

RESEARCH ARTICLE

Gravity anomalies without geomagnetic disturbances interfere with pigeon homing – a GPS tracking study

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ABSTRACT

The gravity vector theory postulates that birds determine their position to set a home course by comparing the memorized gravity vector at the home loft with the local gravity vector at the release site, and that they should adjust their flight course to the gravity anomalies encountered. As gravity anomalies are often intermingled with geomagnetic anomalies, we released experienced pigeons from the center of a strong circular gravity anomaly (25 km diameter) not associated with magnetic anomalies and from a geophysical control site, equidistant from the home loft (91 km). After crossing the border zone of the anomaly – expected to be most critical for pigeon navigation – they dispersed significantly more than control birds, except for those having met a gravity anomaly en route. These data increase the credibility of the gravity vector hypothesis.

KEY WORDS: *Columba livia*, Orientation, Gravity-based navigation, Gravity vector, Horizontal component, Biological GPS, Navigation strategies, Object following

INTRODUCTION

There is currently widespread agreement that pigeons are able to determine and maintain flight (compass) directions based on solar (Schmidt-Koenig, 1960) and magnetic cues (Wiltschko, 2003), possibly also with the aid of infrasonic waves (Hagstrum, 2013). Following compass-aligned topographical features can help in maintaining a direction (Holland, 2003; Lipp et al., 2004). Yet choosing a direction requires determining current position from local cues (the map sense). The underlying mechanisms of the map sense are still debated. Potential candidates for large-scale maps are olfactory cues (Gagliardo, 2013; Wallraff, 2005; Wallraff, 2014) and parameters of the earth's magnetic field (Walker, 1999).

Gravity itself as a principal cue for the orientation process has barely been considered, except by Dornfeldt (Dornfeldt, 1991), who showed that gravity anomalies were the most important geophysical factor accounting for poor orientation and homing of pigeons. In line with his observations, an earlier study had reported a significant correlation between the pigeons' mean vanishing bearings and the day of the lunar synodic month, suggesting that subtle changes in gravitational forces may influence navigation (Larkin and Keeton, 1978). Köhler (Köhler, 1975) proposed a navigation mechanism by assuming that the pigeons were able to use the visual horizon line

for perceiving the difference between the horizontal plane at the home loft and the release site, thus implicitly assuming a role of the gravity vector. Kanevskyi et al. (Kanevskyi et al., 1985) used a helicopter to follow pigeons crossing a tectonic break associated with a gravity anomaly. The pigeons altered their flight paths when crossing the anomaly, some of them showing telemetrically assessed changes of the EEG. In contrast, a study of homing pigeons released within weak negative gravitational anomalies (salt domes) and outside of them could not find a correlation with the initial orientation (Lednor and Walcott, 1984).

Kanevskyi and colleagues explained their findings and the navigational abilities of migratory birds by the 'gravity vector' hypothesis (Kanevskyi et al., 1985). It claims that pigeons become imprinted to the gravity vector at their place of birth, and that this information is stored as a neuronal memory independent of the perception of the actual gravity vector (Fig. 1A, red dashed line). This would represent an analog to a mechanical gyroscope, which maintains the original inclination of the gravity vector plus the orthogonal horizontal plane after displacement – a special form of spatial memory. For example, a rapidly spinning gyroscope with a horizontal disc would preserve the orientation of both the vertical and horizontal plane at the place of activation. Depending on latitude, moving eastwards with such a gyroscope for about 100 km would result in a westward tilt of the horizontal disc by about 1 deg compared with the local plumb. Moving northeast by the same distance would again show a tilt of 1 deg but now towards the southwest. Thus, at any given point on the surface of the globe, a gyroscope (together with a local plumb) permits comparison of the angle between a virtual (memorized) and an actual gravity vector converging in the center of the globe. On the surface, the comparison of two such vectors allows for computing azimuth and distance to the point of departure. For a displaced pigeon, this implies that it always senses, under normal gravity conditions, the approximate home direction and distance. It may then find home by using either a map-and-compass strategy with the support of geomagnetic, olfactory, solar and topographical cues, or, temporarily, a gradient strategy of constantly monitoring a memorized versus actual gravity vector and reducing the difference. Obviously, such strategies are not mutually exclusive.

The gravity vector theory predicts that pigeon navigation should be influenced by gravity anomalies. Gravity anomalies result from the non-homogeneity of underground structures such as rocks with high ore content or tectonic breaks, causing a locally increased force of gravity, or by less dense structures such as salt domes or meteor craters, where the force of gravity is weaker. The gravity vector at a given point at the surface of the earth is described by two scalars: the vertical component pointing to the center of the earth and the horizontal component caused by laterally acting gravity forces.

The horizontal component can change the angle between the remembered and perceived gravity vector and thus cause navigation

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List of symbols and abbreviations

A-pigeon	pigeon released in the center of the gravity anomaly
C-pigeon	pigeon released at the control site
E	eotvos, horizontal component of the gravity vector (0.1 mGal km^{-1})
mGal	unit of gravity-dependent acceleration ($1 \text{ Gal} = 0.01 \text{ m s}^{-2}$)
mhg	horizontal gradient of the gravity vector (measured in E)

problems. In regions with homogeneous underground structures, the horizontal components cancel each other symmetrically (Fig. 1B). In such places, the local plumb coincides with the theoretically expected gravity vector towards the center of the globe, and a pigeon would correctly determine its position in relation to the home loft. However, in locations with asymmetrically distributed masses below the surface, the plumb deviates slightly from the expected direction to the center of the globe (Fig. 1C). This happens preferentially in the border zones of gravity anomalies (Fig. 1D). Depending on the direction and the tilt of the gravity vector caused by the underground masses, the pigeon miscalculates its position and distance to home, and is likely to choose a wrong home direction, except when the tilt of the gravity vector coincides with the home direction. In this case, the pigeon may simply misjudge the distance but has a good chance of finding the loft. Likewise, but depending on navigational strategies, pigeons crossing border zones of anomalies should show correction of their flight paths because a sudden change in the direction of the gravity vector may produce a conflict between the chosen direction and a perceived mismatch.

Between 2009 and 2012, we conducted a series of studies in the Ukraine analyzing the orientation behavior of pigeons in relation to gravity anomalies. The Ukraine was chosen because its central part contains massive and well-mapped gravity anomalies distributed in a predominantly flat countryside without any long-distance visual cues. In a first study (Blaser et al., 2013b), we could verify two predictions of the gravity vector theory: (i) pigeons raised in neighboring lofts yet on anomalies with different inclinations of the gravity vector showed different vanishing bearings, with wrongly departing birds maintaining that direction over long distances, and (ii) pigeons appeared to sense gravity anomalies as indicated by changes of their flight course. However, the gravity anomalies in that study were partially associated with geomagnetic anomalies. Thus, we set out to verify the findings in the first study but without the potentially confounding effects of geomagnetic anomalies.

In this study, we released homing pigeons (*Columba livia* Gmelin 1789) from within a circular gravity anomaly showing normal magnetic values. The Boltishka gravity anomaly was formed by a meteorite impact in the early Mesozoic era (Entin, 2011), which caused a crater of about 25 km diameter, filled with less dense material, and located in a flat countryside. This geological situation causes, on the one hand, negative gravity intensity values (-36 mGal , where $1 \text{ Gal} = 0.01 \text{ m s}^{-2}$; Fig. 2A) and, on the other hand, in the border zone (several kilometers from the center of the anomaly), strong changes in the horizontal component of the gravity vector (75 E , where $1 \text{ E} = 0.1 \text{ mGal km}^{-1}$; Fig. 2B), thought to be navigationally relevant. The magnetic variation in that region is very low, between 50 and 100 nT (Fig. 2C). The shape of the gravity anomaly is fully circular, ensuring that pigeons had to cross the anomaly along any flight direction chosen. If the pigeons headed directly to the loft after leaving the circular anomaly, they would meet a second gravity anomaly, this time arc shaped, characterized by an initial increase of about 12 mGal, followed by a decline to -30 mGal . Thus, we could expect that at least some pigeons would

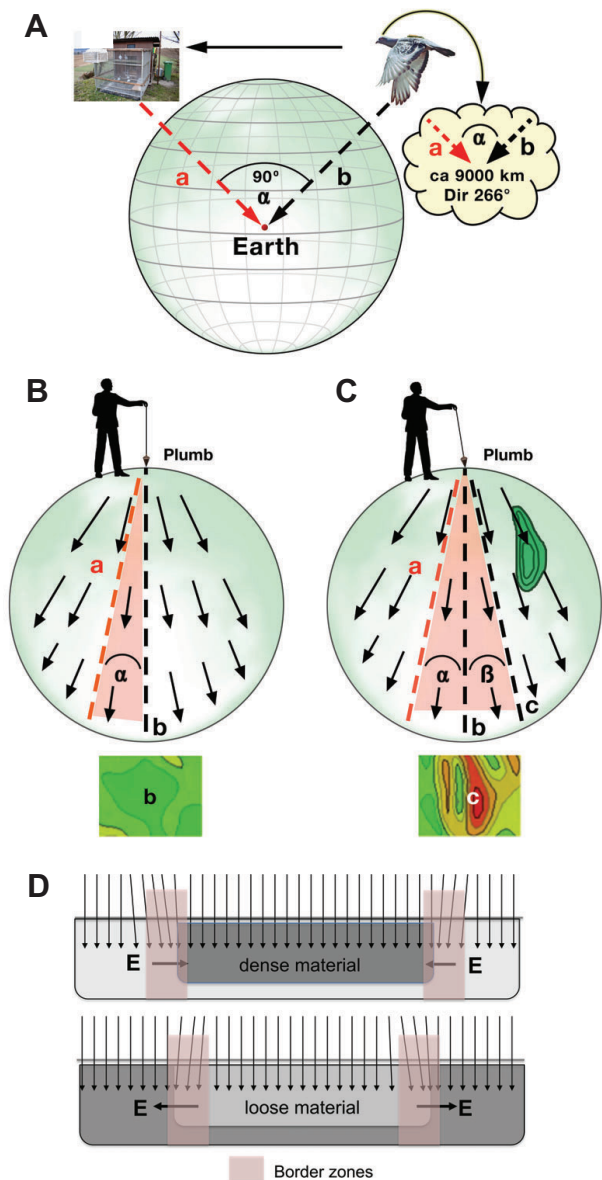


Fig. 1. Why pigeons miscalculate their position in border zones of gravity anomalies. (A) Basic assumption of the gravity vector theory: pigeons possess a neuronal gyroscope to remember the gravity vector at their place of hatching (red dashed arrow labeled a). The black dashed arrow (b) indicates the local gravity vector at the release site. The angle α between a and b indicates the distance, and the tilt of the local gravity vector with respect to the remembered vector indicates the direction (the graph shows only the distance angle). (B) At places with symmetrical distribution of lateral masses, the horizontal component of the gravity vector is balanced in all directions, and the plumb points towards the center of the globe. Maps of the horizontal component of the gravity vector indicate a normal direction of the plumb (color-mapped in green) – the pigeon calculates its position correctly. (C) At places with asymmetrical distribution of underground masses, the plumb deviates (dashed line labeled c) from the normal direction (b) by angle β (color-mapped in yellow/brown) – the pigeon miscalculates its position. (D) Schematic view of large positive and negative gravity anomalies. Within the central region, the horizontal component of the gravity vector does not change, even if the force of vertical gravity is much higher or lower than normal. At such places, the pigeon should determine its position correctly. In the border zones, however, the gravity vector is bent towards the dense material, pointing inwards or outwards, thus biasing the position determination of the pigeon. Color-mapping as in Fig. 2B shows the horizontal gravity gradient as measured in eotvos (E) but does not show the direction of the gradient, which must be deduced from gravimetric maps as in Fig. 2A.

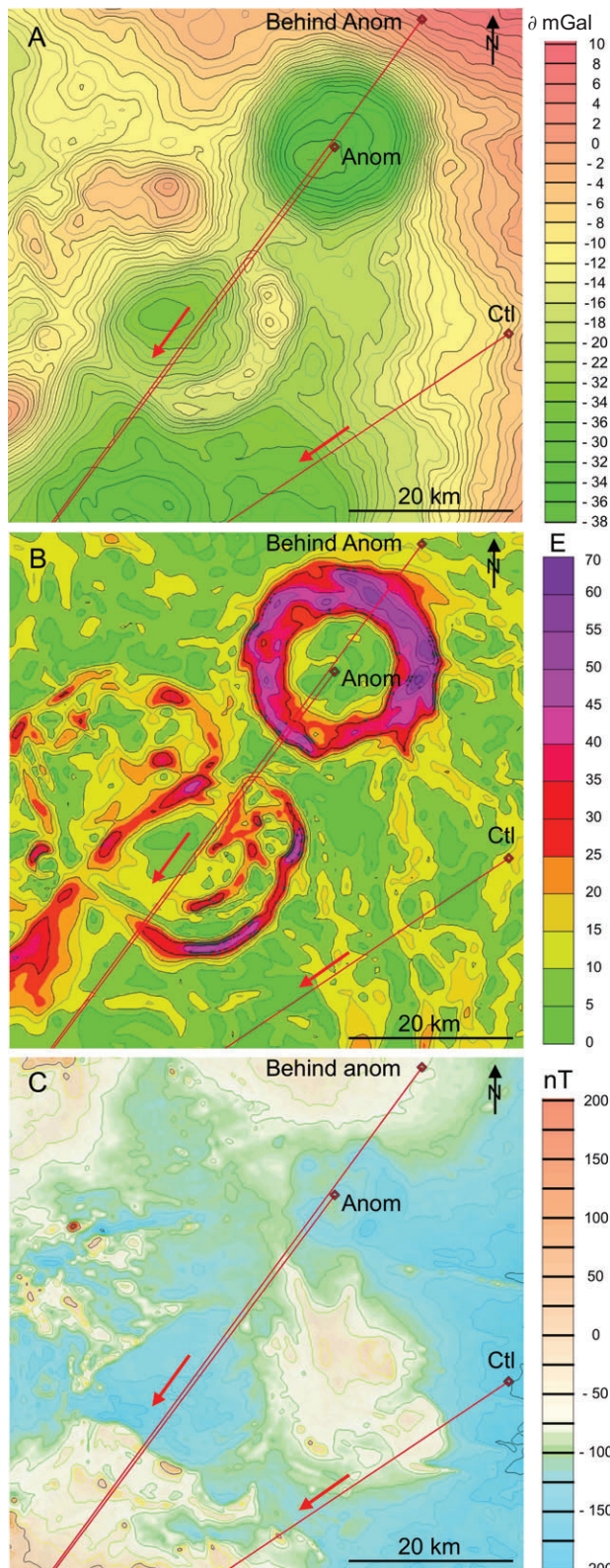


Fig. 2. Relationship between geophysical maps at the release sites and possible relevance for pigeon navigation. (A) Gravimetric map with isolines in steps of 2 mGal (1 Gal=0.01 m s⁻²). This map shows the vertical force of gravity, expressed as the difference (Δ mGal) from the theoretically expected force. The anomaly release sites are located within or behind a strong negative anomaly (Anom) with a steep gradient at the borders. The control site (Ctl) is located on a weak positive gravity anomaly. (B) Map of the horizontal component of the gravity vector color-coded for eotvos (E), isolines in steps of 5 E. The center of the anomaly shows no measurable horizontal gravity gradients. These occur at the border zone of the anomalies and coincide with the steep changes of the force of gravity (dense isolines in A). Local spots with high E-values may also occur in regions with moderate gravity anomalies. According to the gravity vector theory, high E-values bias the pigeon's calculation of its position. (C) Same region showing color-coding of geomagnetic variation in nanotesla (nT). The observed range at the anomaly and control release site is very small. Geomagnetic variations in the Ukraine can peak at 10,000 nT (see also Blaser et al., 2013b). Red diamonds indicate release sites; red lines are beelines between the release site and loft; red arrows indicate the home direction. For satellite maps of the regions, see supplementary material Figs S1 and S2.

