

1 **A magnetic pulse does not affect homing pigeon navigation: a GPS tracking experiment**

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## 22 **Summary**

23 The cues by which homing pigeons are able to return to a home loft after displacement to  
24 unfamiliar release sites remain debated. A number of experiments in which migratory birds have  
25 been treated with a magnetic pulse have produced a disruption in their orientation, which argues  
26 that a ferrimagnetic sense is used for navigation in birds. One previous experiment has also  
27 indicated an effect of magnetic pulses on homing pigeon navigation, although with inconsistent  
28 results. Previous studies have shown that some magnetic-related information is transmitted by  
29 the trigeminal nerve to the brain in some bird species including the homing pigeon. The function  
30 of this information is still unclear. It has been suggested that this information is important for  
31 navigation. Previous studies with trigeminal nerve lesioned pigeons have clearly shown that the  
32 lack of trigeminally mediated information, even if magnetic, is not crucial for homing  
33 performance in homing pigeons. However, this result does not completely exclude the possibility  
34 that other ferrimagnetic receptors in the homing pigeon play role in navigation. Additionally,  
35 recent studies on homing pigeons suggested the existence of a ferrimagnetic sense in a novel  
36 location presumably located in the inner ear (lagena). In the current study, we tested whether any  
37 ferrimagnetic magnetoreceptors, irrespective of their location in the bird's head, are involved in  
38 pigeons' homing. To do this, we treated homing pigeons with a strong magnetic pulse before  
39 release, tracked birds with GPS-loggers and analyzed whether this treatment affected homing  
40 performance. In the single previous magnetic pulse experiment on homing pigeons only initial  
41 orientation at a release site was considered and the results were inconsistent. We observed no  
42 effect of the magnetic pulse at any of the sites used, either in initial orientation, homing  
43 performance, tortuosity or track efficiency, which does not support a role for the ferrimagnetic  
44 sense in homing pigeon navigation, at least not in this geographic area, where magnetic field  
45 variations are in the region of 200 nT intensity and  $0.8^\circ$  inclination.

## 47 **Introduction**

48 True navigation describes behaviour in which an animal is able to return to a known goal from  
49 an unfamiliar area without access to cues emanating from it or information from the  
50 displacement to the unfamiliar site (Able, 2001; Griffin, 1952; Keeton, 1974). The homing  
51 pigeon is a long established model for the study of true navigation because of its motivation to

52 return to a home loft rapidly after displacement to an unfamiliar place (Wallraff, 2005).  
53 However, despite more than 40 years of experimental investigation the cues used by pigeons for  
54 true navigation remain debated (Phillips et al., 2006; Wallraff, 2005). According to the olfactory  
55 navigation hypothesis pigeons perform true navigation by relying on the spatial distribution of  
56 environmental odours learned at the home loft area, by associating the wind-borne odours with  
57 the wind directions (Papi et al., 1972; Wallraff, 1991). An alternative hypothesis argues that one  
58 or more magnetic field parameters can be used for finding the animals position (Lohmann et al.,  
59 2007; Putman et al., 2011), although in some regions of the Earth it seems to be difficult to use a  
60 bi-coordinate magnetic map because different magnetic parameters are distributed at a relatively  
61 small or parallel angle to each other (Åkesson and Alerstam, 1998; Boström et al., 2012). A  
62 number of experiments in which the orientation performance of pigeons appeared to be affected  
63 in various ways by releases in magnetic anomalies have been argued to support this hypothesis  
64 although only with indirect evidence (Dennis et al., 2007; Mora and Walker, 2009; Walcott,  
65 1991; Wiltschko et al., 2009a).

66 As it has been proposed that birds, including pigeons, sense the magnetic field through  
67 sensory cells which contain ferrimagnetic material such as magnetite (Kirschvink and Gould,  
68 1981), another line of evidence in favour of a role for magnetic cues in pigeon navigation comes  
69 from experimental manipulation of the presumed sensory system. Brief strong magnetic pulses  
70 which would re-magnetise magnetic material have been shown to disrupt the orientation of  
71 migratory birds in the laboratory (Beason et al., 1995; Munro et al., 1997; Wiltschko et al., 1994)  
72 and field (Holland and Helm, 2013; Holland, 2010). This sensory system appears to detect some  
73 aspect of the magnetic field and magnetic information would be conveyed to the brain by the  
74 ophthalmic branch of the trigeminal nerve (hereafter V1) (Beason and Semm, 1996; Heyers et  
75 al., 2010; Mora et al., 2004; Semm and Beason, 1990a). The fact that magnetic pulses affect  
76 adult but not juvenile migrating birds (Munro et al., 1997) and the trigeminal nerve does not play  
77 a role in the magnetic compass response (Beason et al., 1997; Zapka et al., 2009) has been used  
78 to argue that this sensory system is used for map based navigation in migrating birds (Wiltschko  
79 and Wiltschko, 2006). A magnetic pulse has been shown to disrupt the orientation performance  
80 of homing pigeons, although not homing performance (Beason et al., 1997). Beason and  
81 colleagues argued that this effect was on a map rather than a compass as releases were under  
82 sunny conditions, where the sun compass has been shown to dominate over the magnetic

83 compass in the cue hierarchy. Local anaesthetic applied to the beak area, a putative site of  
84 magnetoreception in pigeons (Fleissner et al., 2003), has also been shown to reduce the  
85 disrupting effect of being released in a magnetic anomaly (Wiltschko et al., 2010). It is argued  
86 that these results provide evidence that pigeons use a ferrimagnetic sense as part of a redundant  
87 navigation system. However, the results reported by Wiltschko et al 2010 actually speak against  
88 crucial involvement of the trigeminal system in navigation, since the anaesthetised pigeons  
89 showed unimpaired navigational abilities. This is consistent with what was reported in a series of  
90 experiments in which the V1 of homing pigeons were lesioned before release at unfamiliar sites  
91 (Gagliardo et al., 2006; Gagliardo et al., 2008; Gagliardo et al., 2009). In no case did lesioning  
92 V1 result in impairment in homing performance and strikingly, birds with an intact V1 were  
93 unable to home if the olfactory nerve was severed. This suggested that V1 was neither sufficient  
94 nor necessary for true navigation in these birds.

95           Initially iron-containing cells found in the upper beak of the homing pigeons and other  
96 birds (Beason and Nichols, 1984; Falkenberg et al., 2010; Fleissner et al., 2003; Fleissner et al.,  
97 2007; Williams and Wild, 2001) were suggested as magnetoreceptors innervated via the V1.  
98 However, a recent thorough study made on homing pigeons (Treiber et al., 2012) strongly  
99 suggested that the majority of Fe-positive cells, if not all, both in the upper beak and other parts,  
100 such as skin, respiratory epithelium and feathers folliculi are represented by macrophages. This  
101 finding questions the previous model of the upper beak organ (Fleissner et al., 2003; Fleissner et  
102 al., 2007) and clearly shows that the widely used method of Prussian blue staining alone is not  
103 enough when it comes to identification of iron-containing magnetoreceptors. Nevertheless, the  
104 study by Treiber et al. (2012) does not completely rule out the possibility that trigeminal  
105 ferrimagnetoreception in birds exists. There is independent evidence suggesting that V1 in  
106 homing pigeons (Mora et al., 2004) and European robins (Heyers et al., 2010) does transmit  
107 magnetic-related information to the brain (although see (Kishkinev et al., 2012) for failure to  
108 replicate (Mora et al., 2004) with European Robins). These data still support the notion that there  
109 are magnetoreceptors in the areas innervated via V1 (the upper beak, cere, skin at the frontal part  
110 of the bird's head or adjacent areas) though these magnetoreceptors are not yet identified with  
111 certainty (Heyers et al., 2010; Mouritsen, 2012; Treiber et al., 2012). Even if V1 does transmit  
112 magnetic information in homing pigeons, previous studies with trigeminal nerve lesioned  
113 pigeons (Gagliardo et al. 2006, 2008, 2009) have clearly shown that the lack of V1 carried

114 information is not crucial for homing performance in this species. However, this result does not  
115 completely exclude that non trigeminally mediated ferrimagnetic receptor in the homing pigeon  
116 play role in navigation. Recent studies by Wu and Dickman (2011, 2012) on homing pigeons  
117 suggested the existence of a ferrimagnetic sense in a novel location, presumably in the inner ear  
118 (lagena). Despite this neurological evidence, the effect of inner ear lesions on pigeon homing  
119 performance have provided mixed results, with one experiment failing to find an effect on  
120 homing (Wallraff, 1972). Another study did record deficits in performance (Harada et al., 2001),  
121 but only tested birds in a familiar area, and the results suggest that the effect was due to non-  
122 specific effects of the surgery rather than an impairment of navigation by removal of a sensory  
123 system (see (Wallraff, 2005) for discussion). Taken together, there is a possibility that  
124 ferrimagnetoreceptors, irrespective of their location in the bird's head, are involved in pigeons'  
125 homing as a compass, map or both. To test this hypothesis, we treated homing pigeons with  
126 strong magnetic pulse before release, tracked birds with GPS-loggers and analysed whether this  
127 treatment affects homing performance. In the single previous magnetic pulse experiment on  
128 homing pigeons only initial orientation shortly after release, not the whole homing tracks, were  
129 considered, and the result was inconsistent indicating possible effect of the pulse treatments at  
130 some release sites but not in others (Beason et al., 1997).

