Flock Patterns When Pigeons Fly over Terrain with Different Properties

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Abstract: The way in which flocks are organized affects the ability of birds to perceive the landscape over which they fly: if the pattern of the flock changes, then the generalized perception of the terrain over which birds fly will also change. In this paper the features of dynamic spatial organization of pigeons in a flock during flights over landscapes with different characteristics were studied based on the analysis of GPS tracks of birds. The ways of group flight were revealed for typical situations, such as survey of unfamiliar terrain or flight home from remote sites. The spatial distribution of distances between pairs of individual birds and directions of movement were calculated, and then related to the features of terrain over which flights were occurred. The data analysis was performed based on comparison of flock patterns during group flights over terrain of distinct types (sea coast, urban and countryside terrain, and natural landscape). The spatial data was processed using the geographic information system QGIS.

1 INTRODUCTION

This paper considers pigeons' collective behaviour during flight over mixed terrain. The aim of this work is to reveal the relationship between changes in flight trajectories and the distribution of birds in the flock, depending on the terrain over which the flight takes place. Studying the spatial organization of birds in the flock reveals features of group coordination of birds while surveying unfamiliar terrain, returning home from a remote point, foraging or migrating over long-distances. It should be noted that the arrangement of birds in the flock is directly associated with the terrain over which they fly. Reflexively, birds adapt their flight in the flock to the tasks to be solved. Based on the flock configuration at any moment, assumptions can be made about the problem solved by the birds.

Flock spatial structure is determined by the organization of birds within a group, i.e. by their location relative to each other, and by the direction of movement of both individual birds and the whole flock. The individual arrangement of birds changes dynamically during the flight. However, some characteristics of the spatial distribution of birds in the flock can remain steady for long periods of time – such as typical distances between the birds or specific flock patterns.

The coordination of bird trajectories is evident in the adjustment of individual birds to the general direction of flight. Spatial distribution within the flock can change the features of aggregate terrain perception; when changing their distribution parameters during the flight, birds adapt to the new tasks to be solved. For example, a high density of birds in the flock will contribute to multiple observations of one and the same terrain point; a flock pattern with large coverage area will allow simultaneous perception of a large area of terrain. In flocking, there are sets of options for the arrangement of birds, which allow their group observation of visually related elements of the landscape over which the flight takes place. In addition, there are options for the arrangement of birds at nodes and reference points, from which the birds can observe (as a whole) the boundaries and all the nearby points on the terrain with similar attributes. The main parameters of flocks of pigeons are shown in Figure 1.

In this paper, we calculated basic flight parameters from records of GPS tracks of different pigeon flocks: pairwise distances between pigeons, flight directions of pigeons and standard deviations for these parameters, measured at the same time. In

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addition, variation in these parameters was calculated for the intervals +/- 10 seconds.

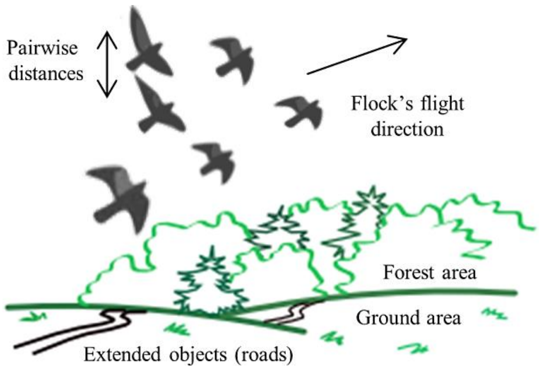

Figure 1: Main parameters of flock of pigeons: general flight direction, individual pigeon's flight direction, and pairwise distance. On the terrain over which the pigeons fly, it is possible to distinguish surfaces with different types of coverage, such as forest and ground area, as well as to select extended objects, such as roads or rivers.

The obtained flight characteristics of the flock were compared at the moments of flight of the flock over extended visually perceived elements of the terrain, such as rivers, roads, and boundaries between different visually homogeneous textures, which were identified via remote sensing data from open sources. The special points that were identified reflect the relationship between fast events (about a second) and long-term changes in flight parameters (about 10 seconds).