pigeons cross the border zone of the anomaly, they experience a tilted gravity vector that might lead to an adjustment of their flight course. Control pigeons from the same loft were released from a site 31 km southeast of the anomaly. The home loft was located in Novoukrainka, 91 km southwest of both sites. We predicted (i) that the vanishing bearings of pigeons released in the center of the Boltishka gravity anomaly should not be different from those of the control pigeons, and (ii) that pigeons crossing the border zone of the gravity anomaly should show changes in their flight direction compared with the control birds.

RESULTS

Initial orientation after 2 and 5 km

Pigeons released in the center of the gravity anomaly (A-pigeons) showed a substantial scatter in their initial headings at 2 km (Fig. 3A; supplementary material Fig. S3A,B). Nine pigeons were oriented towards the loft in a southwest direction, six disappeared northwest and two pigeons headed to the east (Fig. 3A). The Rayleigh test (general unimodal alternative) revealed a random distribution of bearings ($r=0.35$, $P=0.13$), while the homeward component ($hc=0.30$) was low but still significant ($P=0.04$). Pigeons released at the control site (C-pigeons) were mostly heading in the same direction (Rayleigh test, $r=0.84$, $P<0.0001$), showing a strong homeward component ($hc=0.70$, $P<0.0001$). The two groups showed an almost identical mean vanishing bearing at 2 km. The flight times at 2 km distance from the release sites were not significantly different (anomaly, 6.4 ± 6.0 min; control, 4.9 ± 3.4 min; Mann–Whitney U -test). The statistical comparison of the directional scatter between the two groups revealed a significant difference at 2 km (Watson's U^2 -test, $P<0.01$).

After 5 km and still within the gravity anomaly, the homeward orientation of the A-pigeons flying southwest improved; the pigeons were now significantly oriented ($r=0.63$, $P<0.0001$, Rayleigh test) and were clearly homeward oriented ($hc=0.62$, $P<0.0001$), with only four birds maintaining a wrong course (Fig. 3B). The C-pigeons from the control site likewise showed a highly significant uniform distribution of their vanishing bearings ($r=0.91$, $P<0.001$, Rayleigh test) and were highly homeward oriented ($hc=0.90$, $P<0.0001$). Statistical comparison of the directional scatter between A- and C-pigeons showed a non-significant difference at 5 km (Watson's U^2 -test, $P>0.1$).

The initial dispersal of the tracks is visualized using a 3D gravimetric plot (Fig. 4A). The bulk of the pigeons released from the

cross the borders of this gravity anomaly, too. We did not expect a substantially different initial orientation of the pigeons released within the anomaly, as the center of the anomaly does not show a change of the horizontal component of the gravity vector, and because the navigationally critical border zone of the anomaly was several kilometers away from the release site. However, when the

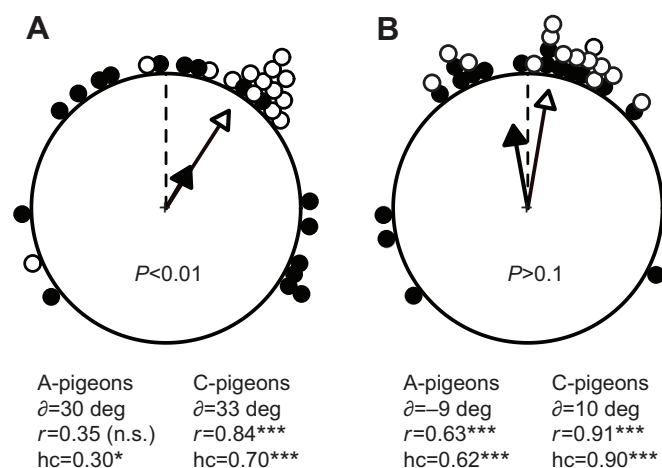


Fig. 3. Initial orientation of pigeons released in the center of the Boltishka anomaly and at the control site. (A) Position of the pigeons 2 km from the release site. (B) Position of the pigeons 5 km from the release site (still before the rim of the anomaly). The black circles refer to A-pigeons (released in the center of the gravity anomaly; $N=17$), the white circles to C-pigeons (released at the control site, $N=14$). Each symbol represents one pigeon. The bold arrows show the mean deviation ($\bar{\theta}$) from the home direction (dashed line) and the mean vector length (r) of the vanishing bearings, for A-pigeons with a black arrowhead and for C-pigeons with a white arrowhead. The home loft direction was normalized for both groups to north, the vanishing bearings were calculated as deviation from the homeward direction. hc is the homeward component. Significance levels for r refer to the Rayleigh test for unimodal uniformity, those for hc to the Rayleigh test with a specified mean direction. Significance levels within the circles refer to Watson's U^2 -test checking for common distribution of A- and C-pigeons. $^*P<0.05$, $^{***}P<0.001$.

anomaly converged into two main southwesterly directions out of the anomaly, one aiming at a zone of increased gravimetric values to the left of the beeline to the loft, the other to a zone of increased gravimetric values to the right of the beeline. We could not identify topographic features causing such channeling (Fig. 4B; supplementary material Figs S1–S3).

Dispersion of A- and C-pigeons

Fig. 5 shows the entire flight tracks of the pigeons released in the anomaly (Fig. 5A) and from the control site (Fig. 5B). A detailed view of the tracks on a 1:50,000 map of gravity anomalies (horizontal components) and geomagnetic anomalies spanning the entire region with all flight tracks is given in supplementary material Fig. S4A,B. Besides some aberrant tracks among the C-pigeons, the flight paths of the C-pigeons appeared much more aligned with the beeline from the release site to the loft than the paths of the A-pigeons, which showed a much wider dispersal (Fig. 5). A quantitative analysis of the closeness of the flight tracks to the respective beelines showed, indeed, that the pigeons released from the center of the gravity anomaly were dispersing widely with distances up to 55 km from the beeline (Fig. 6). The dispersal distances between the pigeons released at the gravity anomaly and those released at the control site were significantly different at distances of 25, 35, 45 and 55 km from the release site (Friedman two-way analysis for related samples $P<0.01$, followed by Mann–Whitney U -tests at different distances; significant values are indicated in Fig. 6). As eight pigeons were released from both sites, an additional analysis of the dispersal distances of these pigeons was performed with the Wilcoxon signed-rank test for paired data: the two pigeon groups were significantly different at distances of 45 and

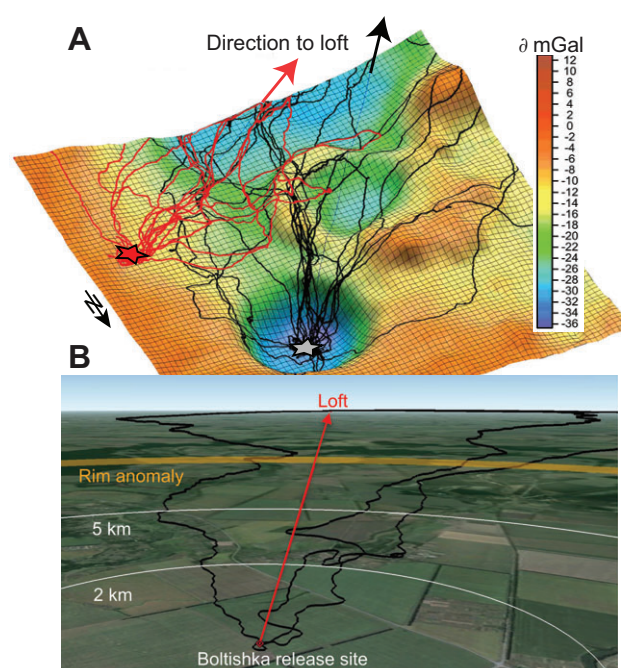


Fig. 4. Initial part of flight tracks of pigeons released from the center of the gravity anomaly and the control site. (A) The flight tracks are superimposed on a 3D-gravimetric anomaly map showing gravity intensity differences in δ mGal (see scale). A steep level change indicates that there is also a change in the horizontal component of the gravity vector. The gray star denotes the release site within the anomaly, the red star the control release site. Red arrow: home direction from control site; black arrow: home direction from anomaly site. (B) Perspective view of the topography of the release site indicating the lack of topographical guidelines. White lines at 2 and 5 km radius show the distances to the release site. The three tracks refer to pigeons b20, 401 and 489. The thick orange band indicates the approximate position of the rim of the gravity anomaly with high values of the horizontal component of the gravity vector. For a larger perspective view with identified pigeon tracks, see supplementary material Fig. S2, and for all tracks, see supplementary material Fig. S4. Picture provided by Google Earth Pro, Image 2014 Digital Globe, 2014 Cnes/SpotImage, Image 2014 CNES/Astrium and Image Landsat.

65 km ($P<0.05$) and the difference was almost significant at distances of 55 and 75 km ($P=0.055$) from the release site. The order of releases of pigeons with two and three tracks is indicated in supplementary material Figs S5–S7) and can also be found in supplementary material Table S1.

The quantitative analysis of all flight tracks did not show a significant difference in any of the track parameters of pigeons released within the anomaly and at the control site. The values of the flight track parameters of pigeons released within the anomaly were: path linearity, $94\pm1.9\%$; path efficiency, $58\pm17.0\%$; home efficiency, $65\pm13.5\%$; and GPS speed, 68 ± 7.2 km h^{-1} . The values of the flight track parameters of pigeons released at the control release site were: path linearity, $94\pm3.0\%$; path efficiency, $62\pm16.5\%$; home efficiency, 63 ± 16.9 km h^{-1} ; and GPS speed, 65 ± 5.5 km h^{-1} . The losses according to the release dates are shown in supplementary material Table S1.

Description of flight tracks

In order to understand the variation of the flight tracks, we made a detailed description of every track from both A- and C-pigeons (available on request from H.-P.L.), and summarize the findings here. In both A- and C-pigeons, one could recognize three

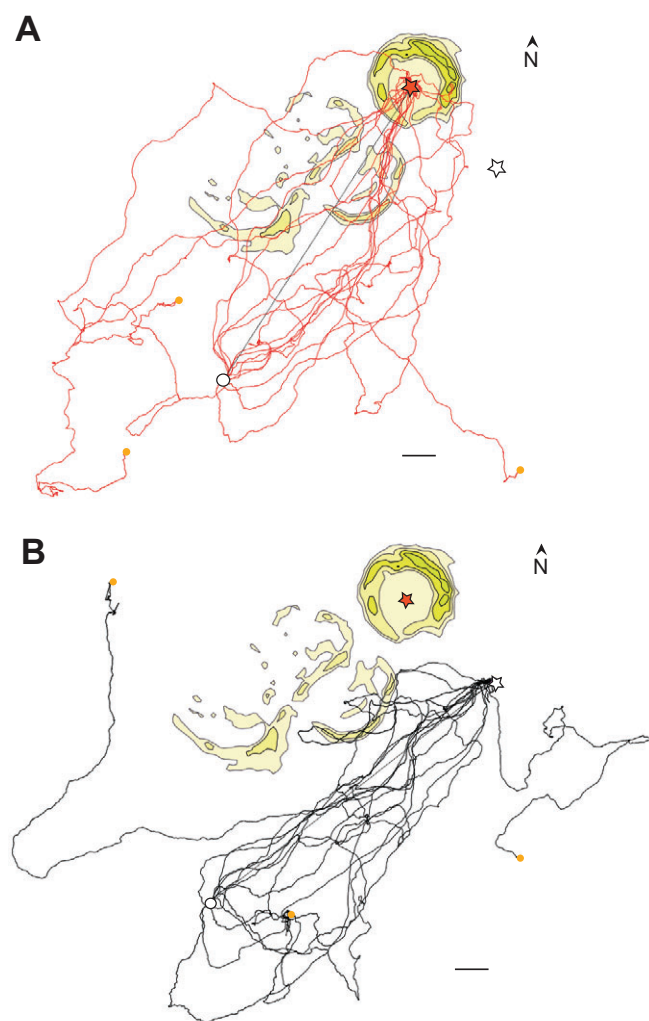


Fig. 5. Tracks of pigeons released from the center of the gravity anomaly (red star) and from the control site (white star). The white circle represents the home loft. The dotted line is the beeline from the anomaly release site to the home loft. (A) Seventeen pigeons flying from the anomaly site (red lines) and (B) 14 pigeons flying from the control site (black lines). Flight tracks are superimposed on a scheme of a horizontal gravity gradient map of the Boltshka anomaly (yellow). The contour lines of the gravity anomaly are in steps of 10 E. The brightness of the color denotes the anomaly intensity: light (20 E), medium (30 E), dark (40 E). Three tracks were disrupted because of exhausted batteries, indicated by orange dots. The scale bar is 10 km. For details, see supplementary material Figs S2–S7.

subgroups characterized by flight speed, directionality, deviations from the optimal flight path, and homing problems.

