

# Characterisation and Identification of the Navigational Processes in Homing Pigeons

Dissertation  
zur Erlangung des Doktorgrades  
der Naturwissenschaften

vorgelegt beim Fachbereich Biowissenschaften  
der Johann Wolfgang Goethe - Universität  
in Frankfurt am Main

von  
Ingo Schiffner  
aus Aschaffenburg

Frankfurt 2010

vom Fachbereich Biowissenschaften

der Johann Wolfgang Goethe - Universität als Dissertation angenommen.

Dekan:

Gutachter:

Datum der Disputation:



For my friends and family



## **Acknowledgments**

This PhD thesis owes a lot to many people. Above all I am deeply grateful to my parents, my brother and my friends, all of whom provided endless and unconditional support throughout this PhD project.

I am especially thankful to my supervisors, Roswitha Wiltschko and Johann Baumeister, for fascinating discussions, constructive criticism, and, overall, for excellent and patient supervision based equally on guidance and support to pursue my own ideas. Furthermore, it was a great honor to be supervised by the late Ulrich Nhemzow, who introduced me to the fascinating field of dynamic systems theory.

I am indebted to Wolfgang Wiltschko for all the stimulating discussions and his constructive criticism of my scientific work during the past years.

I am very thankful to all my colleagues and all the undergraduate students who have helped conducting the experiments. Among them I like to mention Susanne Rausch, who has always taken good care of the birds and has helped greatly with the training of the birds.

Last, but not least, my gratitude is also to the birds. Without them this study would not have been possible. It is their sometimes odd behavior that has made the experiments so much fun. I especially like to mention pigeon 07-410, who liked to hide under the bus and play cat and mouse, and 08-797, who always was the first to reach the home loft and almost always waited until every other bird had arrived before he himself entered the loft.



# Contents

<b>1. Introduction</b>	<b>1</b>
1.1. General Scope . . . . .	1
1.2. Basic Mechanisms of Orientation in Birds . . . . .	1
1.3. A Model Organism . . . . .	3
1.4. Tracking Animals . . . . .	4
1.5. Analyzing Tracking Data . . . . .	5
1.6. Dynamic Systems Theory . . . . .	6
1.7. Characterization of the Navigational Process . . . . .	7
<b>2. Tracking and Experimental Procedure</b>	<b>9</b>
2.1. GPS Tracking . . . . .	9
2.2. Experimental Birds and Training . . . . .	12
2.3. The Release Sites . . . . .	13
2.4. Release Procedure . . . . .	15
2.5. Track Analysis . . . . .	16
<b>3. Traditional Analysis</b>	<b>19</b>
3.1. Introduction . . . . .	19
3.2. Analysis and Evaluation . . . . .	19
3.3. The Tracks . . . . .	21
3.4. Bearings and Efficiencies . . . . .	45
3.5. Differences between Individuals . . . . .	48
3.6. Influence of Experience . . . . .	57
3.7. Influence of Abiotic Factors . . . . .	61
3.8. General Behavior . . . . .	63
3.9. Discussion . . . . .	64
3.9.1. Attraction of Villages . . . . .	64
3.9.2. Influence of Familiarity . . . . .	67