131

## 132 **Materials and methods**

### 133 *General procedure*

134 One hundred and twenty five adult homing pigeons, of at least 6 months of age and  
135 hatched at the Arnino field station (latitude 43° 39' 26'' N; longitude 10° 18' 14'' E), Pisa, Italy,  
136 were used in the study, which took place in 2010 and 2011. The pigeons were raised as free  
137 flyers and were kept and manipulated according to Italian law on animal welfare. The birds had  
138 been subjected to training releases up to 5-7 km around the loft in different directions. Twenty  
139 days prior to the experimental releases all the birds were equipped with a PVC dummy weight,  
140 similar in dimension and weight to the GPS data logger they would be carrying, in order to  
141 accustom them to flying with a load. The dummy was attached to the pigeons' back by means of  
142 a Velcro strip glued on the feathers, which had been trimmed.

### 143 *GPS data logger*

144 Technosmart and iGotU (Mobile Action Technology) GPS data loggers were used in 2010  
145 and 2011, respectively. They recorded positional data of flying birds every second, and only in a  
146 few cases at a lower sampling rate (6-10 seconds). The positional information stored by a GPS  
147 data logger includes latitude, longitude, and time of recording. The devices also provide  
148 information about altitude, but with insufficient precision to allow a reliable analysis. The tracks  
149 for each pigeon for each recorded release were visualised in Google Earth.

150

### 151 *Test releases*

152 Before displacement the birds were divided into two groups and subjected to two  
153 different treatments. Magnetically manipulated birds (MP) received a strong brief pulse from an  
154 SCR-fired capacitive discharge unit (a SOTA™ magnetic pulser, Sota Instruments, Penticton,  
155 BC, Canada) modified by the addition of a double-wrapped, 10cm diameter Lee Whittling coil  
156 (Kirschvink, 1992). The coil system produced a unidirectional magnetic pulse of ~0.1 ms  
157 duration, with peak amplitude slightly over 0.1 T, and a rise time of ~100 ns. The pulse was  
158 administered from a solenoid aligned perpendicular to the Earth's magnetic field, applied  
159 "south anterior" as defined by (Beason et al., 1995) (See Figure 1). A pulse of this strength is  
160 sufficiently large to overcome the coercivity of all known biogenic magnetite and thus re-  
161 magnetise it in the direction of the applied pulse (Dunlop, 1981; Kirschvink, 1983). After  
162 homing the MP birds were excluded from the subsequent releases. Control birds (C) were  
163 placed in the pulser, as well as the magnetically treated pigeons, but although the capacitor  
164 charged and fired in the same way, the current was not delivered into the coil and so the  
165 magnetic pulse was not delivered. After homing the control birds tested at one site could be  
166 released at another site either in the control or MP group in a balanced number.

167 All the birds were released at unfamiliar locations (see Table 1 for details). Prior to release,  
168 the dummy on the back of each pigeon was replaced with a GPS data logger. Each pigeon was  
169 released singly, with at least 10 minutes between releases. All the experimental releases took  
170 place under sunny conditions, with no or light wind.

171

### 172 *Quantitative analyses and statistical procedures*

173 All tracks interrupted within 4 km distance from the release site were excluded from the  
174 analysis. If pigeons belonging to two different experimental groups joined after release they were

175 excluded from the analysis. If two pigeons belonging to the same group joined, only the one  
176 released later was included in the analysis.

177 Homing success was recorded and the performances (homed vs. lost) of the two groups  
178 were compared with the  $\chi^2$  test. For each pigeon we analysed the following aspects of the flight  
179 path.

180 *Distance from home.*

181 The distance from home observed every each hour after release was analysed for the first  
182 10 hours of tracking. The performances of the two groups were compared with a Two Way  
183 Repeated Measures (RM) ANOVA.

184 *Stops.*

185 The percentage of time the birds were perching with respect to the time of recording.

186 *Efficiency index*

187 To compare the length of the homing journey we considered the efficiency index, which we  
188 calculated as the ratio between the track length and the beeline distance between the release site  
189 and home. When the tracks were not complete we added the linear distance from the end of the  
190 track to the loft. The efficiency indices of the experimental groups were compared with the  
191 Mann-Whitney U test. The tracks shorter than the 50% of the beeline were excluded from the  
192 analysis.

193 *Tortuosity per kilometre.*

194 To perform this analysis we drew concentric circles, around the release site, having a radius  
195 increasing by one km from 2 up to 10 kilometres and we considered separately the portions of  
196 the tracks included in the ring delimited by two consecutive circles (see (Gagliardo et al., 2011)  
197 for details). For each portion we considered the direction taken by the bird moving from one  
198 point to the next and therefore we calculated the mean vector. We applied a Two Way Repeated  
199 Measure ANOVA on the mean vector lengths relative to portions of the tracks recorded at  
200 increasing distances in order to compare the tortuosity in the flight path of the two experimental  
201 groups.

202 *Mean vector analysis.*

203 The procedure described above was applied to the section of each track within a range of  
204 1-10 km from the release site. The resulting mean vector gives a good description of the initial  
205 orientation of the bird and of the tortuosity of its flight path. For each group the mean vector  
206 distributions were tested for randomness by using the One Sample Hotelling test. At each release  
207 site the mean vector distributions of the two groups were compared by means of the Two Sample  
208 Hotelling test.

209 *Virtual vanishing bearings.*

210 We recorded the direction of the birds at 2 km from the release site. The circular  
211 distributions were tested for randomness by means of both the Rayleigh and V test and the two  
212 groups were compared with the Watson U<sup>2</sup> test (Batschelet, 1981).

213

## 214 **Results**

215 The tracks used in the analysis are reported in Figure 2-5 for Chiesina Uzzanese, La Sterza,  
216 Montespertoli and Braccagni, respectively.

217 *Homing performance.*

218 The homing success of C and MP were not statistically different according to the  $\chi^2$  test  
219 in each of the four release tests (see Table 1 for details). The Two Way RM ANOVA applied to  
220 the distance from home recorded in the first 10 hours after release (see Figure 6) did not reveal a  
221 significant difference between the C and MP at any site (factor treatment;  $p > 0.1$  in all tests;  
222 Chiesina Uzzanese  $F = 1.825$ , La Sterza  $F = 0.168$ , Montespertoli  $F = 2.131$ , Braccagni  $F = 0.770$ ).  
223 The distance from home (see Figure 2) significantly decreased over time (factor hours from  
224 release;  $p < 0.001$  in all tests; Chiesina Uzzanese  $F = 19.347$ , La Sterza  $F = 22.055$ , Montespertoli  
225  $F = 18.905$ , Braccagni  $F = 19.610$ ). The interaction between treatment and time turned out to be  
226 significant in one ( $p < 0.001$ ; Chiesina Uzzanese  $F = 4.718$ ) out of four test releases ( $p > 0.1$ ; La  
227 Sterza  $F = 1.468$ , Montespertoli  $F = 0.455$ , Braccagni  $F = 0.444$ ). In fact, at Chiesina Uzzanese the  
228 MP pigeons approached home significantly faster than the C birds in the first three hours after  
229 release (Student-Newman-Keuls test, C vs MP, Hour 1  $q = 5.282$   $p < 0.001$ ; Hour 2  $q = 4.042$   
230  $p < 0.01$ ; Hour 3  $q = 3.618$   $p < 0.05$ ).

231 *Stops.*

232 The percentage of time the birds spent sitting during the track recording was significantly  
233 different between the two groups of pigeons only at Montespertoli (Mann-Whitney U test  
234  $p < 0.05$ , median C 57%, MP 79%). In the other three release tests the difference between C and  
235 MP never reached the significance level (Chiesina Uzzanese, C 68%, MP 61%; La Sterza, C  
236 74%, MP 77%; Braccagni C 81%, MP 77%).

237 *Tortuosity.*

238 The analysis of the tortuosity applied on sectors of the tracks at increasing distances from  
239 the release site did not show a significant difference between treatments at any site ( $p > 0.1$ ,  
240 Chiesina Uzzanese  $F = 0.009$ ; La Sterza  $F = 0.346$ ; Montespertoli  $F = 0.109$ ; Braccagni  $F = 0.002$ ).  
241 The tortuosity was not significantly different at various distances from the release site ( $p > 0.05$ ,  
242 La Sterza  $F = 1.677$ ; Montespertoli  $F = 0.611$ ; Braccagni  $F = 1.141$ ), except in the release from  
243 Chiesina Uzzanese where the tortuosity was significantly higher ( $p < 0.05$ ,  $F = 2.471$ .) at a distance  
244 ranging between 2 and 3 km than at a distance ranging from 8 and 9 km from the release site  
245 ( $p < 0.05$ , Tukey test). At no site was there a significant interaction between the treatment and the  
246 distance (La Sterza  $F = 1.413$ , Chiesina Uzzanese  $F = 0.809$ ; Montespertoli  $F = 1.127$ ; Braccagni  
247  $F = 0.745$ ).