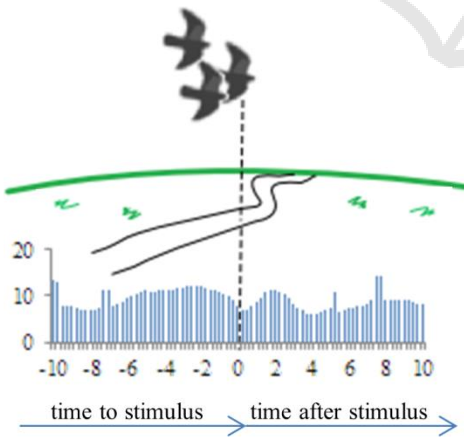

Figure 2: Model of the 'stimulus-reaction' relationship for flight of a flock.

It can be assumed that the biological analogue of such a relationship is a 'stimulus-response' phenomenon (Figure 2), where 'stimulus' is either the specific behaviour of the flock or a special event in the landscape, and the 'response' is the variation in the measured parameters in 10-second interval before and after the stimulus. The analysis of mean value and standard deviation (SD) in distances between pigeons and in flight directions made it possible to identify the relationships between flock structures, and to determine the typical response to external, visually noticeable spatial landmarks.

2 BACKGROUND AND RELATED WORKS

2.1 Characteristics of Birds during Their Flight in a Flock

Flying in a flock allows joint, coordinated spatial migration of birds. The birds gather in flocks to increase their feeding efficiency or decrease their vulnerability to predators (Morse, 1977). Besides, flying in flocks can improve joint spatial orientation during long-distance migrations and enable more exact orientation on the terrain. The coordination of birds during changes in flight direction or height is apparent in the flock pattern and in the distance between birds. The joint flight of the flock of birds is controlled by visual perception and acoustic signals. In ecology, many types of flock patterns are described, such as "straight front", "regiment of starlings", "wedge of geese", and so on.

The structure of pigeon flocks was considered in paper (Mehlhorn and Rehkaemper, 2016). The authors remark that pigeons form flocks with a flexible structure and without any strict hierarchy. During pigeon migrations both single flights and flights in pairs as well as in flocks are possible. The efficiency of flight in the flock differs from that of individuals or pairs of pigeons, and, on the whole, it depends on the number of pigeons flying in the flock.

Research on the behaviour of flocks has been carried out through analysis of GPS tracks. In publication (Dell'Ariccia *et al.*, 2008), comparison of GPS tracks of individual pigeons and pigeons flying in flocks demonstrated that grouping changes flock navigational behaviour. Based on investigation of groups of six pigeons, the authors hold that 'group cohesion facilitates a shift towards more efficient homing strategies: individuals prefer navigating by familiar landmarks, while flocks show a compass orientation'.

Coordination of birds during flights, including typical inter-individual distances, has also been investigated using GPS tracks. Based on this type of data, birds' behaviour during circular movement was investigated for small flocks in publications (Nagy *et al.*, 2013; Yomosa *et al.*, 2015; Chen *et al.*, 2017). In publication (Nagy *et al.*, 2013), track data was recorded using GPS loggers and the leader-follower relationships in the flock were analysed. In publication (Chen *et al.*, 2017), it was found out that pigeons in small flocks coordinate their behaviour with that of their nearest neighbours, which can change during the flight. Pigeons can be considered as flying in a pair if the distance between them is three to four metres less than the average distance between pigeons in the flock.

Grouping of birds within the flock was studied in paper (Ballerini *et al.*, 2008). The authors measured the three-dimensional positions of individual birds in compact flocks of up to 2,600 European Starlings (*Sturnus vulgaris*) in the field. Based on analysis of bird flocks flying above Rome, from pictures taken at an average distance of a hundred metres, aggregation in the combined flock is maintained through the formation of multiple groups of seven to eight birds with a topological interaction.

2.2 Characteristics of the Terrain over which Pigeons Fly

Visual perception of terrain during the flight of birds is based on reflexes. During changes in the observed surroundings, rapid adjustment of the flight trajectory to the terrain occurs. Importantly, the birds perceive not individual objects but consolidated data from the distinct visual elements and attributes of the terrain. These can include the attributes of textures, boundaries and distinct areas.

In landscape perception there is a set of visually connected terrain elements, besides which there is an opportunity for interpolation between sets of data on the terrain with similar and dissimilar attributes. While flying over the terrain it is possible to be guided by elements with previously known attributes. Although birds can see places that they have never seen before, these sites often have already known characteristics, or are simply part of an extended area (e.g. road section, river bank, forest strip). The perceptible elements with well-known attributes ('nodes' or 'reference points') dynamically form the basis for interpolation of spatial data in the area over which movement of the flock occurs. It helps orientation both in a situation that is not well enough known and one in which there is excessive information.