Description of flight tracks of A-pigeons

Efficient A-homers

After initial dispersal in the center of the anomaly, the tracks of seven A-pigeons (released on 12 and 24 August 2011) converged to a small band of about 1.5 km width in the border zone of the anomaly (supplementary material Fig. S3), almost perfectly aligned with the home direction. However, after 15 km, when entering the second gravity anomaly in their flight path and encountering further irregularly spaced gravity anomalies over 12 km, the tracks suddenly split into three directions without apparent topographic obstacles, after which the pigeons arrived home, taking different routes (supplementary material Fig. S8A).

Inefficient A-homers

A second group of seven A-pigeons (released on five different days) left the anomaly in different directions, adopting slower speeds after the release. Their tracks were characterized by many short-lasting directional changes, partly associated with topographic features, partly with gravity anomalies (supplementary material Fig. S8B). The seven inefficient homers showed a total of 20 stops.

Late A-homers

Three pigeons (b25, 451, b20) released from the anomaly showed tracks suggesting severe disorientation and returned to the loft 2–4 days later (supplementary material Fig. S8C). Two of them (b20, 451) followed the western ‘exit’ channel at the rim of the anomaly, aligned their flight partially along gravity anomalies, and passed the loft about 40 km northwest. Pigeon 451 terminated its flight after 210 km, 25 km northwest of the loft, while pigeon b20 (considered as the best bird by his owner) flew over 260 km to the city of Pervomaïsk and stopped its flight 40 km southwest of the loft. Pigeon b25 left the anomaly southwards and took a chaotic course ending 80 km away from its loft (supplementary material Fig. S8C, Fig. S5A). The three errant pigeons made a total of 22 stops.

Description of flight tracks of C-pigeons

The ensemble of the tracks from this site is shown in Fig. 6B. Supplementary material Fig. S9A (inset) shows that the pigeons there had been released within a small gravity anomaly of weak-to-medium strength. In general, the flight tracks converged much better around the beeline from the release site to the home loft than the tracks of the A-pigeons. A detailed analysis revealed again three groups of pigeons according to performance.

Efficient C-homers

Three pigeons (b20, 409, 451) left the control release site well oriented and maintained a straight homeward course along the beeline (supplementary material Fig. S9A).

Inefficient C-homers

Nine of the 15 control releases showed flight paths characterized by detours, partially associated with gravity anomalies (supplementary material Fig. S10), and by the tendency of the birds to fly along landscape features (supplementary material Figs S10, S11). Because of such flight strategies, their actual flight speed was mostly slower than that of the efficient homers, and they showed, as a whole, numerous stops. The most interesting flights were shown by three birds (441, 329 and b25, plus a failing homer, see below), which departed westwards towards the second gravity anomaly (supplementary material Fig. S9B, yellow tracks). Upon hitting the anomaly, they aligned their flight course to the rim for 20 km, and returned along the anomaly before they took a homeward course during which they often joined landscape features (supplementary material Figs S10, S11). There were no topographic cues explaining the changes of the flight path after hitting the anomaly (supplementary material Fig. S10). Other pigeons (b26, 311, 483, 411, 429, 323) deviated from the beeline southwards at different points, often following roads or river valleys that led them variable distances away before correcting homewards. An example of such object following alternating with compass flights is given in supplementary material Fig. S11. They also showed some directional changes associated with local gravity anomalies (supplementary material Fig. S9B).

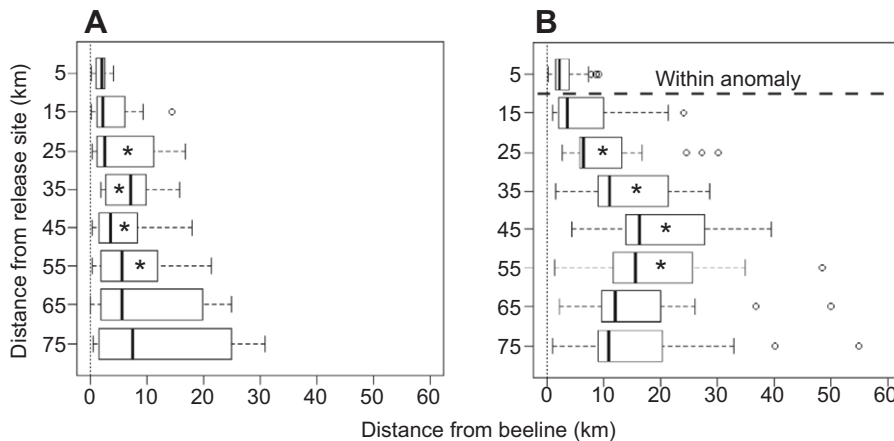


Fig. 6. The dispersal distances of the pigeons from a direct course to the home loft.

(A) Distances of the C-pigeons from the beeline in 5 km steps. (B) Distances of the A-pigeons from the beeline in 5 km steps. The horizontal dashed line in B indicates that the first 5 km are still within the anomaly. The values in both A and B are absolute values, i.e. disregarding the side of the beeline. The box ranges show the upper and lower quartile with the median, and whiskers extend to the most extreme data point no more than 1.5× the interquartile range. Points outside the range are outliers. The asterisks indicate significant differences between the C- and the A-pigeons (* $P < 0.05$, Mann–Whitney U -test).

Late C-homers

Three pigeons (329, 455, 488) that were initially well directed showed severe disorientation, all of them returning to the loft 1–4 days later after having faced gravity anomalies either at the beginning of their journey or after a prolonged flight (supplementary material Fig. S9C). (Detailed descriptions of tracks are available from H.-P.L.)

Releases behind the gravity anomaly

The four pigeons released 4 km behind the anomaly were initially all very well homeward oriented (Fig. 7B; supplementary material Fig. S5, Fig. S7C). One pigeon (b25) then changed course along the eastern rim of the anomaly continuing south and gradually homewards (Fig. 7A; supplementary material Fig. S5A), having shown a similar southerly deviation after crossing the rim of the anomaly when being released from the center of the anomaly. The other three crossed the northern rim of the anomaly mostly following the strongest horizontal gradients, resulting in transient directional changes, but corrected homewards within the center of the anomaly until they hit the second border zone of the anomaly where two pigeons deviated southerly (b20 and b26) and one pigeon more westerly (b31), which were also the two main flight directions we observed in the releases from within the anomaly. The southerly departing pigeons split courses within the gravity anomalies of the second anomaly, as observed before in many other pigeons after releases from the center of the anomaly. Notably, two pigeons familiar with the anomaly deviated again far to the west. Pigeon b31 flew 340 km to reach the loft (supplementary material Fig. S7C), while pigeon b20 got lost again for days (supplementary material Fig. S5C). (Detailed descriptions of their flight tracks are available on request from H.-P.L.)

Losses and meteorological conditions

During all releases, we lost eight pigeons that were released from within the anomaly and 11 pigeons that were released from the control site.

Based on the meteorological records and moon phases given in supplementary material Table S1, we could not identify a clear pattern for success, homing difficulties and losses, the latter being equal from the two release sites. There appeared a trend towards better homing on 29 July 2011, with few clouds but a northerly wind (10 km h^{-1}), and 12 August 2011, with more clouds and a northwesterly wind of 15 km h^{-1} . The most devastating losses (eight out of 10 birds) occurred on 28 August 2011, a day with moderate temperature, clear sky and no wind. For this day, a pigeon was later reported from Uman (a city 110 km west of the loft) as found but, unfortunately, the GPS device had been damaged by the finders so that no track was available.

DISCUSSION

Our data confirm the two predictions made: A-pigeons released from the center of a pure gravity anomaly not associated with magnetic anomalies were nearly as well directed before leaving the anomaly as the C-pigeons from the control site. Yet, they changed their course after crossing the zone with maximal horizontal gravity gradients, deviating significantly more from the beeline homewards than the C-pigeons. We could also replicate our earlier observation that changes in flight directions of both A- and C-pigeons appear to be partly associated with gravity anomalies, occasionally entailing severe disorientation. Taken together, the observed flight paths make it difficult to doubt that pigeons are sensitive to gravity anomalies, even when they are not associated with magnetic anomalies.

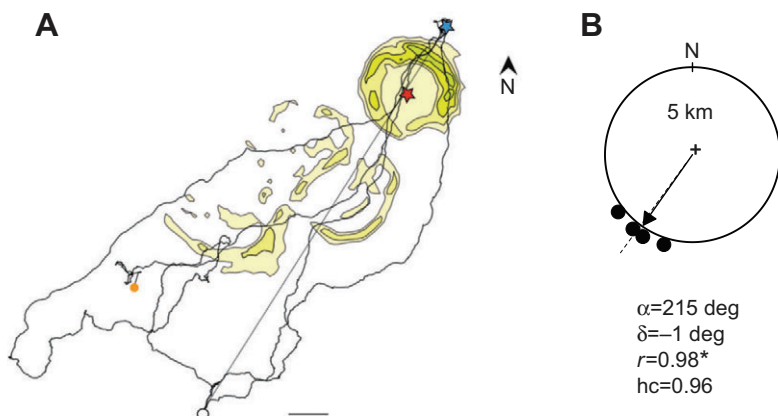


Fig. 7. Tracks of individual pigeons released behind the anomaly. Four pigeons (b31, b20, b26, b25) were released behind the anomaly. (A) The red star is the release site within the anomaly. The blue star is the release site behind the anomaly and the white circle represents the home loft. The tracks are superimposed on a scheme of a horizontal gravity gradient map of the Boltshka anomaly (yellow). The contour lines of the gravity anomaly are in steps of 10 E. The brightness of the color denotes the anomaly intensity: light (20 E), medium (30 E), dark (40 E). The small orange dot indicates a disrupted track. The scale bar is 10 km. (B) The position of the pigeons at 5 km from the release site. α is the mean vanishing vector, δ is the deviation of the mean vanishing bearing from the homeward direction and hc is the homeward component. According to the Rayleigh test, r is significant (* $P < 0.05$). For more details, see supplementary material Fig. S5 and Fig. S7C.

Initial orientation at the release sites

The pigeons seemed to be slightly disturbed when being released within the anomaly, vanishing to the northwest, southwest and east. The disorientation at 2 km could be an effect attributed to specificities of the release site, as geomagnetic values were low and the horizontal component of the gravity vector normal. Alternatively, the pigeons might have sensed the distorted gravity vectors at the rim of the anomaly at some distance. Based on other observations in the Ukraine, we cannot exclude the possibility that pigeons somehow and mysteriously perceive gravity anomalies at a considerable distance. Whatever the reason, after 5 km, the disturbance of most A-birds was overcome and the pigeons showed, as predicted, a clear and significant homeward orientation. In comparison, the vanishing bearings of the control pigeons were extraordinarily aligned to the homeward direction, in spite of the fact that this release site was located on a small gravity anomaly and was, like the A-release site, close to a small city. In judging the vanishing bearings at the center of the anomaly, we are inclined to give more weight to the dispersal pattern at 5 km from the release site. In our experience, directional orientation at 5 km from the release site indicates the characteristics of a release place more reliably.

Crossing the border zone of the Boltishka gravity anomaly

Most pigeons crossed the border zone towards the southwest, showing distinct yet rather discrete course directions when crossing zones of maximal horizontal gradients. We have no explanation for why these corrections converged in two visible southwestern 'exit channels' – the topography gave no clues for this phenomenon (supplementary material Figs S1, S2). However, release data from 2012 showed exactly the same pattern (H.-P.L., unpublished observations). Two pigeons, both of them flying initially eastwards, flew a large circle exactly in the border zone before heading south. Flying in circles is considered to show a positional uncertainty of the bird, and it is suggested that the bird determines its position again by flying in a circle. The same interpretation has been used for a similar behavior, turning around, observed in a variety of other animals such as ants (Wehner and Raber, 1979) and dung beetles (Baird et al., 2012). We are aware that circling may occur for other reasons, mostly when joining a flock of other pigeons. In such cases, however, circling lasts longer before the pigeon resumes its course. Interestingly, the behavior of the birds released behind the anomaly showed identical patterns. Being initially very well aligned, one pigeon (a late homer) deviated eastwards along the anomaly and headed south, as it had shown during the release from the center of the anomaly. Taken together, it appeared as though the pigeons were deriving some directional information from crossing the zone with maximal horizontal gravity gradients, and this was most evident soon after they left the anomaly zone. In particular, the pigeons leaving through the more western exit channel were prone to maintaining long and errant compass flights deviating westwards from the home direction, an observation confirmed by releases in 2012 (H.-P.L., unpublished observations).

Impact of gravity anomalies encountered en route

Perhaps the most impressive directional changes associated with gravity anomalies were observed for the C-shaped second anomaly lying across the beeline from the Boltishka release site to the loft. On this route, the birds had to cross a mosaic zone of positive and negative smaller anomalies, most of them with strong horizontal gravity gradients. Efficient homers released from Boltishka, being

on an apparently perfect course homewards, suddenly split courses as if they had encountered a topographic obstacle, none of which were visible on satellite maps (supplementary material Fig. S1, Fig. S7A). The birds were not flying together or following each other. Their subsequent route appeared to depend on either topographic features or unknown factors leading them away from the beeline over considerable distances before they corrected homewards. Whatever the reason, such splitting of tracks among fast flying pigeons at a given point has never been observed by us before. The northern rim of this C-shaped anomaly seemed to have seriously misleading properties, chiefly for the pigeons passing through the exit channel from the anomaly to the right of the beeline: they mostly followed the northern contours westwards, deviating further and further from the home direction, partially along a third large anomaly (Mala Vyska), while one pigeon zigzagged across the anomaly to leave it in an easterly direction. It should be noted that, in 2012, we had conducted releases from the Mala Vyska region that entailed high losses among pigeons from different lofts (H.-P.L., unpublished observations). The C-shaped anomaly was also associated with very unusual flight tracks of four control birds that, having deviated northward from their beeline, were hitting the anomaly while flying westward. Except for one pigeon changing course homewards when meeting the anomaly, they not only aligned to the rims of the gravity anomaly over longer distances but also flew back towards the release site, aligning partially again to the rims of the anomaly. Returning to the release site is a typical behavior of disoriented pigeons, and one of these got lost for 3 days.