248 *Efficiency index.*

249 The efficiency index did not differ between groups according to the Mann-Whitney U  
250 test in the four test releases (median efficiency index (e.i.): Chiesina Uzzanese, C  $n = 8$  e.i.=0.52,  
251 MP  $n = 9$  e.i.=0.64; La Sterza, C  $n = 14$  e.i.=0.56, MP  $n = 11$  e.i.=0.58; Montespertoli C  $n = 11$   
252 e.i.=0.74, MP  $n = 10$  e.i.=0.67; Braccagni C  $n = 12$  e.i.=0.71, MP  $n = 8$  e.i.=0.72).

253

254 *Virtual vanishing bearings.*

255 The two groups of pigeons were significantly oriented at 2 km from the release site and  
256 their mean vector direction was close to the home direction in all test (see Figure 7 and Table 2

257 for details). The Watson U2 test did not reveal a significant difference between C and MP  
258 pigeons at any site ( $p > 0.1$  in all tests).

259 *Mean vector analysis.*

260 The initial orientation of the birds at a distance ranging between 1 km up to 10 km from  
261 the release site is summarised by the mean vector diagrams represented in Figure 8 (see also  
262 Table 2 for the second order mean vector values). The Hotelling test applied to the mean vector  
263 distributions revealed that both C and MP group mean vector distributions were different from  
264 random at all release sites (Chiesina Uzzanese C  $p < 0.01$ , MP  $p < 0.001$ ; La Sterza C  $p < 0.001$ , MP  
265  $p < 0.01$ , Montespertoli and Braccagni both C and MP  $p < 0.001$ ). The Two sample Hotelling test  
266 did not reveal a difference between the C and MP distribution in any of the release tests ( $p > 0.1$ ).

## 267 **Discussion**

268 It has been argued that if animals possess a ferrimagnetic sense then applying strong  
269 magnetic fields should disrupt or damage the sensory receptor, as shown by *in vitro* experimental  
270 tests demonstrating the disruption of a cluster of superparamagnetic particles when treated with a  
271 strong magnetic pulse (Davila et al., 2005). Therefore such a treatment is expected to produce  
272 loss or change of magnetic information-based navigation performance (Kirschvink and Gould,  
273 1981). Magnetic pulse treatments have previously been shown to affect the orientation of  
274 migratory birds in laboratory (Wiltschko et al., 1994) and field based tests (Holland and Helm,  
275 2013; Holland, 2010). In studies using orientation cages, the cancelling of the effect when a local  
276 anaesthetic is applied to the trigeminal nerve (Beason and Semm, 1996) or the upper beak  
277 (Wiltschko et al., 2009b) is argued to indicate that the effect is on a magnetosensory receptor  
278 involved in navigation, located in the beak and mediated by the trigeminal nerve. A magnetic  
279 pulse has also been shown to affect the orientation of homing pigeons in some circumstances  
280 (Beason et al., 1997). A significant difference was only observed at 2 out of 16 sites in the  
281 comparable south anterior treatment, and not consistently (Figure 2, table 1, in Beason et al.,  
282 1997). Our results show no difference in orientation or homing performance between control and  
283 magnetic pulse treated birds at any distance, with a maximum (but not significant) difference in  
284 mean vectors of  $23^\circ$  at Braccagni, 106 km from the loft. Taken together with the results of  
285 Gagliardo et al. (2006, 2008, 2009) this result strongly suggests that putative ferrimagnetic

286 receptors in the upper beak, lagena or elsewhere do not play a role in homing of pigeons in this  
287 study. Whether this result is because pigeons do not use magnetic cues for map navigation is a  
288 matter of discussion. The results of Gagliardo et al. (2006, 2008, 2009) indicate that an intact  
289 trigeminal nerve does not allow anosmic pigeons to home within 100 km of the home loft. This  
290 finding speaks against a multicue system for true navigation in homing pigeons at these  
291 distances. On the other hand Wiltschko et al. (2010) argue that improved initial orientation  
292 performance at magnetic anomalies located within 90 km from home after the application of  
293 local anaesthesia on the beak was due to the removal of confusing magnetic information. The  
294 results of Treiber et al. (2012), which indicate that the putative site of magnetoreception in the  
295 upper beak appear to be macrophages, make it unclear as to whether this treatment would affect  
296 a magnetoreceptor or not (although see (Wiltschko and Wiltschko, 2012) for other behavioural  
297 evidence consistent with magnetoreceptors in this region and discussion of this issue in the  
298 introduction of this paper).

299           Possible experimental differences between this study and Beason et al. (1997)  
300 include the pulse strength and the distance of release sites. The pulse strength varied between the  
301 current study and that of Beason et al., with a 0.1T pulse used in this study and a 0.5T pulse in  
302 the previous study. However, previous (Holland, 2010; Holland et al., 2008) and a subsequent  
303 experiment (Holland and Helm, 2013) using this pulse device, have indicated significant effects  
304 on initial orientation in both bats and migratory birds. Furthermore 0.1T is greater than the  
305 coercivity of all known biogenic magnetite so this seems an unlikely explanation for these results  
306 (Dunlop, 1981; Kirschvink, 1983).

307           Why is the distance of release argued to be important? One hypothesis suggests that  
308 difference in intensity of the magnetic field between current position and desired goal provides a  
309 cue to latitude (Phillips et al., 2006). Differences in intensity are argued to be too variable or too  
310 small at distances <75 km from the goal (Phillips, 1996). We acknowledge that Beason et al.  
311 (1997) had several release sites greater than our 106 km from the loft, although significant  
312 effects were seen at only two of those in the south anterior group. The sample sizes between  
313 papers were comparable however, with no more than 12 bearings analysed at any site in the prior  
314 study. However, distance alone is not an explanation unless it corresponds with differences in the  
315 magnetic field parameters that the birds were exposed to in the two regions. Examining the

316 magnetic field parameters of the four release sites used in our experiment with respect to home  
317 highlights the variability inherent in the magnetic field (supplementary Table 1, values obtained  
318 from a global field model). While three of the sites (Braccagni, La Sterza and Chiesina  
319 Uzzanese) have field parameters that vary as expected in comparison to the home loft values (i.e.  
320 increasing inclination and total intensity from south to north), one site, Montespertoli, has a total  
321 intensity that is greater than the home site, despite being on the same latitude. The largest  
322 difference in intensity is between Braccagni and home (214 nT less at Braccagni than at the loft),  
323 as one would expect because it is approximately south of the loft and 106 km away, i.e. the  
324 furthest latitudinal displacement. Beason et al. (1997) found a correlation between distance of  
325 release site from home and the size of deflection from controls. They also had three sites at  
326 distances further than our furthest release site (123km, 128 km and 169 km). However, this does  
327 not take into account intensity or inclination differences between the home loft and the release  
328 site, upon which the hypothesis of magnetic navigation is based (see supplementary table 1 for  
329 values of Beason et al. (1997)). Closer examination of the intensity and inclination parameters at  
330 the sites used in both studies in relation to observed significance of the effect reveal a more  
331 complicated picture which is not easy to explain by a simple intensity/inclination/distance vs.  
332 effect relationship. First, if significantly oriented groups are considered, Beason et al. (1997)  
333 only had two sites out of 16 at which a significant effect of treatment was observed in the south  
334 anterior treatment (comparable to ours). Two of these releases were at a site 107.8 km from the  
335 loft, with distance, and inclination values comparable to our furthest site, but with a higher  
336 intensity (60 nT higher). The other site 169 km from the loft, where the experimental group  
337 became non oriented, had a lower intensity (40 nT lower) and inclination (0.39° lower). The  
338 other two sites at greater distance than our furthest site (123 km and 128 km) did not show a  
339 significant effect in the comparable south anterior treatment in fact showing smaller deflection  
340 from controls (12° and 14°) than at our furthest site (23°), despite in one case (123km) having  
341 the highest intensity and inclination values that of any site used (294 nT). The fact that the  
342 intensity and inclination difference of our furthest site, 106km from the loft is greater than the  
343 difference in the site at 169km in Beason et al. (1997) also highlights that greater distances in the  
344 Beason et al. (1997) study *per se* do not necessarily mean greater difference between magnetic  
345 parameters and are not necessarily a stronger predictor of effect. Thus, if the effects seen at in the  
346 Beason et al. study are related to magnetic parameters, it is in a way that is not explained simply

347 by greater differences in magnetic parameters and it does not easily explain the lack of an effect  
348 at our furthest site. It is not currently clear whether the magnetic sense of a homing pigeon is  
349 sensitive enough to detect the changes in intensity reported here. Changes in intensity of 3000 nT  
350 have been shown to affect the orientation behaviour of migratory birds (Henshaw et al., 2010),  
351 and electrophysiology studies suggests sensitivity between 50 and 200 nT (Beason and Semm,  
352 1987; Semm and Beason, 1990b) but see (Mouritsen and Hore, 2012) for criticisms of early  
353 electrophysiology works. No direct behavioural test indicates sensitivity as low as required for  
354 detecting 200 nT changes. On this basis, it would be important to test the effect of magnetic  
355 pulses selecting sites where intensity differences are clearer indications of differences in latitude  
356 and approach potentially more realistic sensory thresholds.