Multi-scale integration of perception is also based on the aggregate interpolation of visual attributes. Distances between flowers, or trees, or shades can set the different scales for spatial data generalization. Simplification to single-scale perception can occur after a reduction from a multi-scale integration of perception.

2.3 Correlation of Bird Flock Flight and Terrain Characteristics

The role of visual reference points for pigeons in getting around terrain is considered in paper (Mann *et al.*, 2011). The authors have found that the most informative elements of flight trajectories coincide with landscape features that have previously been suggested to form important components of the homing task.

Perception of the surrounding landscape during the flight and the influence of landscape on way-finding and training of pigeons during the flight was studied in (Guilford and Biro, 2014), and the authors demonstrated that memorised guidance control is likely to relate to geocentrically fixed, local features of the landscape. However, in the case of a familiar route, the importance of snapping to the reference points on the terrain may decrease. Nevertheless, route memorizing depends on the terrain type: 'birds follow single memorised routes more readily, or more faithfully, over some landscape types than others'.

In publication (Pearce *et al.*, 2014) it was demonstrated that terrain perception cannot depend directly on the distribution of pigeons in the flock, but, for dense flocks, it plays an immediate role in the joint perception of the terrain. The behaviour of birds is specific to the density of flock, and observations of real bird flocks show that a bird usually reacts to six to seven of its nearest neighbours.

2.4 Mathematical Simulation of Behaviour in Flocks

The distribution of directions and, in a similar way, distribution of velocities can be characterised in a similar way to spatial distribution, by finding out the common, regular factors. For each individual, the spatial characteristics and direction of movement are determined at a specified moment and compared with the average parameters of the flock.

A typical mathematic model ('Boids algorithm') of bird behaviour in a flock was suggested by Craig Reynolds (Reynolds, 1987). Firstly, each bird in the model aimed to avoid collisions with the other birds. Secondly, each bird moved in the same direction as the nearby birds. Thirdly, each bird aimed to move at the same distance from other birds. The flock size is insignificant for the model.

The 'Vicsek Model' (Vicsek *et al.*, 1995) is used to describe large flocks, and demonstrates how individual birds in the flock adjust their movement in the presence of noise depending on location of their neighbours. Allocation of aggregated data is presented in publication (Topaz, Ziegelmeier and Halverson, 2015) using simulation snapshots of the 'Vicsek Model'.

Models for explaining and predicting pigeon flock flights in real-time mode ('Pigeon Model') were suggested in publication (Wallentin and Oloo, 2016), where the authors used specific algorithms to identify an optimal range of parameters that can be used to reproduce realistic navigation paths of homing pigeons. In (Oloo and Wallentin, 2017) the authors combined an agent-based model of social pigeon flights with a simulated data stream from recorded GPS tracks.

Directions were calculated for individuals in schools of fish to analyse joint behaviour in publication (Jolles *et al.*, 2017) based on the example of free-swimming three-spine stickleback shoals (*Gasterosteus aculeatus*).

3 MATERIALS AND METHODS

3.1 Materials

In this work the behaviour of pigeon flocks – consisting of three to eight birds – during flights over unfamiliar heterogeneous terrain was studied. During the investigation, calculations were carried out based on data on pigeon flights published in open repositories (*Dryad Digital Repository* and *Movebank Data Repository*). The calculations were made for six flocks.

The first three flocks (data package from https://datadryad.org/resource/doi:10.5061/dryad.f9n8t, paper (Watts *et al.*, 2016)) flew over mixed terrain near the seashore: sea coast, urban terrain and agricultural fields. The specific distance between the individual values of coordinates for pigeon GPS tracks is presented within the range of three to five metres. Measurements of coordinates between separate points of GPS tracks were taken five times per second. The number of pigeons in the first, second and third flock were four, five, and three, respectively.

The other three flocks (data package from www.datarepository.movebank.org/handle/10255/move.365, paper (Santos *et al.*, 2014)) flew over the mixed terrain in the foothills: natural forests, populated countryside and agricultural fields The specific distance between the individual values of coordinates for pigeon GPS tracks is presented within the range of three to six metres. Measurements of coordinates between individual points of GPS tracks were taken four times per second. The number of pigeons in the fourth, fifth and sixth flock were eight, seven and eight respectively.