Another (gravitomagnetic) anomaly associated with regular sudden changes in flight course was the westernmost turning point of all errant pigeons located near Tarasivka (supplementary material Fig. S12). This anomaly appeared like an invisible barrier for the probably exhausted birds. We believe that it did not contain positional information, as two disoriented pigeons had been resting there, one having arrived from the control site and one from the Boltishka anomaly; however, they resumed flight in opposite directions (supplementary material Fig. S12). Thus, it appears that this location provided a strong signal to the pigeons but induced an unpredictable change of course. Control pigeons deviating southwards from the beeline faced two other regions inducing navigational uncertainty. One of them was located in the small town of Rivne, harboring a smaller gravity anomaly in the neighborhood of an unusual point-like negative geomagnetic anomaly ['Mineta' (Entin, 2011)]. C-pigeons appeared to be stuck there for a long time (supplementary material Fig. S9B,C), even though the loft was only 20 km away. The other zone was a relatively strong gravity anomaly located 15–20 km south and southeast of the loft where a C-pigeon bounced back for a considerable distance (supplementary material Fig. S9C).

Confounding factors: individual flight strategies

Clearly, pigeons can adopt different flight strategies (Filannino et al., 2014) and pooling data from birds with different strategies for statistical analysis must be done with consideration. Variations in performance appeared to reflect a conflict between two homing strategies: compass flying and following topographic cues. Compass fliers were a minority of birds departing rapidly (even in the wrong direction), adapting a regular speed flight between 60 and 80 km h⁻¹ over long distances that appeared not to be modified much by topographic distractors such as rivers, villages, highways and railways (Guilford and Biro, 2014; Lipp et al., 2004). Compass fliers rely on idiosyncratic routes only when approaching the loft, or they

show a despair-like object-following behavior in the case of complete disorientation at the end of an errant flight. Examples of compass fliers were pigeons b20, b26, b31, 441 and 451. In our data, such birds either homed perfectly, reacting only minimally to gravity anomalies, or, after having chosen a wrong direction within the first 10–15 km, continued for a long distance and homed very late. Most pigeons, however, showed a mix of following landscape features and compass flying, and are termed here opportunistic fliers. Examples include pigeons b25, 311, 323 and 418. Opportunistic fliers appear to change their flight paths unpredictably, alternating between aligning their flight path to external cues seemingly ignorant of the homeward direction, then following for some time a steady compass course ignoring external cues, like the compass fliers (e.g. supplementary material Fig. S11). Again, the repeated alignment to landscape cues occurred more frequently during the later part of the homing flight. In our data set, these birds were those that reacted most clearly to gravity anomalies encountered en route. Finally, opportunistic fliers showed frequent rests, after which the birds resumed a different flight direction. While this mix of strategies facilitated qualitative detection of changes in flight paths related to gravity anomalies, it made a quantitative analysis difficult, particularly so because the other main distractors such as canopies and field roads are not digitized in the Ukraine. It should be noted that the distinction between compass fliers, which neglect features en route, and opportunistic fliers, which are reactive, may be related to the function of the pigeon hippocampus, as suggested by a recent paper: birds with hippocampal lesions were more likely to adopt a straightforward course while intact pigeons appeared to be more perceptive (Gagliardo et al., 2014).

Compass setting versus on-flight reading of gravity-related cues

The gravity vector theory holds that pigeons (and possibly other birds as well) are able to determine their position in relation to the home loft by comparing an actual gravity vector and its associated horizontal planes with a memorized one (Kanevskyi et al., 1985). This would allow two homing strategies: (i) the pigeons might calculate their position with a mental map and calculate a compass direction and flight distance homewards (Blaser et al., 2013a), or (ii) the pigeons might just try to minimize the perceived difference, reaching home automatically. Our data imply that pigeons might use both strategies, but that, at the release site, an initial map-and-compass mechanism is more likely. This is indicated by two observations. Firstly, some pigeons departed with high speed and without circling, heading almost perfectly homewards. In the case of sensing gradients, one would expect an obligatory period of circling to help determine the local distribution of horizontal gravity gradients as indicators of the inclination of the gravity vector. Secondly, pigeons headed for a long time in the wrong direction after having crossed the rims of the anomaly – some got lost for days. In the case of simple gradient-reduction strategies, pigeons should correct homewards soon after leaving an anomaly zone, and there should be no birds missing the loft. Another argument for compass use is the robustness of the sun compass (Wallraff, 2005). In the case of a gradient reduction strategy, such a mechanism would not seem necessary. However, the data here make it difficult to ignore the notion that the pigeons somehow sensed the presence of gravity anomalies encountered en route.

From the data obtained, it appears that the compass-setting mechanism is active for some distance (10–15 km) after release, otherwise the systematic deviations westwards after passing

through the second anomaly exit remain inexplicable. It remains unclear why hitting the second anomaly through this exit had such detrimental effects on homing performance even of experienced homers, but it appears that they must have suffered from a map orientation problem. Perhaps the best example is pigeon b20, which got lost westwards during its first release, showed perfect homing from the control site, and got lost again after being released from behind the anomaly (supplementary material Fig. S5C).

Gravity versus magnetic anomalies

The data show clearly that massive disorientation of pigeons may occur when they face gravity anomalies associated with negligible magnetic variation, certainly for the releases from the Boltishka anomaly. Thus, they confirm the analysis of Dornfeldt (Dornfeldt, 1991), who concluded that gravity anomalies are the strongest geophysical predictors of poor initial orientation and homing performance in pigeons, pure geomagnetic anomalies having the least impact. Our results are also compatible with the earlier negative findings with respect to orientation observed over negative gravity anomalies (Lednor and Walcott, 1984). The gravimetric anomalies (caused by underground salt domes) in this study were much weaker (–2 to –10 mGal) than the gravity anomalies reported here (–38 to +10 mGal) and no information about horizontal gravity gradients was given.

We do not ignore an additional confusing impact by magnetic anomalies (e.g. at the Tarasivka anomaly), as we assume that the pigeons are aware of the inclination and intensity of the Earth's magnetic field. We also assume that the perception of learned directional cues (including atmospheric information) was contributing to the erratic behavior of many pigeons encountering anomalies, because they conflicted with the actual position assumed by the pigeon. Without knowledge of the own position, most directional cues are of little use to the pigeons, which may explain the rather dramatic impact of gravity anomalies compared with other disturbed directional mechanisms. We are less convinced, however, that gravity anomalies are disturbing the map sense by altering the reference system (the gravity vector) against which a map sense based on magnetic inclination and intensity is calibrated. For one, there is sufficient experimental evidence that interfering with the magnetic sense of birds has sometimes visible but quite often no detrimental effects on navigation (e.g. Bonadonna et al., 2005; Moore, 1988). The other argument is, at present, of a conceptual nature only, but has often served as a guideline for developing theories: the gravity vector theory is the simpler and thus the more elegant one. The stumbling stone for both the gravity vector theory and the magnetic map theory is the extremely small angular differences that must be perceived and remembered by the bird's brain. But if this must be assumed for the magnetic map theories, there is no reason to exclude it for gravity vector-based navigation.

Conclusions

As expected by the gravity vector theory, releasing the pigeons from the center of the large anomaly had no significant impact on their vanishing bearings after 5 km. This implies that most birds had a normal position determination and compass setting towards their home loft when released within and behind the Boltishka circular gravity anomaly.

Pigeons seemed to be alert to changes in gravity gradients for about 10–15 km after the release. In this phase, anomalies appeared to induce new and often inappropriate compass

directions, as evidenced by the significant differences in dispersal of the tracks. Given that many birds did not return for a long time, this implies recalibration of the map and their own position during flight.

Reactions to gravity anomalies encountered en route (after course setting) were frequent but their magnitude appeared to be a personality trait: efficient compass fliers corrected rapidly or not at all, while navigationally distractible pigeons showed unpredictable and mostly erratic alterations of flight paths.

Most GPS tracks in the rim of the Boltishka anomaly showed temporary yet subtle corrections, with a few showing more distinct changes. Likewise, a lower number of GPS tracks showed clear alignment of flight paths along the contours of the second gravity anomaly. As the geomagnetic variation in these zones was very low, in the range of normal zones, these observations suggest that some pigeons can also show a strategy of following gravity gradients temporarily.

The high number of lost pigeons from control sites too implies that future studies should refrain from control releases in the vicinity of gravity anomalies, unless it becomes possible to track lost pigeons. Methodologically, one must also assess by GPS tracking all training flights of the experimental pigeons.

If the gravity-based map-and-compass theory of bird navigation is correct, then future releases from border zones of gravity anomalies that show maximal gravity gradients should entail strong and persistent directional changes and losses of birds.

MATERIALS AND METHODS

Pigeons and loft situation

We placed a former Swiss military pigeon loft near the city of Novoukrainka (48°16'21.78"N, 31°30'30.0"E). The topography around the area is flat with no visible beacons such as hills, high towers and distant mountains. The loft was populated with pigeons from local pigeon breeders 1 year earlier. The pigeons we used were mixed in sex, most of them were 1–2 years old with little flight experience, a few were 3–4 years old and were provided by the local pigeon breeder caring for the loft (mostly designated by the number prefix 'b'). They were mated and were in various stages of breeding. All pigeons were trained up to 20 km in flock and afterwards in pairs and then singly up to 60 km from the east. Early in the training phase, we mounted PVC dummies on the pigeon's back to accustom them to the mass and the size of a GPS logger. The PVC dummies stayed on the pigeons for the whole training period. The GPS loggers (GiPSy2, Technosmart, Rome, Italy) had a mass of 12 g and recorded the position of a pigeon every second with an average accuracy of about 4 m.

Ethics statement

The experiments were conducted according to Swiss regulations on animal welfare and experimentation, licenses 99/2008 and 92/2011 issued by the Zurich Cantonal Veterinary Office. Keeping homing pigeons and conducting pigeon releases with GPS in the Ukraine does not need governmental permission.

Maps

Details of the maps are shown in Fig. 2. The maps presented show gravitational anomalies (Δg_a) either expressed as reduced gravimetric values (Bouguer anomaly) obtained by pedestrian surveys in mGal (gravimetric map, Fig. 2A) or depicting the horizontal gradient of the gravity vector (mass \times height \times acceleration due to gravity, mhg), i.e. the horizontal change in the gravitational acceleration vector from one point on the Earth's surface to another (horizontal gradient map, Fig. 2B) (see also supplementary material Figs S3–S10, S12). This is customarily measured in units of eotvos (E): 1 E is 0.1 mGal km⁻¹. The magnetic anomaly maps (Fig. 2C; supplementary material Fig. S4B) show the intensity of the Earth's magnetic field in nanotesla (nT). In the Boltishka area, there is no concurrence of magnetic anomalies with gravity anomalies.

Experimental releases

Releases took place on different days to balance meteorological conditions and save GPS devices, the pigeons being released either at the anomaly or at the control site on the same days. We released pigeons within the Boltishka circular gravity anomaly (48°56'27.38"N, 32°14'32.49"E), 91 km northeast of the home loft. The control release site was 31 km southeast of the release site (48°44'17.51"N, 32°31'49.01"E) and also 91 km from the home loft. The direction from the experimental release site and from the control release site to the home loft was 217 and 236 deg, respectively. On five different days (26 and 29 July 2011, and 12, 24 and 28 August 2011), we released a total of 26 pigeons from the anomaly, of which 18 returned to the home loft (70%) and of which 17 tracks were recorded. We released 27 pigeons from the control site, of which 16 returned successfully (59%) and of which 15 tracks were recorded (supplementary material Table S1). Because of the losses, we had GPS tracks of only eight pigeons from both release sites. After the releases from within the anomaly and from the control site, on 29 August 2011, we released five pigeons 4 km northeast behind the circular anomaly at Ivanka, 111 km from the home loft (49°4'51.01"N, 32°23'13.95"E). The weather conditions at 06:00 h and the identity of the pigeons released that day are shown in supplementary material Table S1. The pigeons were released singly with 5 min intervals between releases, starting at 05.30 h to avoid the high summer temperatures during flight. After the return of the pigeons to the home loft, we collected the GPS loggers and downloaded the data to the computer with GiPSy2 software (Technosmart).

Analyses

Vanishing bearings were calculated manually from tracks in Google Earth referring to the first crossing of tracks with circles of 2 and 5 km radius from the release site. Vanishing time and flight track parameters were calculated from GPS tracks using the freeware program Wintrack (<http://www.dpwolfer.ch/wintrack>) (Wolfer et al., 2001). Circular data distributions (Batschelet, 1981) were analyzed with the statistical program Oriana (Kovach Computing Services, Pentraeth, Anglesey, UK) and with the R package for circular distributions (Pewsey et al., 2013). To quantify dispersal as a measure of navigational problems, we calculated the distance of the pigeons from the beeline to the loft. To this end, circles with radii from 5 to 75 km in steps of 10 km were drawn around the release site. The dispersal distance was defined as the length of the line (in km) that connected the point of a recorded pigeon track with the point on the beeline at the same distance from the release site. As eight out of 25 pigeons flew from both release sites, we additionally tested them with the Wilcoxon signed-rank test for pairs.