357 A number of tracking studies that tested the navigation ability of Procellariiformes  
358 bearing strong magnets on their head failed to find an effect of the treatment on navigation  
359 (Benhamou et al., 2003; Bonadonna et al., 2005; Mouritsen et al., 2003), suggesting that they  
360 rely on other cues, possibly olfaction, for navigation (Nevitt and Bonadonna, 2005). The only  
361 previous tracking study on the effect of magnetic pulses on birds navigation was conducted on  
362 catbirds displaced during migration (Holland et al., 2009) and tracked by aerial survey from a  
363 light aircraft. This study also failed to find an effect on birds' orientation. However, in the latter  
364 case, the delay between treatment and departure meant that it was possible that the birds had  
365 recalibrated, as previous evidence suggests the pulse is temporary, lasting approximately 10 days  
366 (Holland and Helm, 2013; Wiltschko et al., 1998). In the present experiment homing pigeons  
367 homed within hours of the treatment, so this cannot be an explanation for the lack of an effect.  
368 This study strongly suggest that ferrimagnetic receptors do not play role in homing of pigeons.  
369 This result together with previous studies with trigeminal nerve lesioned pigeons (Gagliardo et  
370 al., 2006; Gagliardo et al., 2008; Gagliardo et al., 2009) questions the hypothesis of magnetic-  
371 based navigation in homing pigeons at least for intensity differences in the range of 200 nT.  
372 Whether (ferri)magnetoreceptors and the trigeminal nerve play a crucial role for long-distance  
373 navigation in birds remains to be demonstrated.

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379 performing the releases. We thank Daniele Santerini for his help in preparing the figures.

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383 Grocott award, a prize from the Royal Institute of Navigation.

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535

536 Table 1. Homing success of birds released at the 4 test sites. Tr= treatment (C= control,  
 537 MP=magnetic pulse). N=number of birds released, n=number of birds considered in the analysis.

538

RS	Tr	N	n	homed	lost	$\chi^2$
La Sterza 299°, 39 km 29-30/07/2011	C	18	16	14	2	1.26
	MP	19	17	11	6	
Chiesina Uzzanese 241°, 40.3 28/07/2011	C	12	10	8	2	0.20
	MP	12	11	9	2	
Montespertoli 270°, 61 km 15/08/2010	C	17	17	16	16	0.47
	MP	17	16	15	18	
Braccagni 326°, 106.3 7-10/08/2010 1/08/2011	C	38	38	22	16	0.01
	MP	40	39	21	18	
						ns

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542 Table 2. Initial orientation at the 4 test release sites. Tr= treatment (C=control, MP=magnetic  
 543 pulse), r= mean vector length,  $\alpha$  = mean vector direction, hc=homeward component. \*=  
 544 significance level \* $<0.05$ , \*\* $<0.01$ , \*\*\* $<0.0001$ .

545

RS	Tr	n	Virtual vanishing bearing			Mean Vector 1-10 km		
			r	$\alpha$	hc	r	$\alpha$	hc
La Sterza 299°, 39 km 29-30/07/2011	C	14	0.59**	295°	+0.59***	0.43***	292°	+0.43
	MP	11	0.64**	295°	+0.64**	0.43**	294°	+0.43
Chiesina Uzzanese 241°, 40.3 28/07/2011	C	8	0.80**	204°	+0.64**	0.56**	232°	+0.63
	MP	9	0.94***	218°	+0.87***	0.65***	233°	+0.64
Montespertoli 270°, 61 km 15/08/2010	C	10	0.80***	275°	+0.80***	0.58***	287°	+0.55
	MP	11	0.88***	287°	+0.84***	0.63***	269°	+0.63
Braccagni 326°, 106.3 7-10/08/2010 1/08/2011	C	16	0.89***	328°	+0.89***	0.56***	323°	+0.56
	MP	11	0.56*	305°	+0.54**	0.51***	319°	+0.51

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553 **Figure legends**

554 Figure 1. Schematic of the orientation of the bird to the pulse when placed in the pulse coil. The  
555 large arrow with the lightning bolt indicates the direction of the pulse. The small arrow indicates  
556 the orientation of the Earth's magnetic field (after (Holland 2010)).

557 Figure 2. Release from Chiesina Uzzanese. Tracks of control (C) and magnetic pulsed (MP) are  
558 reported in the left and right panels, respectively. Release and home sites are indicated by the  
559 white square and circle, respectively. Whithin the same panel different tracks are indicated with  
560 different coloured lines. The tracks are plotted over a Google Earth map.

561 Figure 3. Release from La sterza. Other explanations as in Figure 2

562 Figure 4. Release from Montespertoli. Other explanations as in Figure 1

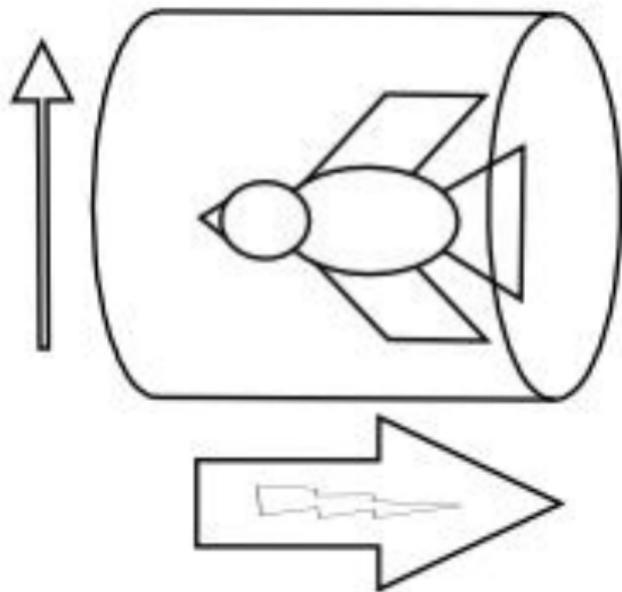
563 Figure 5. Release from Braccagni. Other explanations as in Figure 1