Earth remote sensing data – satellite images – in the form of OpenLayers (http://openlayers.org) were applied as a source of information about terrain surfaces. The coordinate system for the project was WGS 84/Pseudo-Mercator (EPSG:3857).

3.2 Methods

To determine how the behaviour of each flock changed – in response to changes in the terrain over which it flew – pigeon GPS tracks were analysed and characteristics of the movements of individual

Figure 3: Points at which the flock flew apart, according to the local maximums of pairwise distances between pigeons at the same time. Dotted points show the trajectories of individual pigeons, the circle is a special point.

birds during their flight in the flock and the aggregated parameters of the flock were calculated.

The analysis was made for all flight trajectories for each of the six flocks specified in subsection 3.1 and for all periods of time during which the flights of these flocks were performed. The distance between the departure and destination points for all six flock flights was about ten kilometres.

During analysis the following groups of data were processed:

I) Analysis of trajectories of individual pigeons, taking into account their collective behaviour in the flock during the flight.

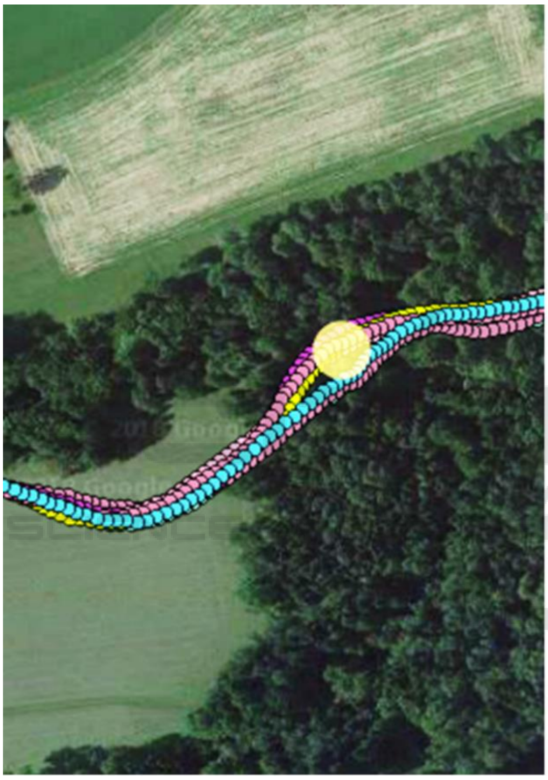

Figure 4: Points of breaks in direction (points of sharp changes in flock direction during one second). Dotted points show the trajectories of individual pigeons, the circle is a special point.

The spatial distribution of distances between pairs of individual birds and directions of movement were determined during the analysis. The following parameters were compared to determine:

- distance between pairs of individual birds in the flock and standard deviation of distances between pairs for all birds in the flock taken at the same moment of measurement;
- directions of movement for each bird and standard deviation of directions for all birds in the flock taken at the same moment of measurement.

Based on analyses of trajectories, special points in six flock flights were calculated in coordinates and in time:

- points at which the birds in the flock flew apart, according to the local maximums of distances between pairs of birds (Figure 3);

points of breaks in direction (points of sharp changes in flock direction during one second) of the flock trajectories, i.e. points corresponding to significant changes in the standard deviation of directions (

- Figure 4).

II) Analysis of terrain over which the pigeon flocks flew

Based on analyses of remote sensing data from OpenLayers, the spatial locations of the visually perceived terrain elements were determined. In order to do this, terrain isolines were contoured along the boundaries of distinct terrain textures. The isolines revealed the significant extended objects on the terrain, as well as the boundaries between territories with different surface features.

Figure 5: Points of intersection of the flock flight trajectories and the terrain isolines. Yellow lines indicate the isolines identified on the surface. Dotted points show the trajectories of individual pigeons. The circles indicate special points of intersection.

III) Comparison of characteristics of pigeon flights and terrain features

Based on analyses of additional special points – points of intersection of the flock flight trajectories and the terrain isolines – were determined for different types of surface (Figure 5).

3.3 QGIS Plugins

The data were processed using the open source software program QGIS (http://qgis.org), including additional analysis plugins: QGIS geoalgorithms and GDAL tools (http://www.gdal.org) integrated into QGIS. The source data layers were added using the OpenLayers Plugin in QGIS, which allows to obtain Google Maps, Bing Maps and another open layers.