Analysis of flight track parameters of both groups was calculated with the freeware program Wintrack as described previously (Blaser et al., 2013a) (see also Appendix). In brief, it included path efficiency, homing efficiency, path linearity and GPS speed. Of the 17 recorded GPS tracks from the anomaly site, we could use 17 for vanishing bearing and vanishing time analysis, and 16 for the flight parameter analysis excluding one track because it showed many errors for position determination at the end of the record. Of 15 recorded GPS tracks from the control site, we could use 14 for vanishing bearings and vanishing time analysis. One pigeon paired with another pigeon while flying and therefore we calculated the two as one data point.

APPENDIX

Comments on maps

As the regions with the maximal E-values overlap with the steepest gradient of gravimetric values and might thus be of greater relevance for navigation, we prefer the horizontal gradient maps assembled by one of us (S.I.G.) after clearance of the formerly classified data in 2012. Detailed maps in 1:50,000 and 1:200,000 scales revealed numerous smaller gravity anomalies with horizontal gradients ranging from 10 to 40 E.

At the beginning of the studies, the control release site was thought to be in a region without gravity anomalies. However,

detailed maps that became available at the end of 2012 showed that the control site was located on the rim of a small gravity anomaly (up to 30 E; see also supplementary material Fig. S9A).

Details of release procedures

The evening before the experiment, two cars transported the pigeons to the two release sites. The crates with the pigeons were placed on top of the car with a view of the surroundings. Before sunrise, the crates were placed in an open field and the start of the pigeon releases was coordinated between the release sites to give similar flight times. The pigeons were released singly with 5 min intervals between releases. They were not tossed but were allowed to start spontaneously from the opened door of the release crate. This allowed assessment of their starting motivation. We started releasing at 05.30 h because the daily temperature rose very quickly after sunrise to above 30°C in the later morning, which increased the risk of pigeons pausing to avoid flying during the heat. After the return of the pigeons to the home loft, we collected the GPS loggers and downloaded the data to the computer with GiPSy2 software (Technosmart).

Details of analysis

Circular data

The scatter of vanishing bearings was assessed by the Rayleigh test for uniform distribution of vanishing bearings. The significance of the homeward component was calculated using the Rayleigh test for a specified mean direction. The Watson U^2 -test was used to reveal any differences between the groups at 2 and 5 km from the release site. Other group differences were assessed with non-parametric statistical tests.

Dispersal data

Group differences at a given distance were statistically compared using Friedman two-way analysis for related samples first, and then by pairwise comparison at different distances by means of the Mann–Whitney U -test. As eight out of 25 pigeons were flying from both release sites, we additionally tested them with the Wilcoxon signed-rank test for pairs.

Definitions of flight track parameters calculated with the freeware program Wintrack

Path efficiency, homing efficiency, path linearity and GPS speed

Path efficiency is the beeline distance between the release site and the home loft divided by the track length as a percentage. Homing efficiency adds the homeward component as a percentage of the track with a homeward component >75%. Path linearity is the sum of the ratio of the distance between two positions 32 s apart and the track length of two positions 32 s apart (in %) and shows how straight the pigeon's tracks were regardless of the home direction. The GPS speed is the ground speed in km h⁻¹ (without rests, i.e. speed <5 km h⁻¹). The parameters between the two groups were analyzed for any difference with the Mann–Whitney U -test. For the calculation of the flight parameter homing efficiency, three tracks from pigeons released from the anomaly ($N=14$) and three tracks of pigeons released from the control site ($N=12$) could not be used because the tracks ended outside of the home loft area.

Qualitative analysis of the flight paths in relation to gravity anomalies and topography

We checked every flight path using Google Earth's tour feature. This allows the flight path to be followed from a bird's eye perspective (altitude 300 m) and recognizes whether the pigeon aligned its flight to landscape features. We also superimposed flight tracks color

coded for speed in order to visualize flight speeds in different segments of the tracks. Color-coding of GPS flight tracks was done with the help of the website <http://www.gpsvisualizer.com>, using a sliding average of 5 s.

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Competing interests

The authors declare no competing financial interests.

Author contributions

H.-P.L. and V.K. conceived and designed the experiments; N.B. and H.P.L. performed the experiments; N.B., S.G., H.P.L. and D.P.W. analyzed the data; S.G. and V.E. assembled geophysical maps and analyzed pigeon tracks; N.B. and H.-P.L. wrote the manuscript; H.-P.L. created the supplementary graphs.

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Supplementary material

Supplementary material available online at <http://jeb.biologists.org/lookup/suppl/doi:10.1242/jeb.108670/-DC1>

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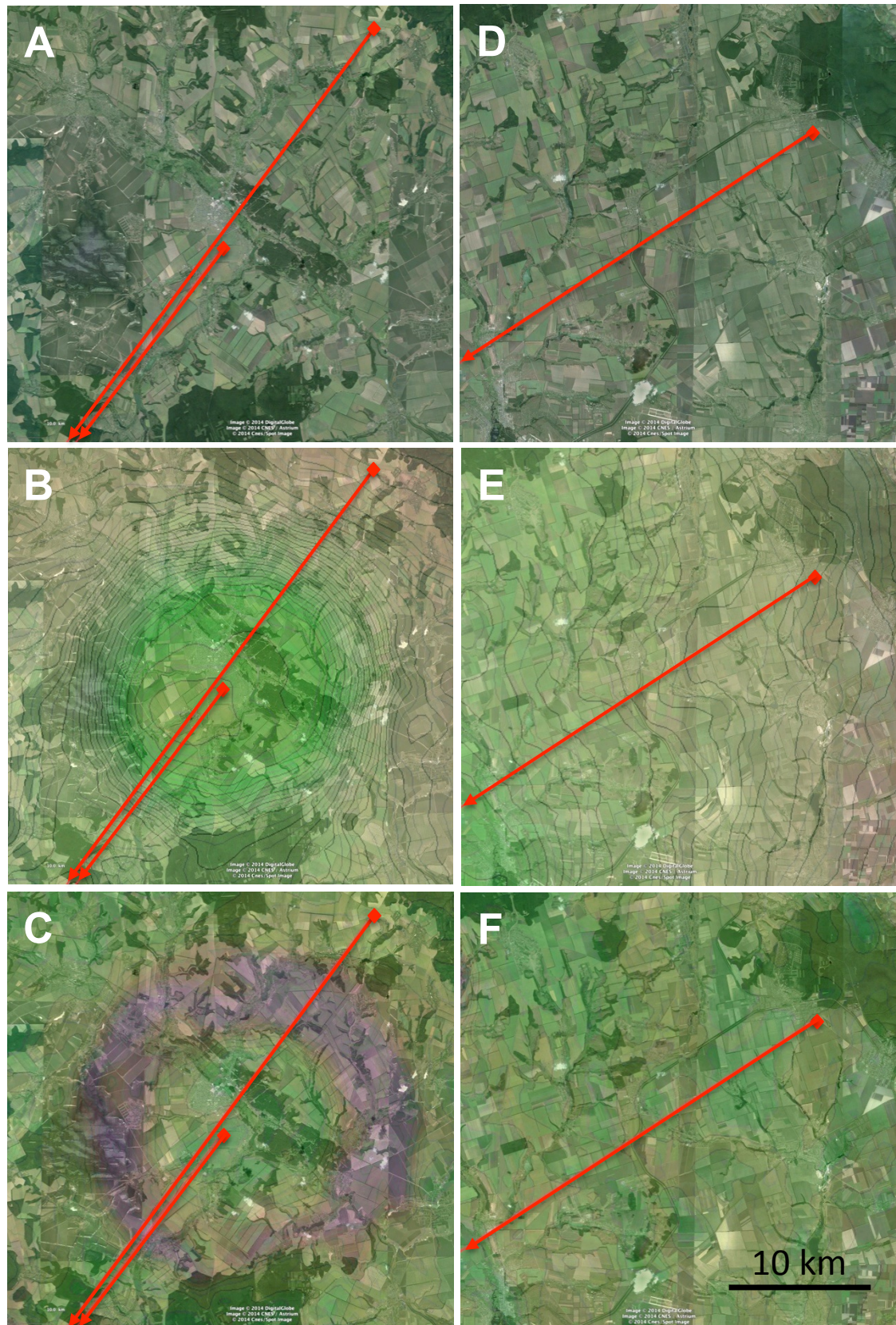


Fig S1. Transparent gravity anomalies superimposed on Google Earth pictures reveal lack of associated landscape features. A) Release sites (red diamonds) and home directions (red arrows) within and behind the Boltishka gravity anomaly. The small city is Oleksandrivka, see also Fig S3. B) Overlap of Google Earth picture with gravimetric values (dG) of Boltishka anomaly. C) Overlap of Google Earth picture with horizontal gravity gradient corresponding to the rim of the gravity anomaly of Boltishka anomaly. See also Fig. s S2 – S6, and S8-S10). Note the lack of landscape features influencing flight directions of the pigeons. D) Google view of control site at Bogdanivka. There is also a small city in the neighborhood, and railways. E) Overlap of Google Earth picture with gravimetric values (dG) at Bogdanivka. F) Overlap of Google Earth picture with horizontal gravity gradient at control release site (see also Fig S5A). Google Earth Images from 2014 Digital Globe, 2014 CNES Astrium and 2014 Cnes Spot/Image.

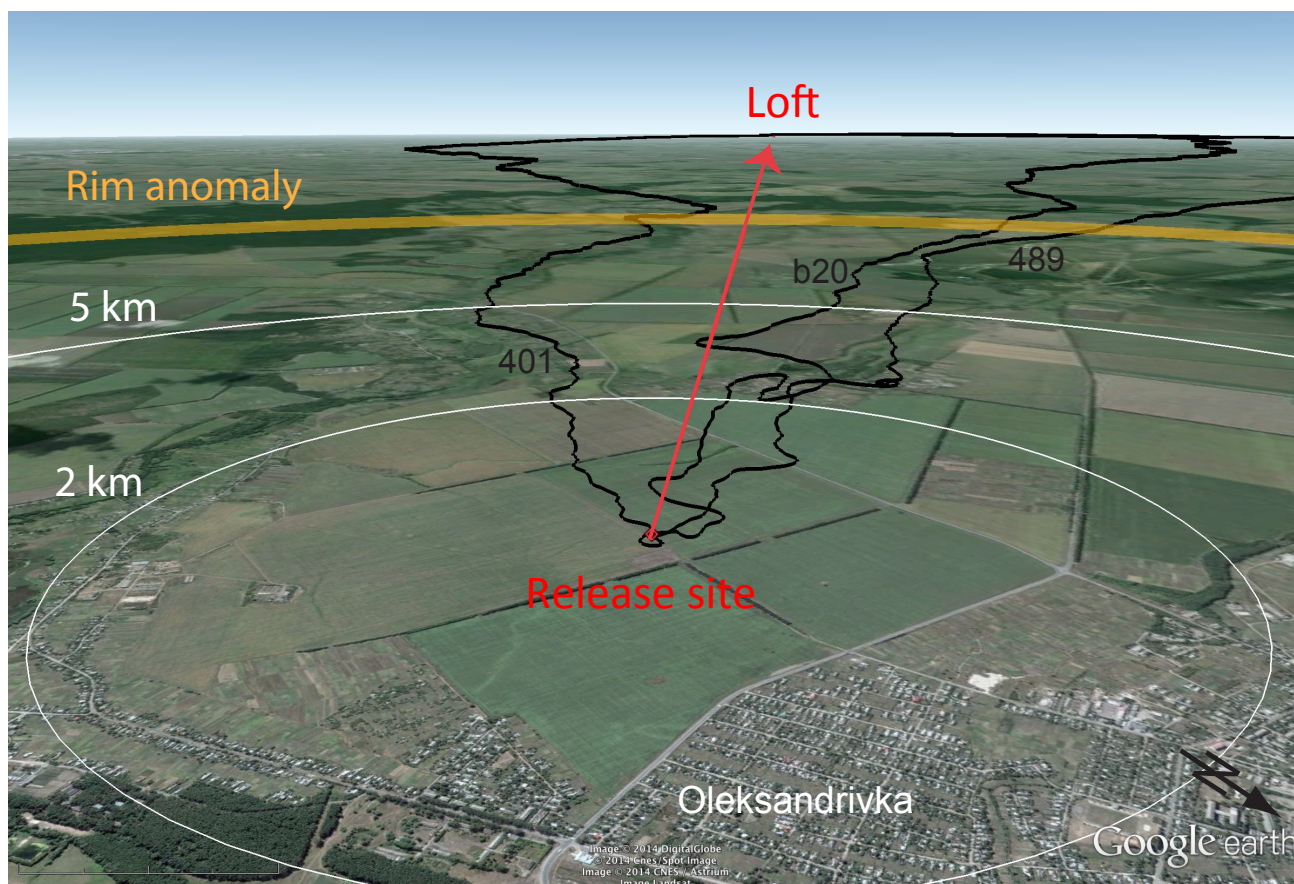


Fig S2. Large perspective view of Boltishka anomaly release site with three pigeon tracks. Orange line: approximate position of rim of gravity anomaly. Pigeon **401** follows the eastern of the two SW “exit channels” from the anomaly, pigeons **b20** and **323** follow the more western “exit channel”. For details of tracks see also Fig. S5C (track 1 of **b20**), Fig. S6A (track 2 of **323**) and Fig. S8A (**401**). Picture provided by Google Earth Pro, Image 2014 Digital Globe, 2014 Cnes/SpotImage, Image 2014 CNES/Astrium an, dImage Landsat.