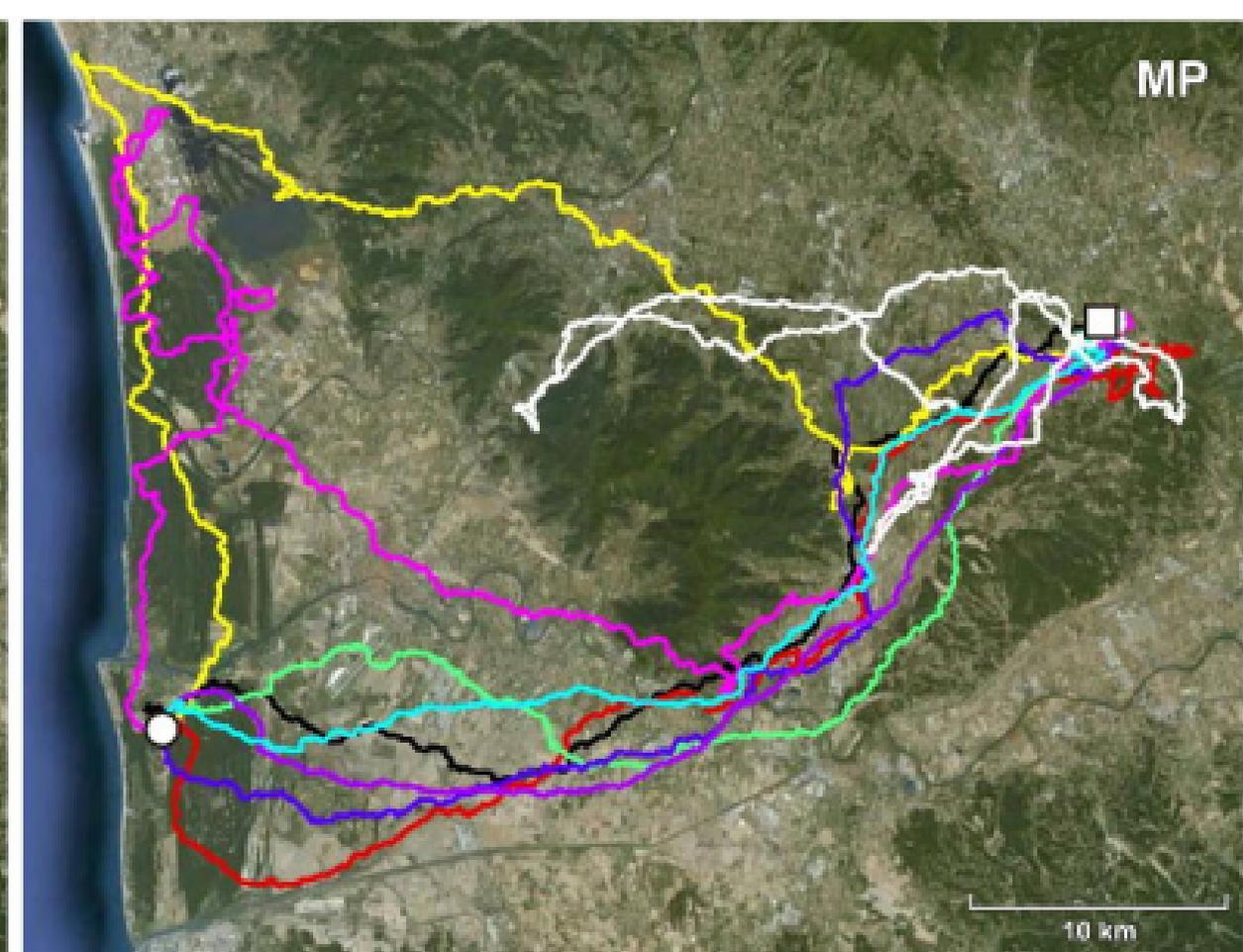
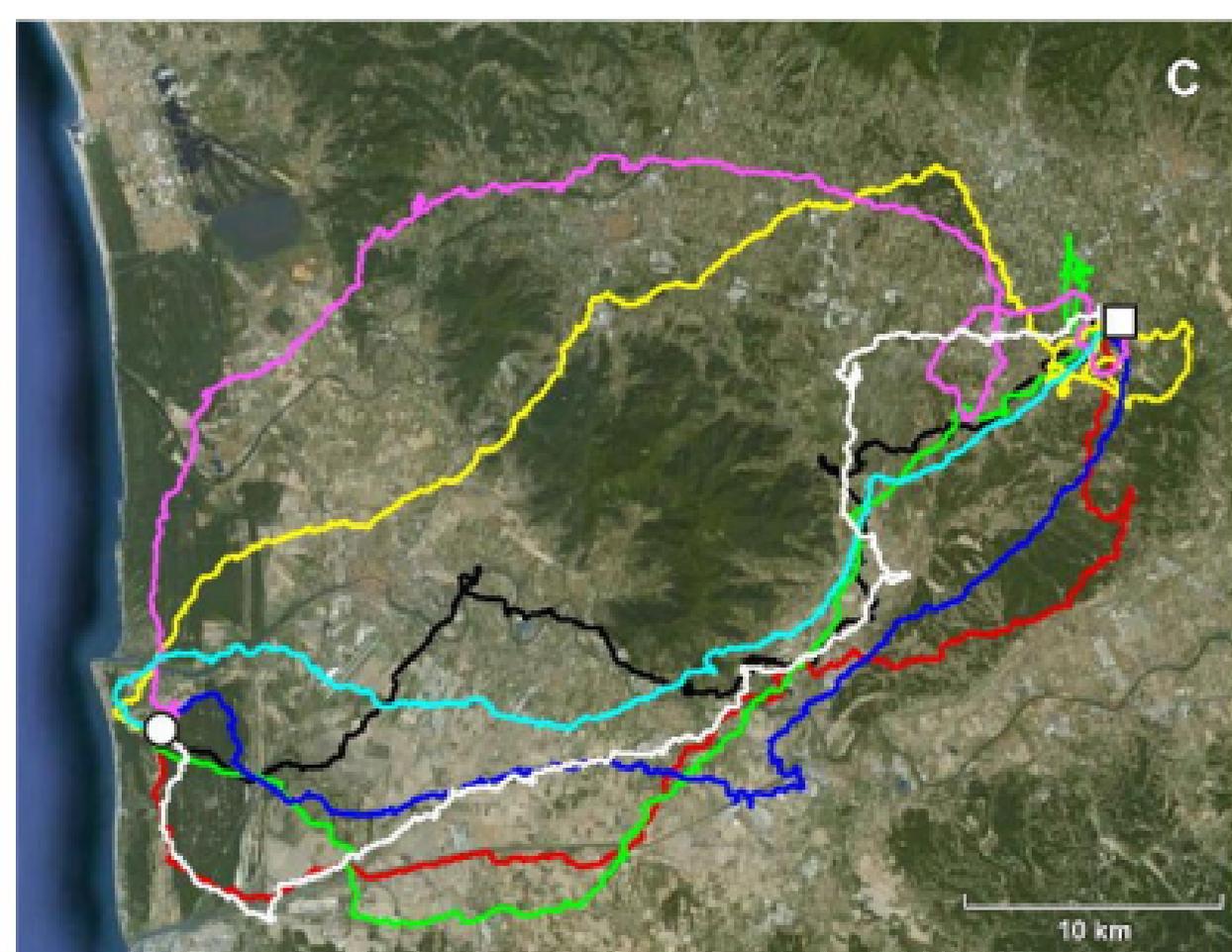
564 Figure 6. Distance from home plotted as a function of time for experimental and control groups  
565 at the four release sites. Control birds (C) are plotted in red and experimental birds (MP) are  
566 plotted in blue in all graphs.

567 Figure 7. Virtual vanishing bearings of C (open circles) and MP (filled circles) groups at each of  
568 the four release sites. Mean vectors are shown (C, open arrow, MP, filled arrow). Arrow outside  
569 the circle represents the home direction.

570 Figure 8. Initial orientation analysis performed on the section of the tracks recorded from 1 up to  
571 10 km distance from the release site. Each mean vector has been calculated from the directions  
572 taken by a bird while moving from one fix to the next (see material and methods for details).  
573 Second order mean vector length ( $r$ ) and direction ( $\alpha$ ) is reported for each diagram. Triangles  
574 outside each diagram represent the direction of the mean vectors plotted inside each circle.  
575 Confidence ellipses of the distributions according to the One Sample Hotelling test are reported:  
576 significance levels of  $p < 0.05$ ,  $p < 0.01$ ,  $p < 0.001$  are represented by the inner, intermediate and  
577 outer ellipses, respectively