Geographic information system QGIS allow to process GPS data of the pigeons' flight paths with precise reference to the locations and terrain features:

- Create vector track lines by points of GPS measurements.
- Calculate variation in directions of motion and variation in distances by vector data.
- Build summary diagrams of the dependence of different flight parameters with reference to time and to coordinates along the flight trajectories.
- Calculate the terrain features obtained from remote sensing data, such as the boundaries between different types of terrain, and select contour isolines.
- Calculate the density of special lines on the surface in the form of a 'heat map'.

The applied QGIS tools and plugins are presented in Table 1.

Table 1: Applied QGIS tools and external plugins.

Plugin	Description
OpenLayers Plugin: https://github.com/sourcepole/qgis-openlayers-plugin	QGIS plugin embeds OpenLayers (http://openlayers.org) functionality. It allows to obtain Google Maps, Bing Maps, OpenStreetMap and another open source layers.
Points2One: http://plugins.qgis.org/plugins/points2one	Create lines and polygons from vertices. Connects points in a layer to form lines and polygons.
Line intersections: https://www.qgis.org/en/docs/index.html	Locate intersections between lines, and output results as a point shapefile.
Heatmap Plugin: http://www.qgistutorials.com/en/docs/creating_heatmaps.html	Create a density raster of an input point vector layer based on the number of points in a location, with larger numbers of clustered points resulting in larger values.

4 RESULTS

In this work three types of special points were calculated (points at which the birds in the flock flew apart, points of breaks in direction with sharp changes in flock direction during one second, points of intersection of flock flight trajectories and terrain isolines) for the flights of six flocks using three different methods.

Based on special points, peri-stimulus histograms were forming as histogram of flight parameters around stimulus events – 'triggers'. Peri-stimulus histograms were plotted for: directions, distances and deviations by direction and distances, as well as detection of dependencies between flock flight parameters and terrain properties. Peri-stimulus histograms were constructed (using 200 or 250 ms bins) for the epoch between 10 seconds before passing over a special point and 10 seconds after passing over a special point ('trigger stimulus'). Typical phenomena occurring during the flights of the flocks were analysed for points where:

- individual birds flew apart;
- there was sharp changes in flock direction;
- trajectories of pigeons crossed selected isolines.

Basic flight parameters and calculated results are presented in Table 2 (SD - standard deviation).

Table 2: Basic flight parameters and calculated results.

Dryad Digital Repository			
Flock number	1	2	3
Number of pigeons	4	5	3
Time interval between GPS measurements, ms	200	200	200
Number of GPS measurements	5395	3685	4800
Mean SD of pairwise distances, m	10.8	9.4	8.6
Mean SD of flight directions, degrees	5.8	5.6	5.5
Isoline contour accuracy, m	5	5	5
Movebank Data Repository			
Flock number	4	5	6
Number of pigeons	8	7	8
Time interval between GPS measurements, ms	250	250	250
Number of GPS measurements	3501	3501	3844
Mean SD of pairwise distances, m	3.8	3.8	6.8
Mean SD of flight directions, degrees	3.9	4.0	4.2
Isoline contour accuracy, m	5	5	5

The typical histograms for the different cases are shown in the Figures below.

4.1 Results of Data Processing by Distance

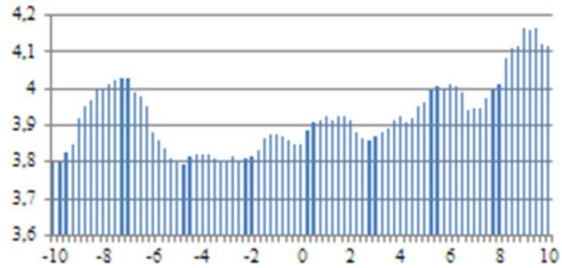

Figure 6: Histogram of distance deviations, in relation to the moments when the flock crossed the isolines. The x axis shows the timescale in relation to events ‘isoline’, s. The y axis shows standard deviation of the distances between pairs of pigeons, m.