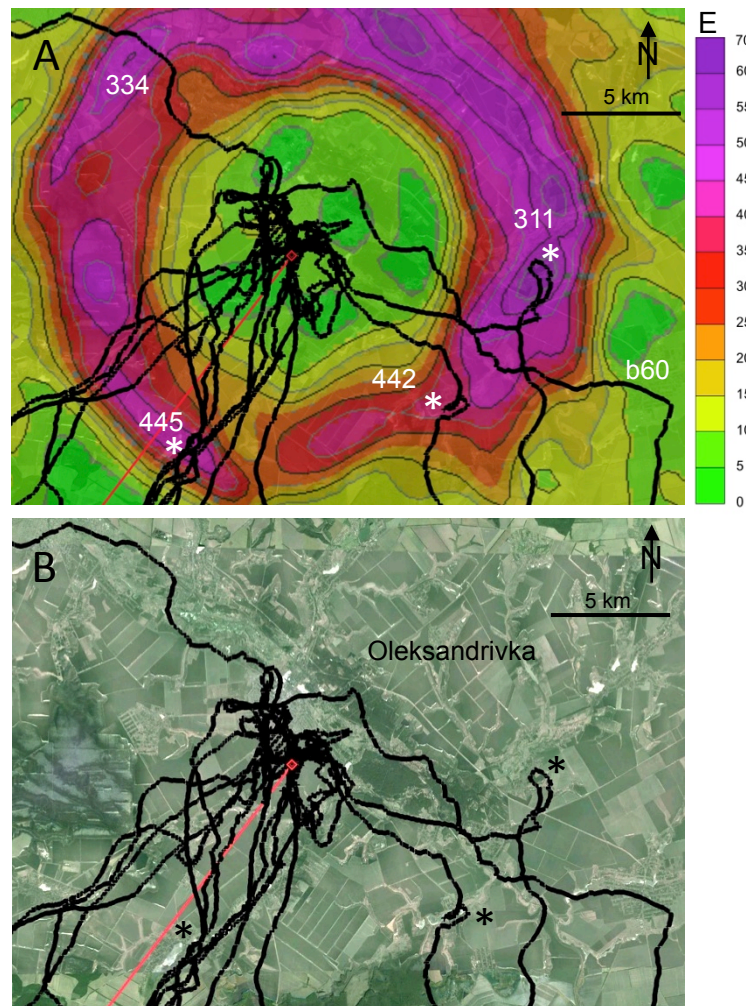


Fig. S3. Flight tracks of pigeons released from the center of the anomaly and flying across the rim of the anomaly. A) Upon approaching the rim of the anomaly with stronger horizontal gradients (yellow to purple), most pigeons changed course to cross the anomaly. Well oriented birds made minor changes, their tracks converging towards the home direction, ineffective homers (see Fig. S5B) showed more distinct directional changes, sometimes with circling. B) Satellite view of the release region indicating lack of prominent landscape features guiding pigeons. Asterisks: pigeons showing circling at sites of maximal gravity gradients. White numbers refer to individual pigeons. Red lines indicates the beeline between release site and loft. Color scale/isolines: horizontal gravity gradient in eotvos = E . . Google Earth Images from 2014 Digital Globe, 2014 CNES Astrium and 2014 Cnes Spot/Image.

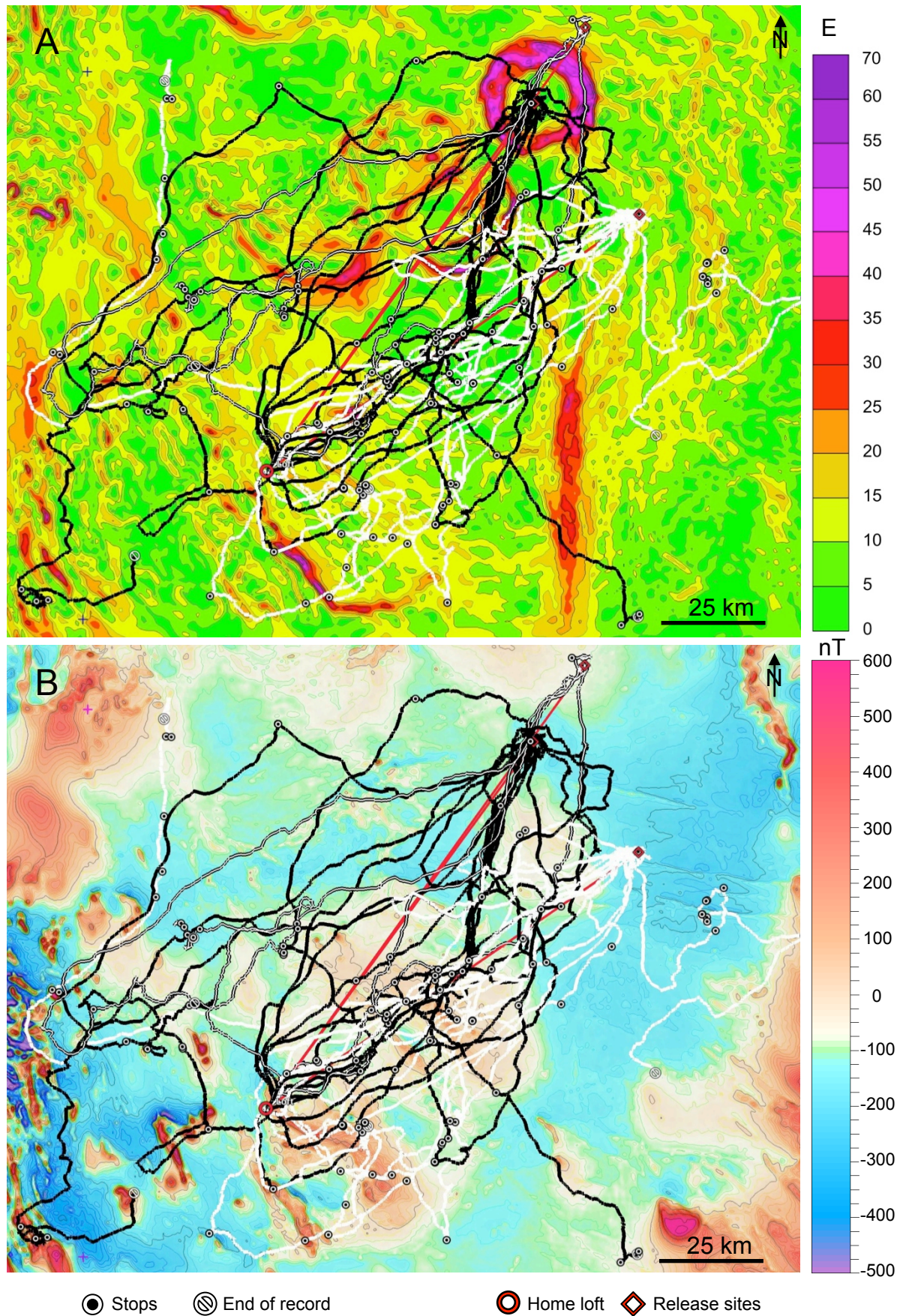


Fig S4. Overview of all GPS tracks on magnetic and gravity anomaly maps. A) Gravity anomaly map (1:50'000) showing the distribution of gravity anomalies according to gradients in their border zones – the steeper the gradient (E), the darker the color. Color scale/isolines: horizontal gravity gradient in eotvos = E. B) Geomagnetic variation across the entire track region, nT = nanotesla. White tracks: control releases; black tracks, releases from center of Boltishka anomaly; black-white tracks: releases behind gravity anomaly. Red lines: beelines between release site and home loft. The westernmost turning points are shown in detail in Fig. S12.

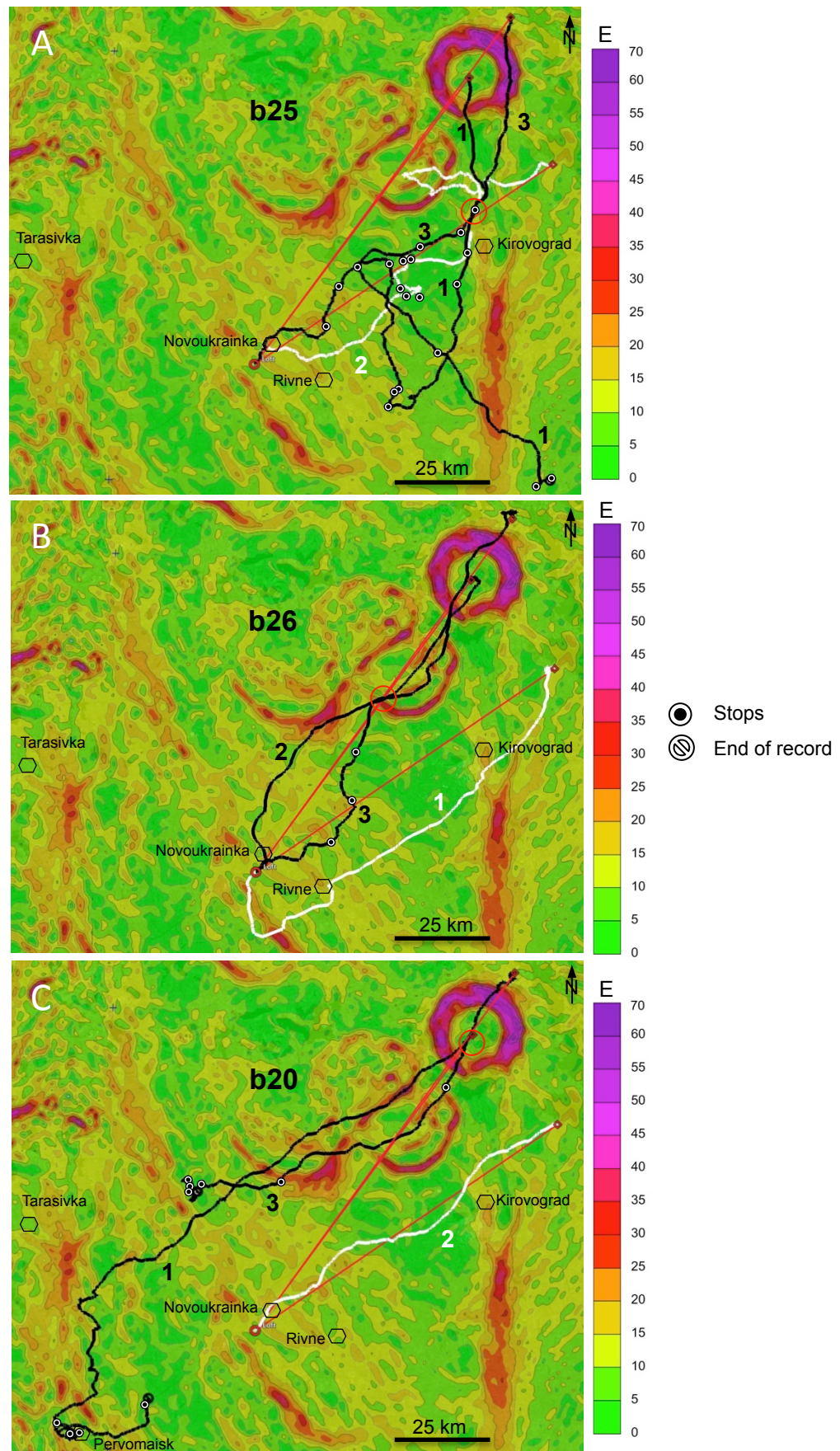


Fig S5. GPS tracks of pigeons that were released 3 times each, one track from the control site (white numbers), one track from the center of the anomaly (1), showed very inefficient homing from the control site after hitting a gravity anomaly (2), and, after release behind the anomaly (3) deviated from the beeline along the rim of the anomaly, following mostly landscape guidelines afterwards. B) Pigeon **b26** was an efficient homer yet changing course three times after encountering gravity or gravitomagnetic anomalies. C) Pigeon **b20**, a fast flyer, showed perfect homing from the control site (2), but when crossing the second gravity anomaly it always deviated westwards and got lost for some days (1,3). Red circles, common flight paths; Color scale/isolines: horizontal gravity gradient in eotvos = E.

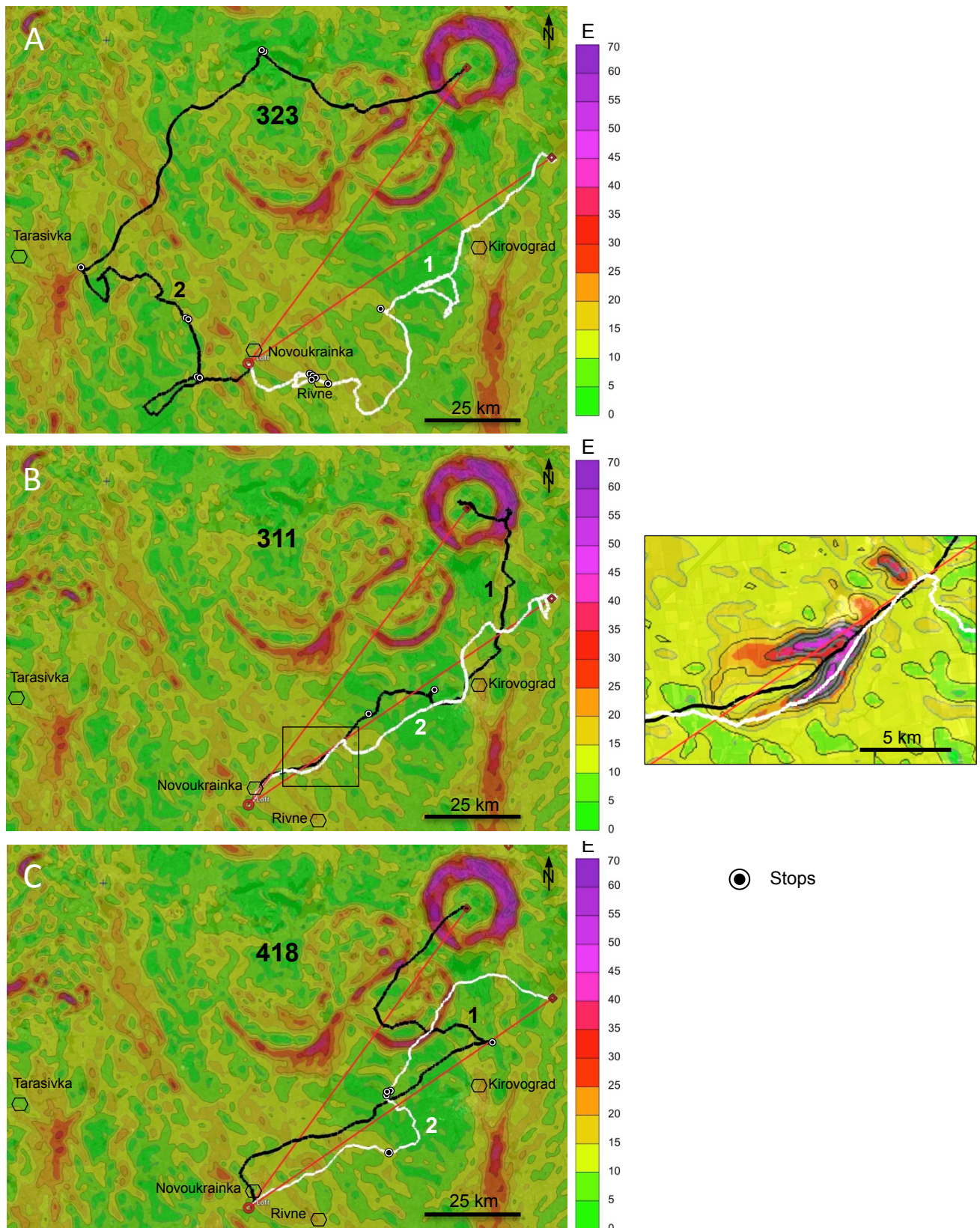


Fig S6. GPS tracks of pigeons that were released twice, one track from the control site (white numbers), one track from the center of the anomaly (black numbers). A) Pigeon **323** deviated from the beeline southwards and appeared disoriented at the gravity and magnetic anomaly at Rivne (1). After passing the rim of the Boltishka anomaly it deviated westwards flying a large detour (2). B) Pigeon **311** changed course in the rim of the Boltishka anomaly, but showed a relatively efficient flight path from the control site (2). Inset: aligning to a small gravity anomaly located on the beeline (scale 1:50'000). C) Pigeon **418** changed course when encountering gravity anomalies, both from the Boltishka anomaly (1) and from the control site (2). Red lines: beelines from release site to loft. Color scale/isolines: horizontal gravity gradient in eotvos = E.