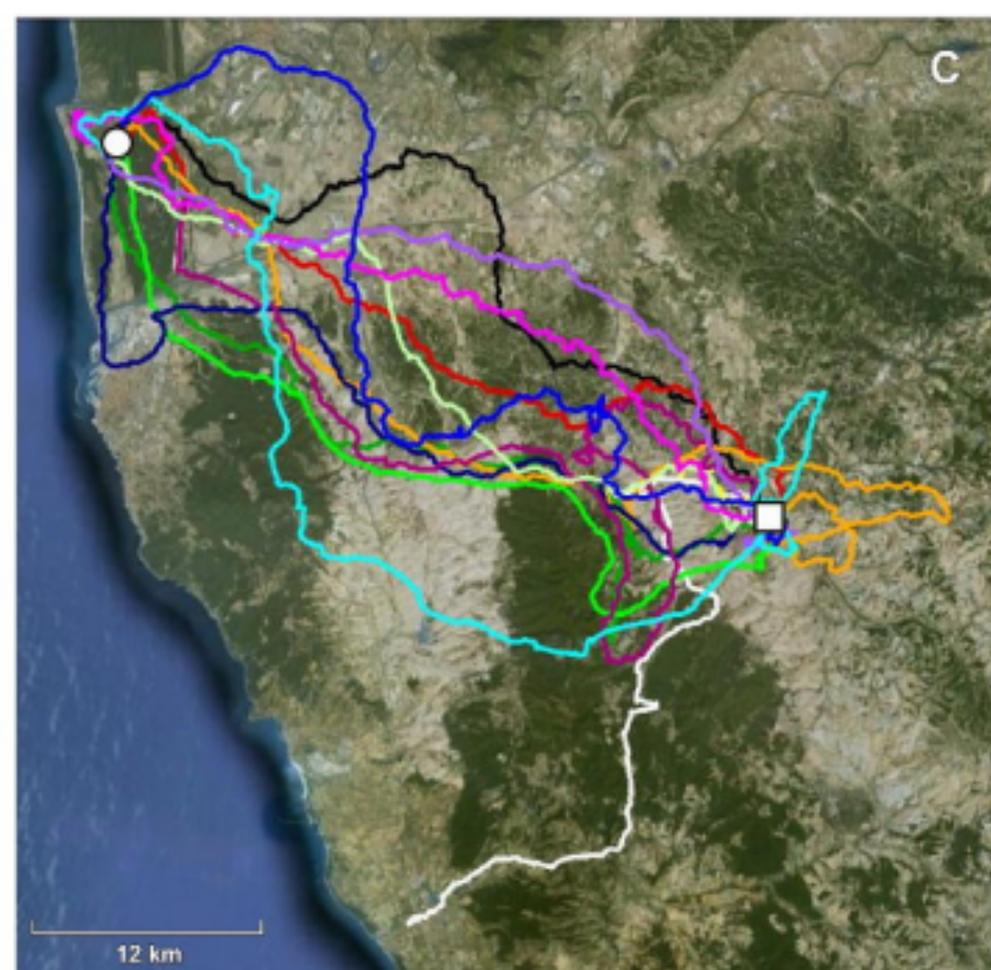
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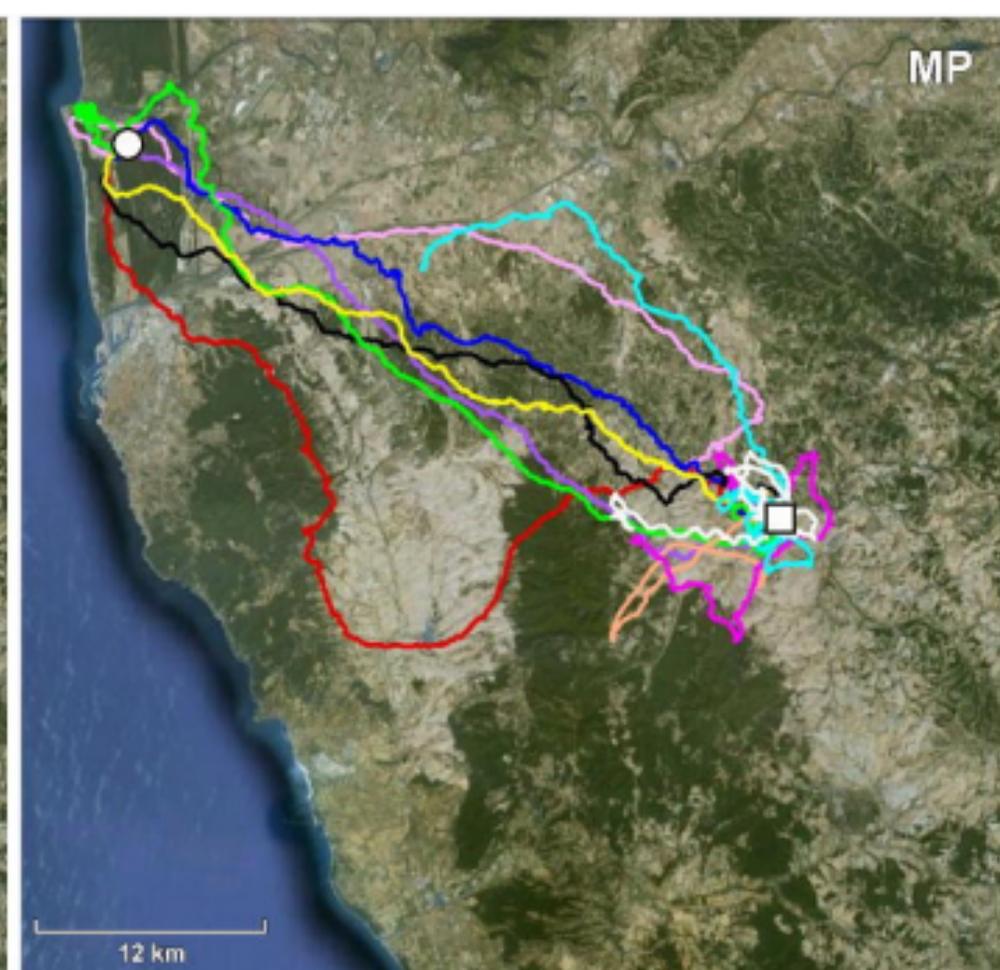


Chiesina Uzzanese

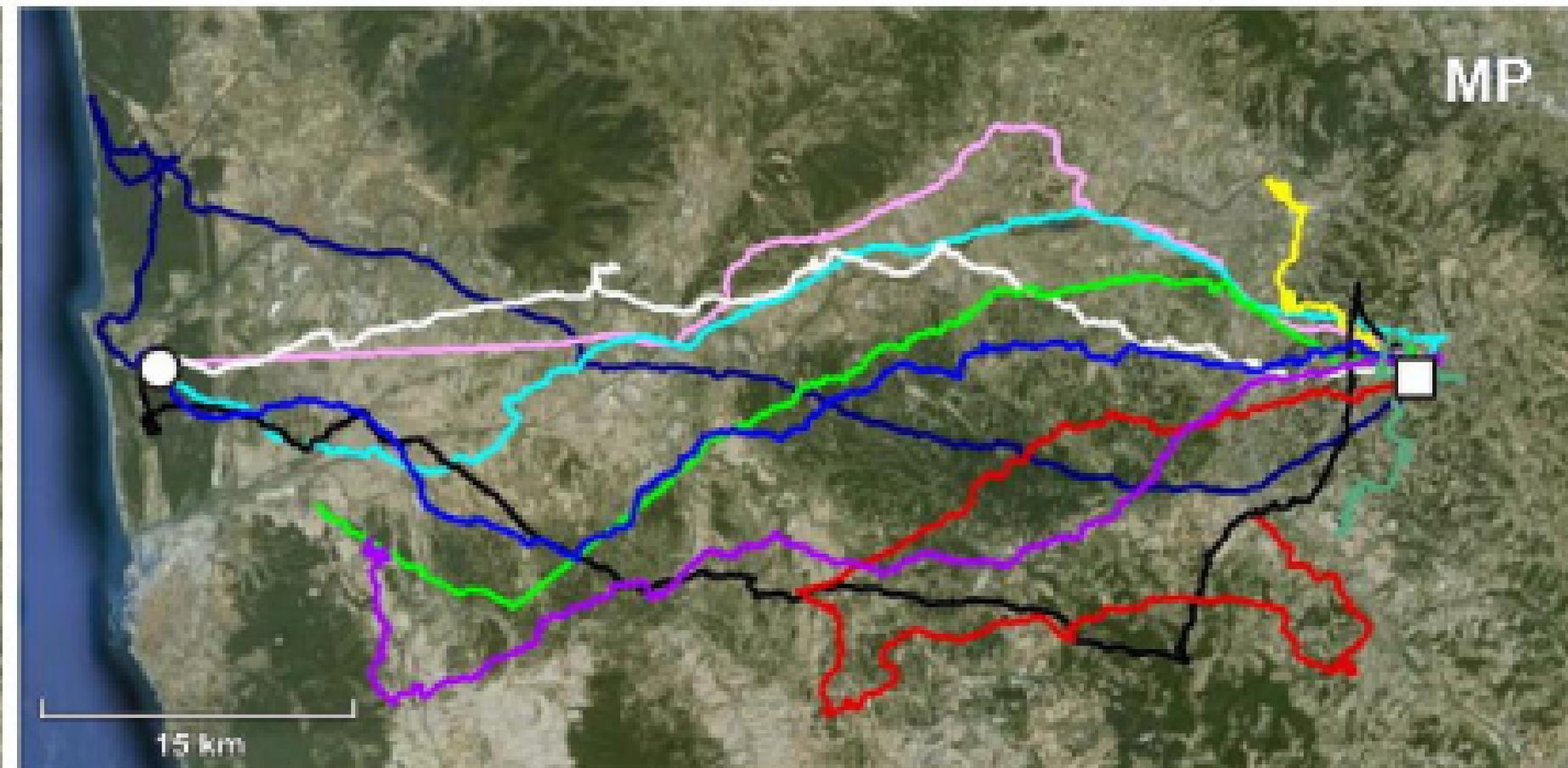
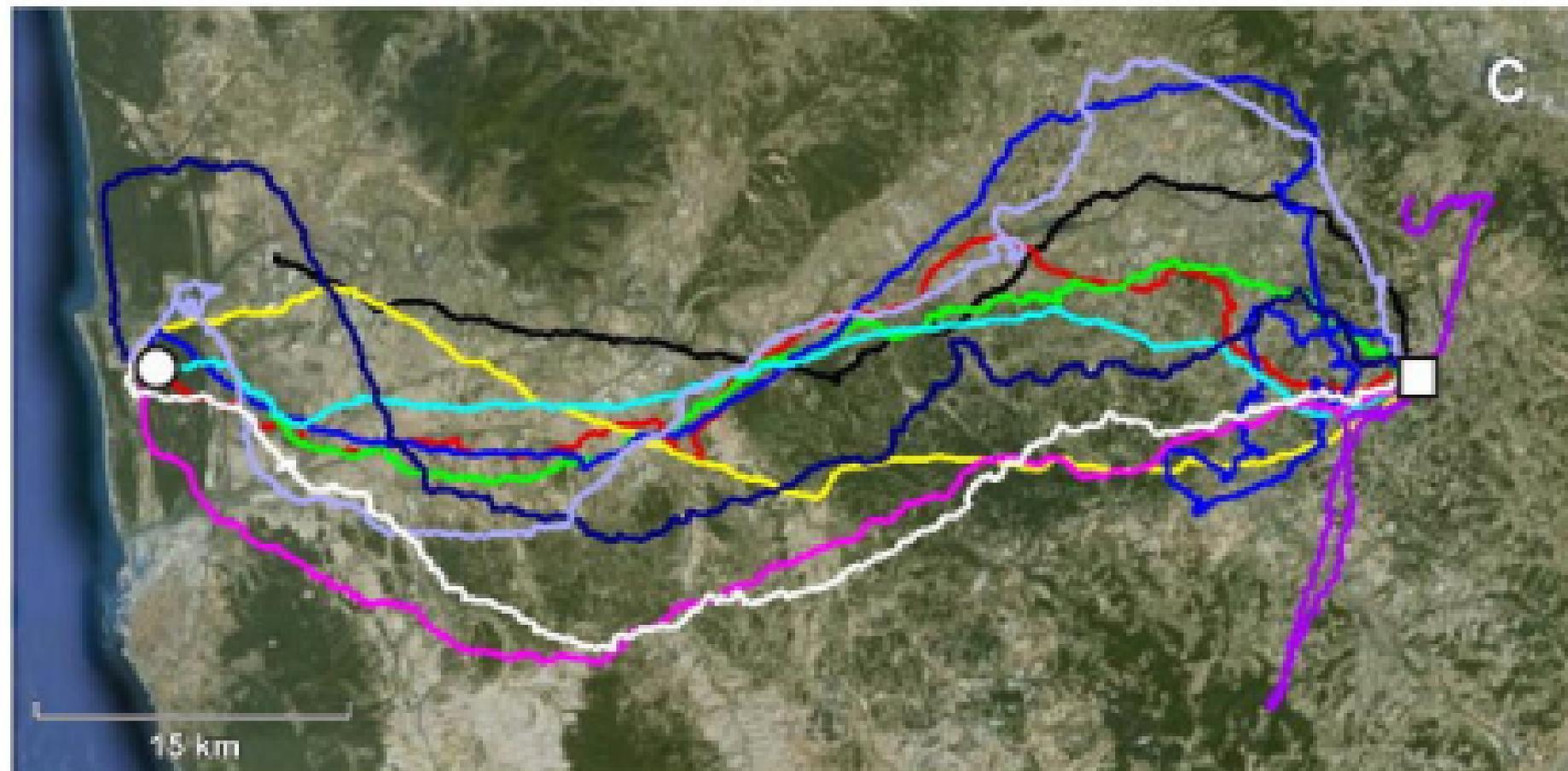
C