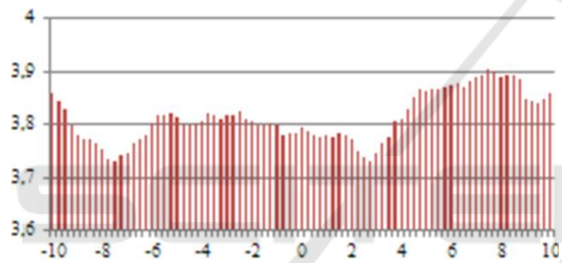

Figure 7: Histogram of distance deviations, in relation to the moments of break in flock direction. The x axis shows the timescale in relation to events ‘breakpoint’, s. The y axis shows standard deviation of the distances between pair of pigeons, m.

4.2 Results of Data Processing by Directions

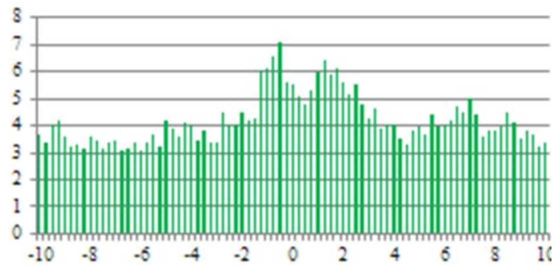

Figure 8: Histogram of direction deviations, in relation to the moment at which the flock flew apart. The x axis shows the timescale in relation to events ‘flock flying apart’, s. The y axis shows standard deviation of the direction of pigeons, deg.

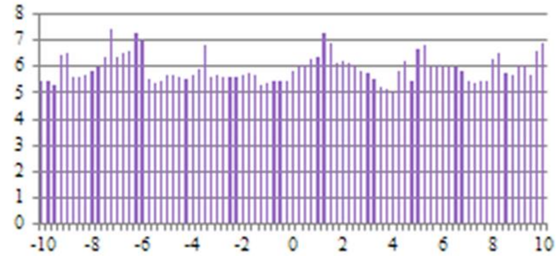

Figure 9: Histogram of direction deviations, in relation to the moments when the flock crossed the isolines. The x axis shows the timescale in relation to events ‘isoline’, s. The y axis shows standard deviation of the direction of pigeons, deg.

5 DISCUSSION AND CONCLUSIONS

The aim of this work was to reveal the flight properties of a small flock (three to eight indistinguishable pigeons tracked using GPS loggers) over homogeneous and combined homogeneous and heterogeneous terrain. The paper discusses typical flock behaviour related to specifics of the terrain over which birds fly. Specific features of the flight, revealed during turns of the flock, and changes in the terrain colour characteristics or lighting condition in landscape, presented the principle interest for this study.

Reflexively, the pigeons arrange themselves within the flock over the terrain. Moreover, part of visual data about landscape, perceived by the pigeons, forms the basic points and areas that determine both continuity and change in pigeon trajectories during flights (flight along the river maintains consistency of trajectories, and flying out of the forest into the fields can cause the flock to turn around). With that, other visual data may be not perceived as significant for navigation during the flight (for example, a particular house among the abundance of single houses in low-rise built-up area), in such case no behavioural response is associated with changing trajectories.

The pigeons can fly over heterogeneous and homogeneous terrain. The scope of navigation tasks solved by the pigeons when flying over homogeneous terrain with a small number of reference points is also limited and generally stable. The arrangement of pigeons in the flock and their flight trajectories will be maintained during the whole flight over homogeneous terrain. The pigeons pay attention to a limited and fixed number of objects – for example, the river bank along which the flight occurs. Repetition of terrain textures and structures enables stable behaviour and does not require additional attention of pigeons. Any changes or additional information – changes in weather conditions or light, or the appearance of a predator – may result in changes in the pigeons' arrangement in the flock and trajectories. In contrast to individual birds, the flock perceives the terrain jointly and in coordination and responds to changes in terrain cooperatively – with changes not only in trajectories but also in the flock structure itself.

During a flight over heterogeneous terrain, a great amount of diverse information is observed. This information can be generalized and become typical. Sets of data are extracted from it and can be applied even when the birds have become accustomed to operating in other situations. Accordingly, the responses to similar sets of data will be alike. This promotes both fast and consistent responses during flight over similar terrain and adaptation during flight over different terrain. When current situation change, the sets of reference points and regions also change.

Generally, pigeons prefer to fly over already familiar terrain, gradually extending the survey areas. But even well-known territories can change – at different times of day and seasons of the year – and therefore flock navigational strategies can change completely, and the flock can even fly away from previously interesting terrain.

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