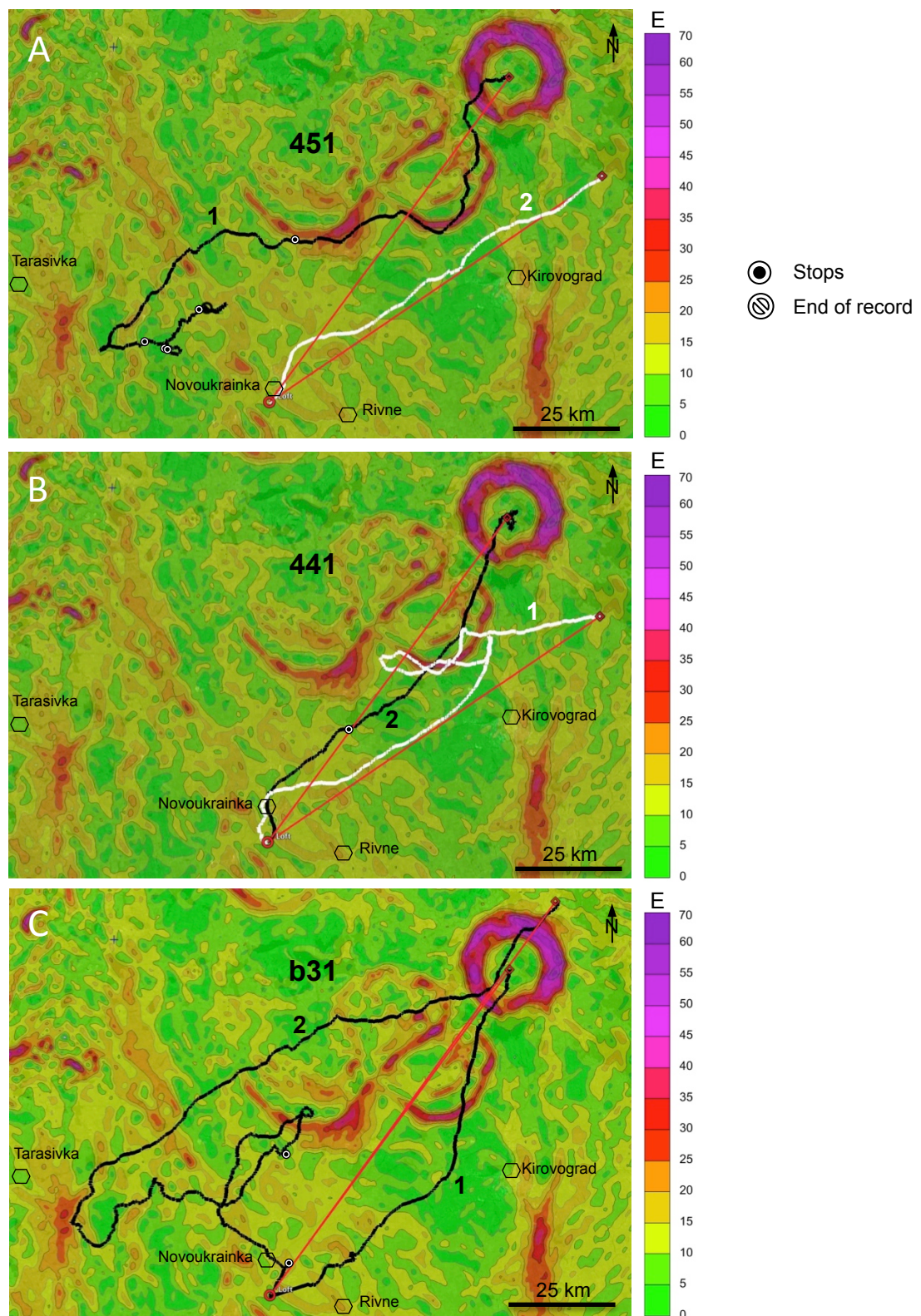


Fig S7. GPS tracks of pigeons that were released twice, one track from the control site (white numbers), one track from the center of the anomaly or from behind (black numbers). A) Pigeon **451**: After passing the rim of the Boltishka anomaly it deviated southwards and followed the contours of two gravity anomalies, getting lost for two days after stopping 30 km from the loft (1) but showed perfect homing from the control site (2). B) Pigeon **441** changed course after flying into a gravity anomaly, but corrected perfectly homewards after having left the anomaly (1). From the Boltishka anomaly, it showed efficient homing showing only small corrections while crossing the second anomaly (2). C) Pigeon **b31** homed well from the center of the Boltishka anomaly, showing a minor deviation in the second anomaly. When released behind the Boltishka anomaly, it changed twice course westwards while crossing it, flew then WSW and then SW till meeting the Tarasivka anomaly where it reversed direction towards another gravity anomaly after which it reversed again to reach the loft after 344 km of flight. Red lines: beelines from release site to loft. Color scale/isolines: horizontal gravity gradient in eotvos= E.

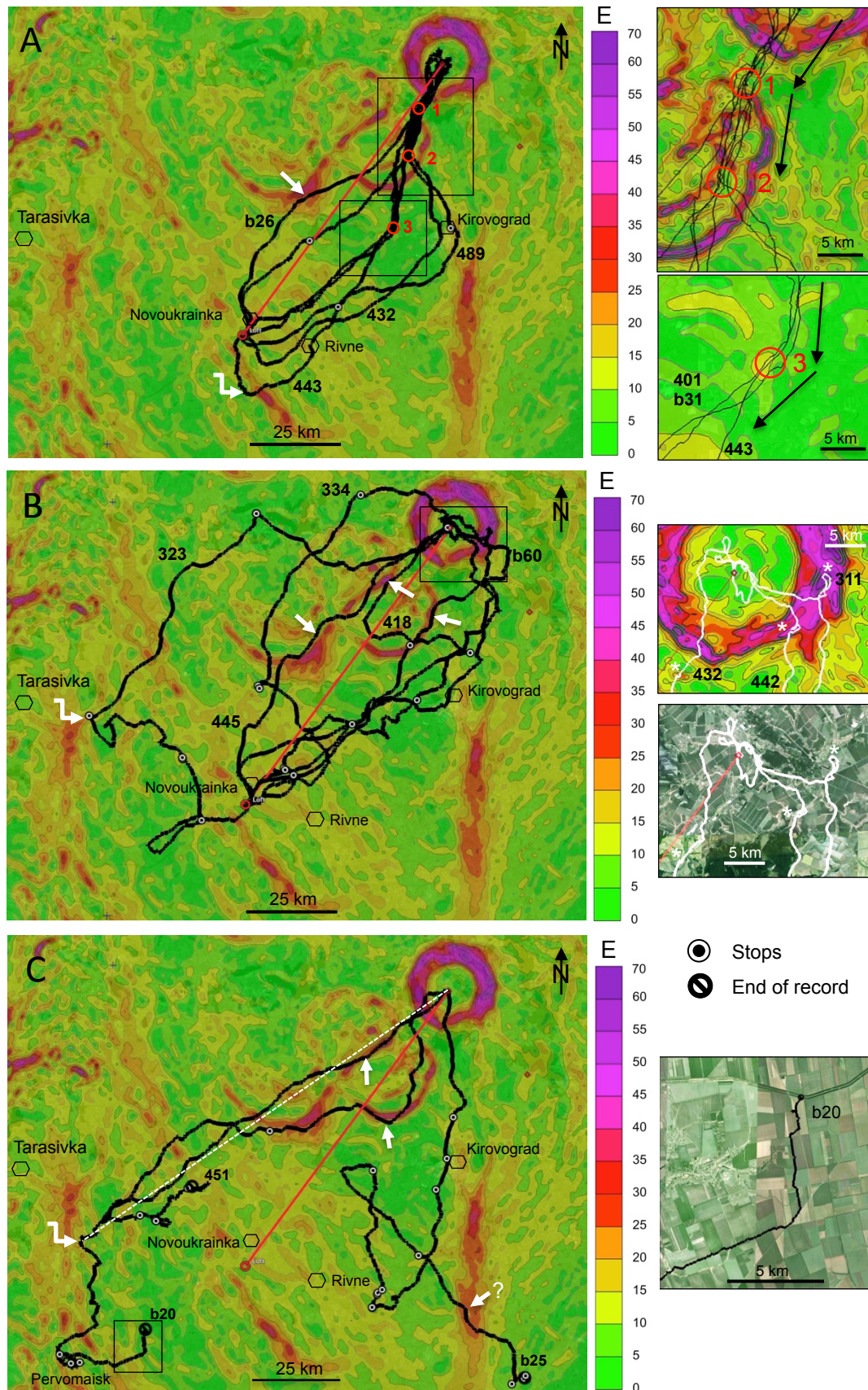


Fig. S8. Pigeon tracks from center of gravity anomaly grouped according to performance. A) Efficient homers (7 tracks). These fast and initially well-directed pigeons change flight paths upon hitting the next anomaly (red circle 1) and disperse after passing more anomalies (red circle 2). Three birds fly a common route at different days (red circle 3). B) Inefficient homers (7 tracks) change frequently their flight direction according to both gravity and topographic cues. Inlets show tracks of 3 pigeons circling over peaks of gravity anomalies (asterisks) with no obvious topographic cues. C) Poor homers (3 tracks) choosing wrong directions. **Pigeon b25** adopted a wrong direction after crossing the rim of the circular anomaly, **pigeon 451** appeared to be misrouted by gravity anomalies. **Pigeon b20** maintained an increasingly deviating compass direction (dotted white line) for 120 km, its last leg of 20 km showing a road-following strategy (Inset). White arrows: alignment of flight to gravity anomalies; white angular arrows: sharp turns associated with gravity anomalies in last flight segments. Color scale/isolines: horizontal gravity gradient in eotvos = E. Google Earth Images from 2014 Digital Globe, 2014 CNES Astrium and 2014 Cnes Spot/Image.