MP



La Sterza

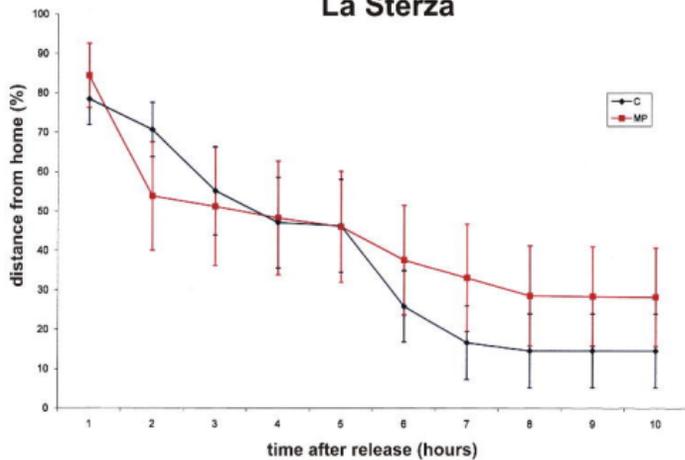


**Montespertoli**

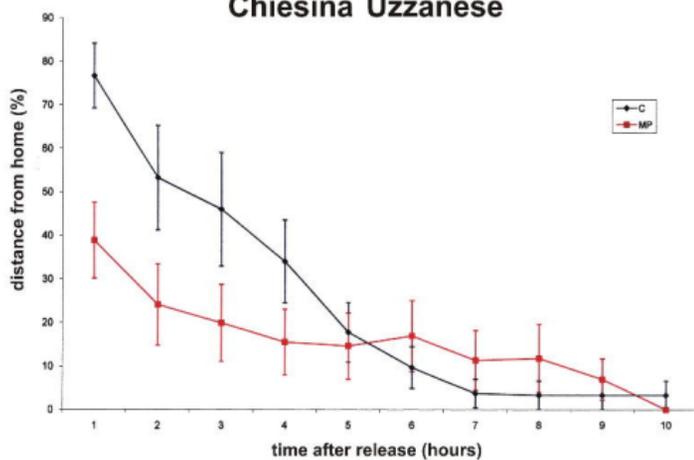


**Braccagni**

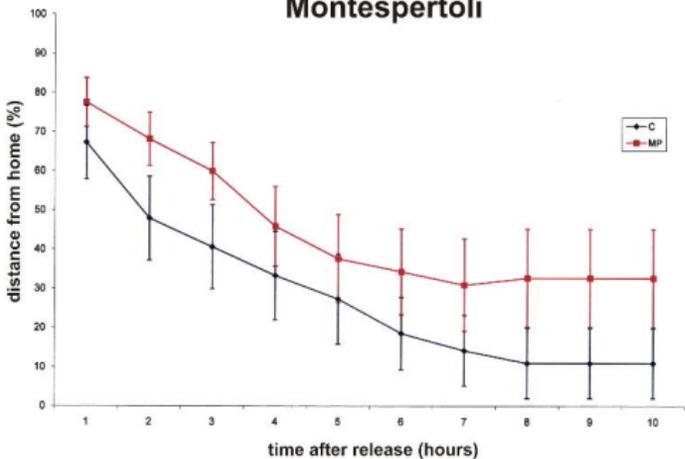
### La Sterza



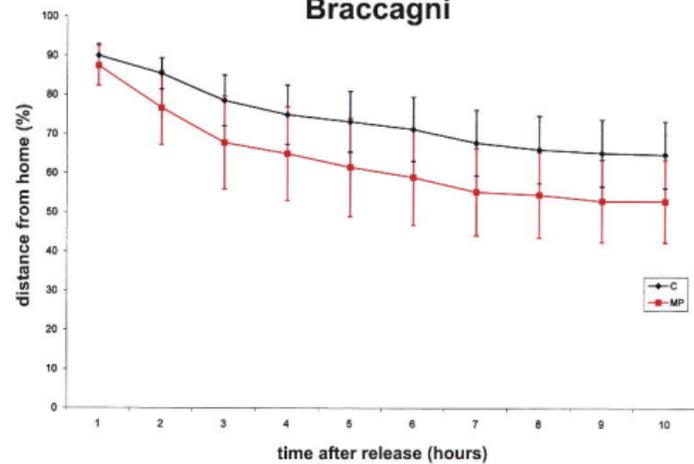
### Chiesina Uzzanese



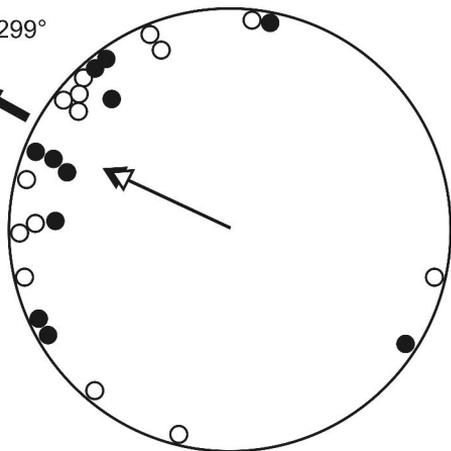
### Montespertoli



### Braccagni

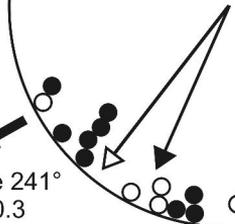


Home 299°  
km 39



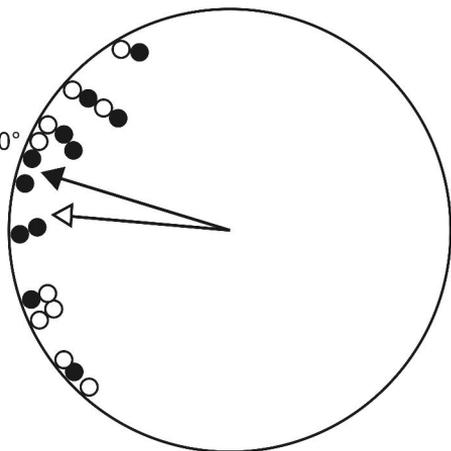
La Sterza

Home 241°  
km 40.3



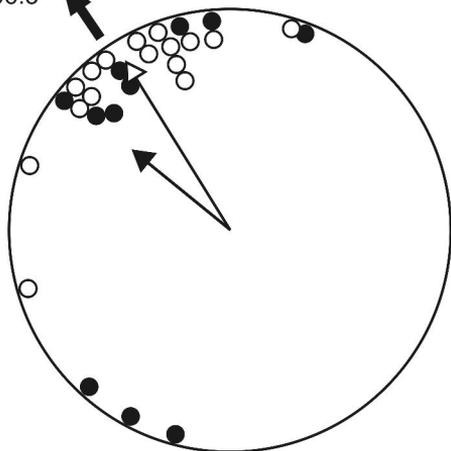
Chiesina uzzanese

Home 270°  
km 61



Montespertoli

Home 326°  
km 106.3



Braccagni

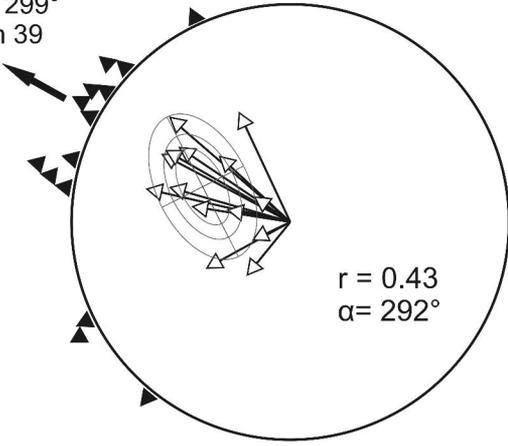
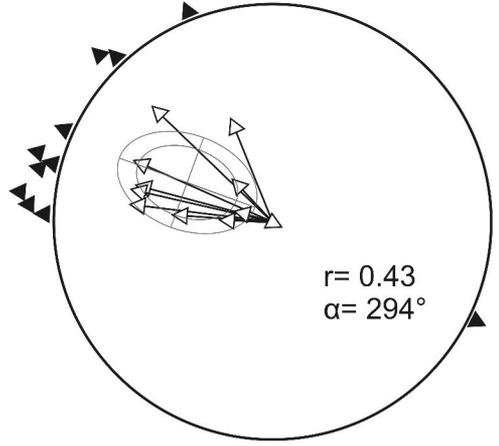
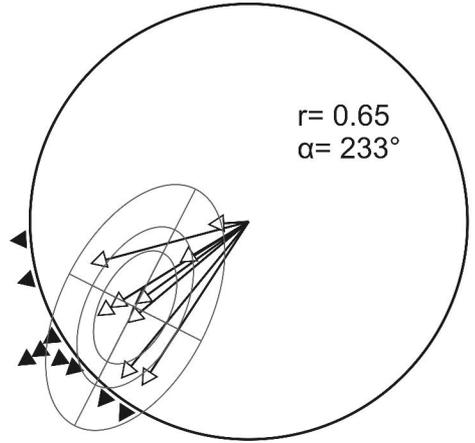
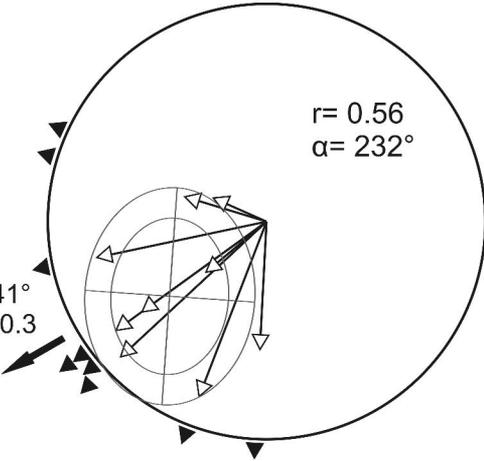
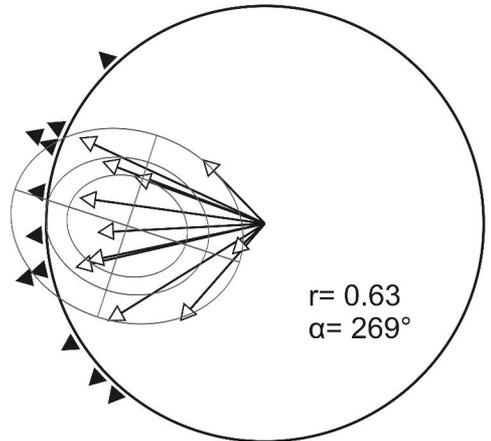
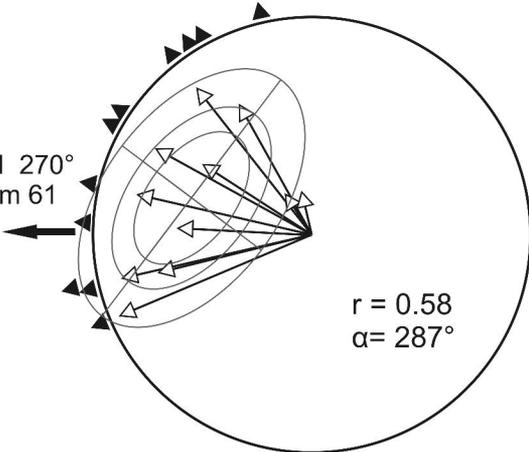
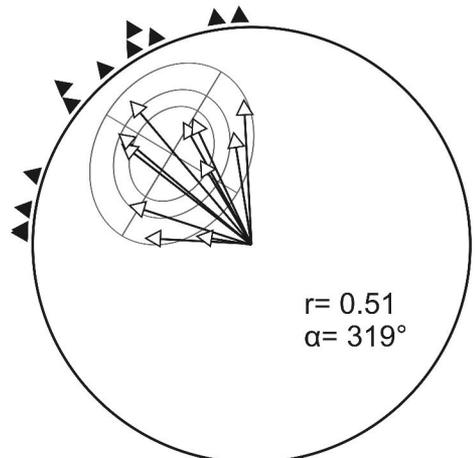
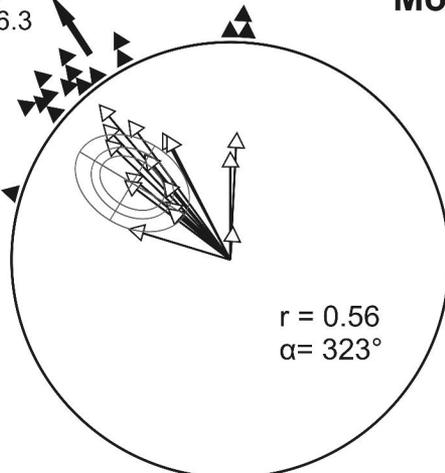
**C**H 299°  
km 39**MP****La Sterza**H 241°  
km 40.3**Chiesina Uzzanese**H 270°  
km 61H 326°  
km 106.3**Montespertoli****Braccagni**

Table 1. Homing success of birds released at the 4 test sites. Tr= treatment (C= control, MP=magnetic pulse). N=number of birds released, n=number of birds considered in the analysis.

