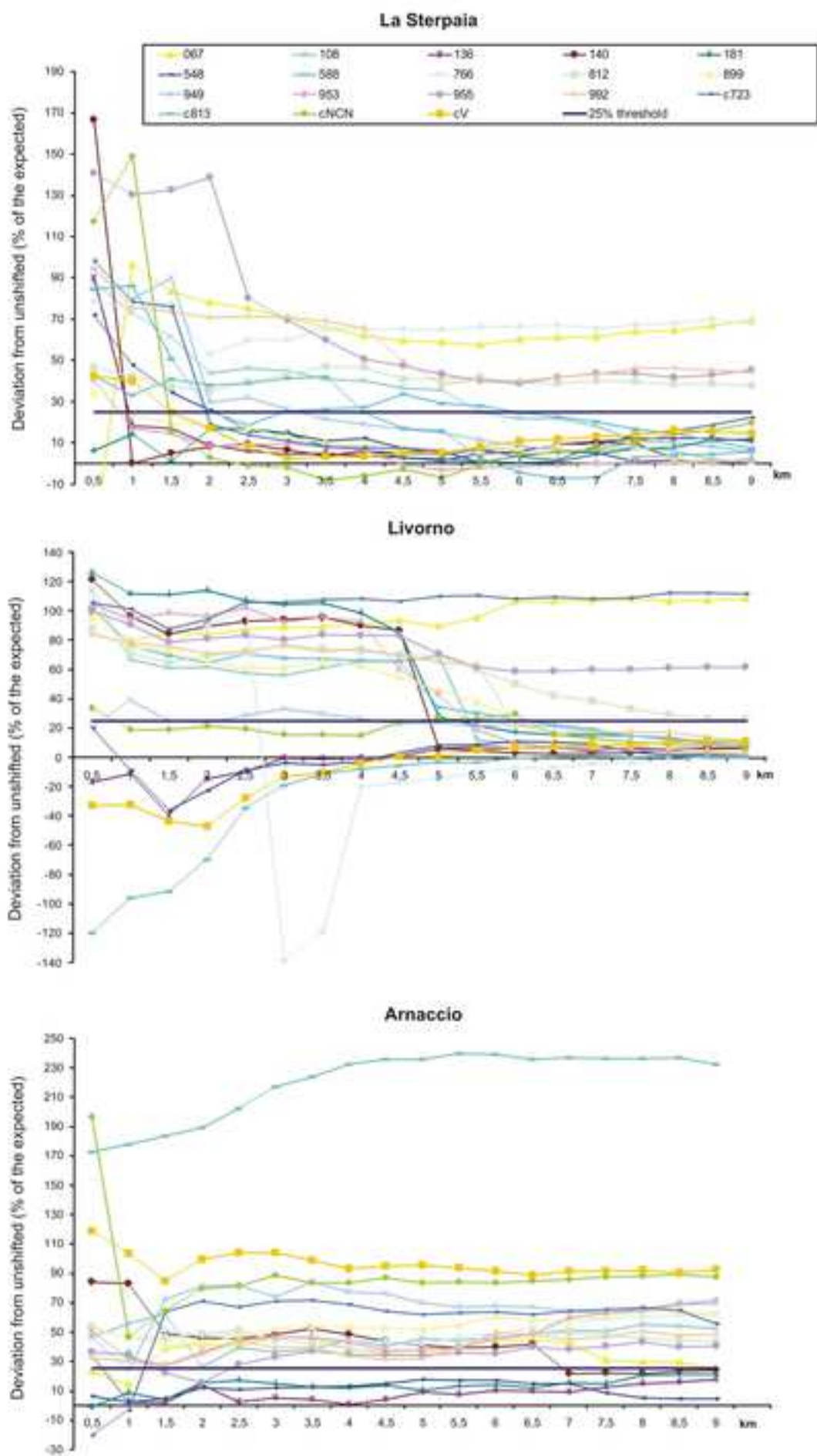
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Fig.5

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Supplementary Material

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