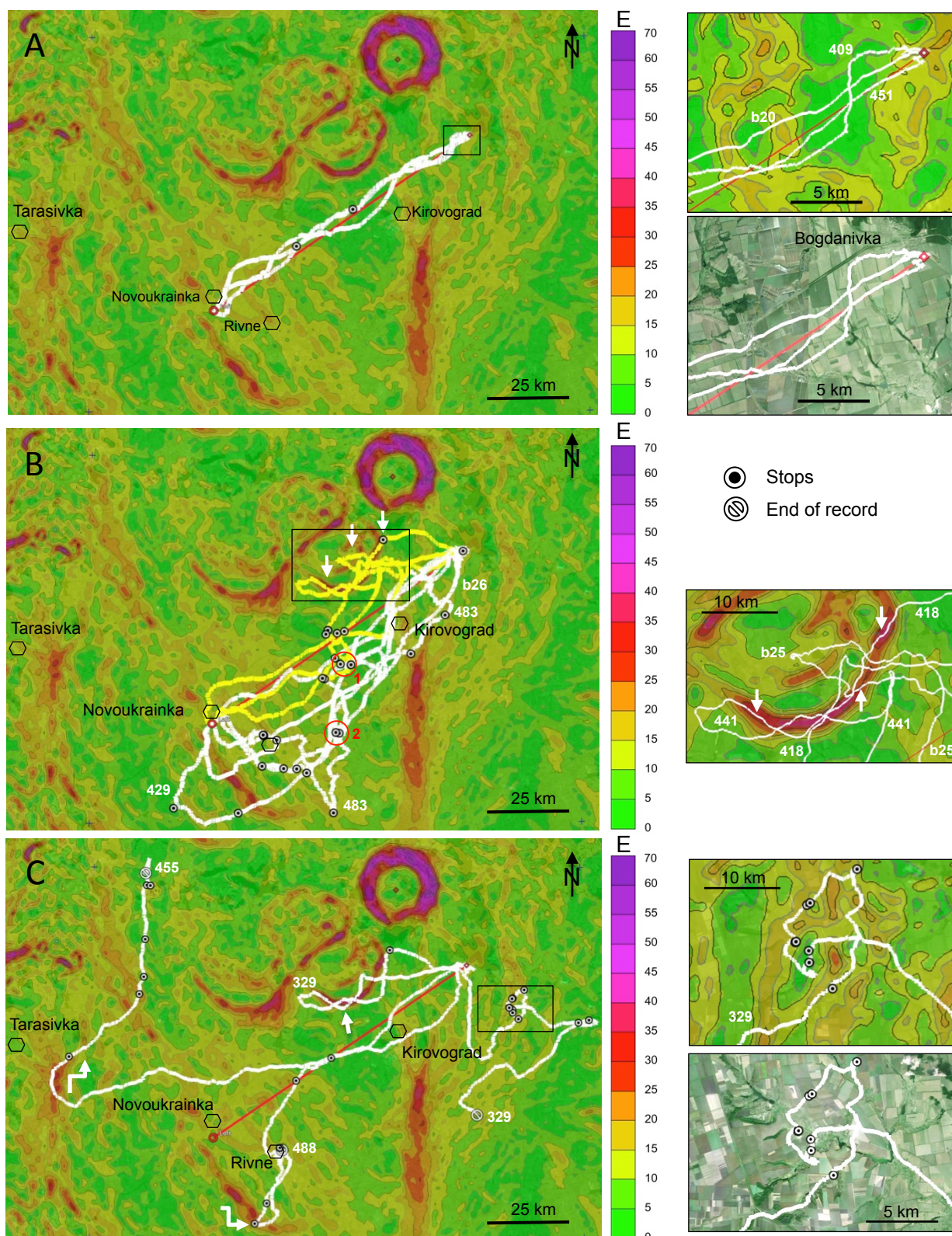


Fig. S9. Pigeon tracks from the control site, grouped according to performance. A) Efficient homers (3 tracks) flew fast and remained aligned to the beeline from release site to loft (pigeons **b20**, **409**, **451**). Insets show that the release site was located on a moderate gravity anomaly unrelated to topography. B) Inefficient homers (9 tracks) either departed westwards (yellow tracks, **b25**, **418**, **441**), hitting a gravity anomaly associated with dramatic changes in flight direction (Inset), or they departed from the bee-line to the south, often following shallow valleys and small lakes, changing their flight direction according to both gravity and topographic cues, interspersing many stops. Red circle: convergence site of 4 tracks from the same day. C) Late homers (3 tracks) choosing wrong directions. Pigeon **329** flew first westwards, met a gravity anomaly, returned to the release site and then took a disoriented course with many stops inside a maze of small gravity anomalies (Inset). Pigeon **488** was initially well directed and deviated later from the home direction following a river system, continuing southward and, after having met a gravity anomaly, returning to the end-of-record point at Rivne, site of a combined gravitomagnetic anomaly. Pigeon **455** departed southwards, corrected towards home but maintained a deviating flight course for 100 km until hitting a gravity anomaly near Tarasivka, where it turned northwest and north till the end of record. White arrows: alignment of flight to gravity anomalies; white angular arrows: sharp turns associated with gravity anomalies in last flight segments. Red lines: beelines from release site to loft. Color scale/isolines: horizontal gravity gradient in eotvos = E. Google Earth Images from 2014 Digital Globe, 2014 CNES Astrium and 2014 Cnes Spot/Image.

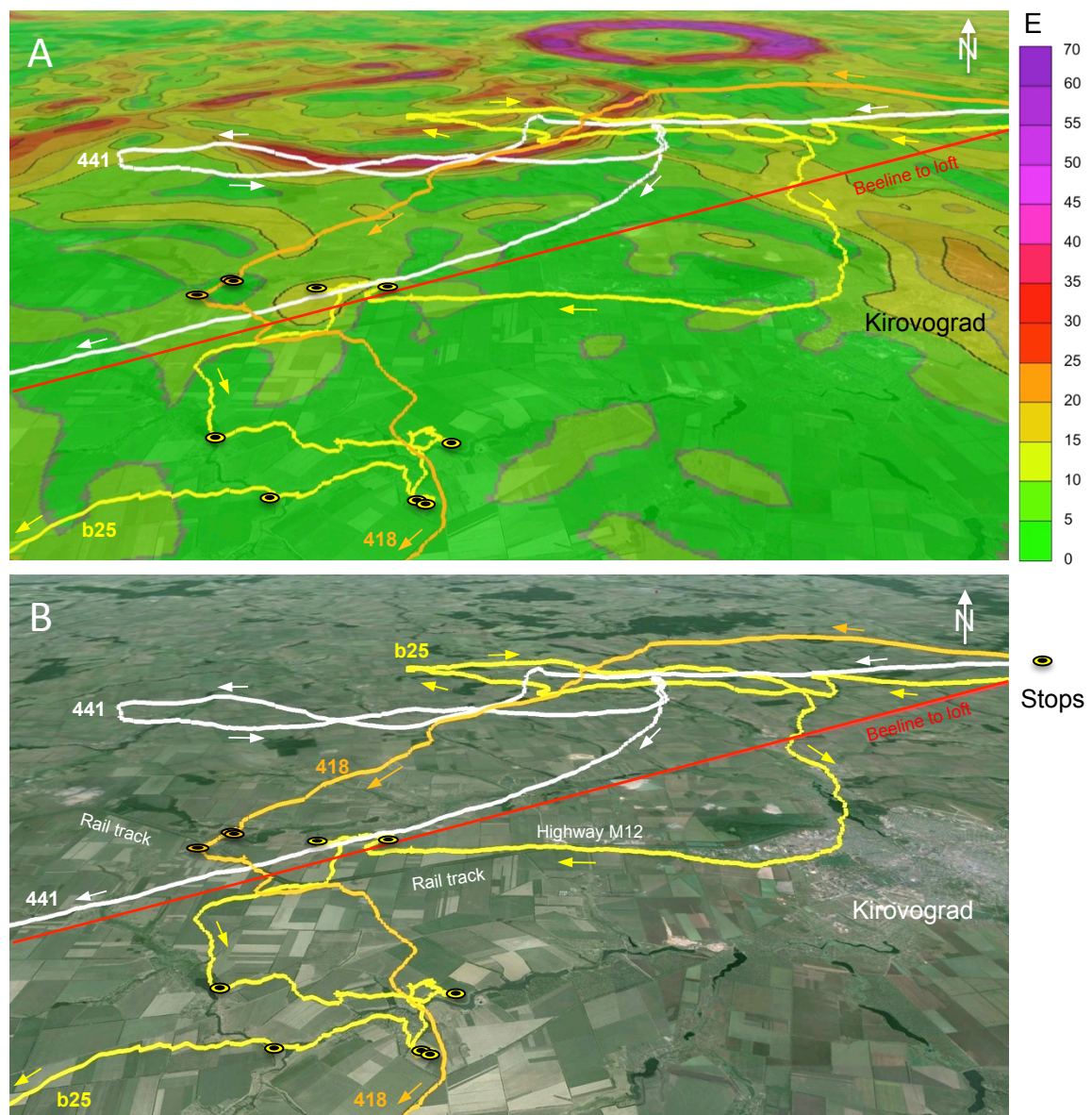


Fig S10. Alignment of 3 tracks of control pigeons first to gravity anomalies and then to landscape cues. A) Perspective view of gravity anomalies without topographic cues, north of the beeline (in red). Pigeons tracks changed without apparent reactions to landscape features. B). Tracks of the same pigeons after having passed the anomaly zones. Pigeon **b25** (yellow) followed rivers and partially the highway M12. Pigeon **418** (orange) changed flight course by 90° after meeting highway M12 which it followed before taking gradually a homeward course that frequently joined shallow river valleys. Pigeon **441** (white) took, after returning from the anomaly, a hairpin turn and then a course gradually aligning to the beeline, which it continued without further topography-induced deflections. Arrows: direction of flight. Color scale/isolines: horizontal gravity gradient in eotvos = E. Images from Digital Globe 2014,



Fig S11. Examples of flight strategies in pigeon 411. A) After start, precise following of a railway track running parallel to the bee-line to the loft. B) In-between segment of the home flight, the pigeon maintaining a compass direction ignoring guiding landmarks. C) Last leg of flight showing a compromise between home direction (white line from last stop to loft) and adherence to visual guidelines. Bottom of picture: pigeon 411 joining a river valley, afterwards flight along canopies lining agricultural fields, the bird taking 90° turns to the left and re-aligning by 90° towards the actual home direction. Last segment: aligning to bee-line in familiar territory. Google Earth Images from 2014 Digital Globe, 2014 CNES Astrium and 2014 Cnes Spot/Image.

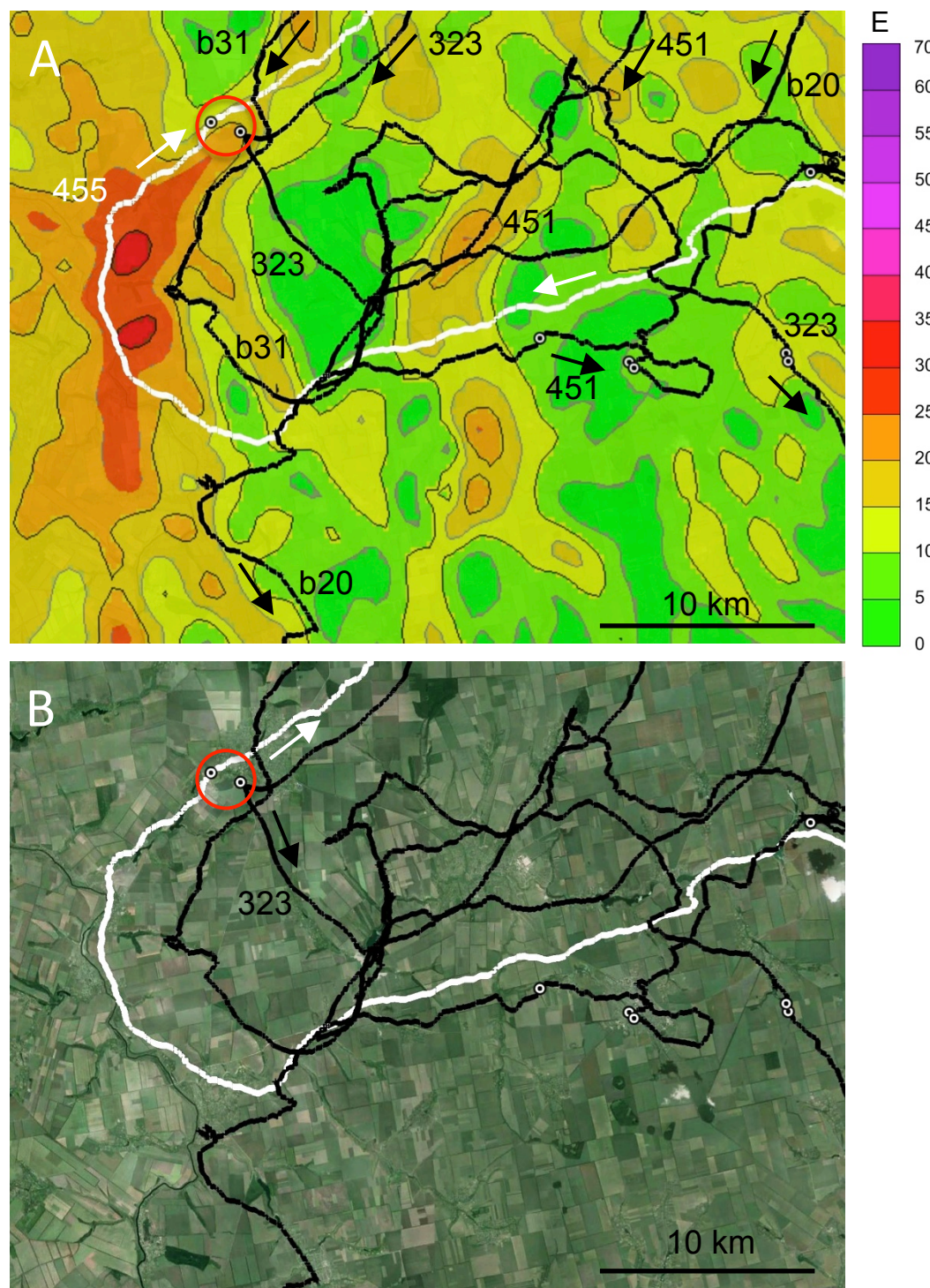


Fig S12. Westernmost turning point of errant pigeons at the Tarasivka gravity anomaly (see also Fig. S4 for a general overview). A) Tracks of 3 pigeons released from the center of the Boltishka anomaly (**b20**, **323**, **451**), from behind the Boltishka anomaly (**b31**) and from the control site (**455**). B) Satellite view of same tracks. Note that the three pigeons arriving from Boltishka (black tracks) arrived from NNW and reversed the flight direction eastwards after some erratic flight patterns, pigeon **b20** turning southwards along the gravity anomaly. Pigeon **455** was released at the control site and arrived from West to turn NE. Red circles denote two sites where two pigeons rested, 1.5 km apart. Yet pigeon **455** departed towards NE, pigeon **323** towards SE. Color scale/isolines: horizontal gravity gradient in eotvos = E. Google Earth Images from 2014 Digital Globe, 2014 CNES Astrium and 2014 Cnes Spot/Image.

Table S1. Number of released and lost pigeons

Date	Anomaly			Control site			Moon	Wind speed	Cloud cover	Temp.	% loss/day	Pigeons	
	released	back	lost	released	back	lost						Boltishka anomaly	Control site (Bogdanivka)
26.7.	5	4*	1	5	3	2	22.1% d	none	clear	20°	30.0%	311,442,451, 348*	329, 441 , 455
29.7.	2	2	0	3	3	0	new moon	N 10 km/h	clear	17°	0.0%	b25,b60	b20, b26
12.8.	6	5	1	6	4	2	full moon	NW 15 km/h	60-80%	14°	25.0%	b20,b26,b31,441,445	311 , 409, 451 , b25
24.8.	8	6	2	8	5	3	27.7% d	none	clear	15°	31.3%	334,401, 418 ,432,443,489	323 ,411,429,483,488
28.8	5	1	4	5	1	4	new moon	none	clear	12°	80.0%	323	418
29.8.	5	4	1				new moon	none	clear	12°	20.0%	b26,b20,b25,b31 (behind anomaly only)	
Totals	31	22	9	27	16	11					34.5%		

d = decreasing moon
N = north
NW = northwest

bold print: 2-3 tracks
plain text: one return only
* pigeon back with no GPS record