RS	Tr	N	n	homed	lost	$\chi^2$
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Chiesina Uzzanese 241°, 40.3 28/07/2011	C	12	10	8	2	0.20 ns
	MP	12	11	9	2	
Montespertoli 270°, 61 km 15/08/2010 29-30/07/2011	C	17	17	16	16	0.47 ns
	MP	17	16	15	18	
Braccagni 326°, 106.3 7-10/08/2010 1/08/2011	C	38	38	22	16	0.01 ns
	MP	40	39	21	18	

Table 2. Initial orientation at the 4 test release sites. Tr= treatment (C=control, MP=magnetic pulse), r= mean vector length,  $\alpha$  = mean vector direction, hc=homeward component. \*= significance level \* $<0.05$ , \*\* $<0.01$ , \*\*\* $<0.0001$ .

RS	Tr	n	Virtual vanishing bearing			Mean Vector 1-10 km		
			r	$\alpha$	hc	r	$\alpha$	hc
La Sterza 299°, 39 km 29-30/07/2011	C	14	0.59**	295°	+0.59***	0.43***	292°	+0.43
	MP	11	0.64**	295°	+0.64**	0.43**	294°	+0.43
Chiesina Uzzanese 241°, 40.3 28/07/2011	C	8	0.80**	204°	+0.64**	0.56**	232°	+0.63
	MP	9	0.94***	218°	+0.87***	0.65***	233°	+0.64
Montespertoli 270°, 61 km 15/08/2010 29-30/07/2011	C	10	0.80***	275°	+0.80***	0.58***	287°	+0.55
	MP	11	0.88***	287°	+0.84***	0.63***	269°	+0.63
Braccagni 326°, 106.3 7-10/08/2010 1/08/2011	C	16	0.89***	328°	+0.89***	0.56***	323°	+0.56
	MP	11	0.56*	305°	+0.54**	0.51***	319°	+0.51