3.9.3. Flight Corridors . . . . .	70
3.9.4. Navigational Factors . . . . .	72
3.10. Conclusion . . . . .	74
<b>4. Phases of the Flight</b>	<b>75</b>
4.1. Introduction . . . . .	75
4.2. Analysis and Evaluation . . . . .	76
4.3. The First Decision . . . . .	78
4.4. The Final Homing Phase . . . . .	85
4.5. Differences between Individuals . . . . .	88
4.6. Influence of Experience . . . . .	94
4.7. Influence of Abiotic Factors . . . . .	96
4.8. General Behavior . . . . .	97
4.9. Discussion . . . . .	99
4.9.1. A First Decision . . . . .	99
4.9.2. Behavior after the First Point of Decision. . . . .	102
4.9.3. Individual Behavior . . . . .	104
4.9.4. Influence of Abiotic Factors . . . . .	105
4.9.5. Influence of the Earth's Magnetic Field . . . . .	106
4.10. Conclusion . . . . .	108
<b>5. Time Series Analysis</b>	<b>109</b>
5.1. Introduction . . . . .	109
5.2. Time Series Analysis . . . . .	112
5.2.1. The Correlation Dimension $d_2$ . . . . .	112
5.2.2. The Largest Lyapunov Exponent $\lambda$ . . . . .	113
5.3. Data Filtering . . . . .	114
5.4. Data Evaluation . . . . .	117
5.5. Influence of the Release Site . . . . .	121
5.6. Differences between Individuals . . . . .	122
5.7. Influence of Experience . . . . .	123
5.8. Influence of Abiotic Factors . . . . .	125
5.9. Precision of the Flight . . . . .	126
5.10. Complexity of the Flight . . . . .	127
5.11. Mapping the Navigational Process . . . . .	131

5.12. Discussion . . . . .	133
5.12.1. Non-Navigational Phases . . . . .	133
5.12.2. Navigational Strategies and Processes . . . . .	133
5.12.3. Precision of the Navigational Process . . . . .	135
5.12.4. Complexity of the Navigational Process . . . . .	136
5.13. Conclusion . . . . .	138
<b>6. General Discussion and Conclusion</b>	<b>141</b>
6.1. The Navigational System . . . . .	142
6.1.1. Navigational Strategies . . . . .	143
6.1.2. Navigational Factors . . . . .	146
6.1.3. The Role of Landmarks . . . . .	146
6.1.4. Navigational Gradients . . . . .	150
6.1.5. The Earth's Magnetic Field . . . . .	151
6.1.6. Identification of Navigational Factors . . . . .	152
6.1.7. Simulating Navigation . . . . .	154
6.1.8. A Redundant System . . . . .	156
6.2. A General Model for Navigation in Birds? . . . . .	156
6.2.1. Homing in Other Birds . . . . .	156
6.2.2. Physiological and Behavioral Similarities . . . . .	159
6.2.3. The Routes Chosen . . . . .	163
6.2.4. The Bottom Line . . . . .	164
<b>7. Summary</b>	<b>165</b>
<b>8. Zusammenfassung</b>	<b>171</b>
<b>Appendix</b>	<b>181</b>
<b>A. Dynamic Systems Theory</b>	<b>181</b>
A.1. Introduction . . . . .	181
A.2. Definition of Dynamic Systems . . . . .	181
A.3. Phase Space Reconstruction. . . . .	182
A.4. Choosing the Embedding Parameters . . . . .	185
A.4.1. Choosing the Embedding Dimension . . . . .	185
A.4.2. Choosing an Embedding Lag . . . . .	186

## Contents

A.5. Correlation Dimension $d_2$ . . . . .	187
A.5.1. Concepts of Dimensionality . . . . .	187
A.5.2. Basic Ideas and Principles . . . . .	189
A.5.3. Calculation of the Correlation Dimension $d_2$ . . . . .	192
A.6. Lyapunov Exponents $\lambda$ . . . . .	193
A.7. Application on Data . . . . .	195
<b>B. Algorithms Explained</b>	<b>197</b>
B.1. Introduction . . . . .	197
B.2. Choosing a Embedding Dimension . . . . .	197
B.3. Choosing a Embedding Lag . . . . .	199
B.4. Correlation Dimension Estimation . . . . .	202
B.5. Estimation of the Largest Lyapunov Exponent . . . . .	203
B.6. Conclusion . . . . .	206
<b>C. Tracks of Individuals</b>	<b>219</b>
<b>D. Additional Tables</b>	<b>255</b>
D.1. Abiotic Data . . . . .	255
D.2. Traditional Analysis . . . . .	256
D.3. Phases of the Flight I - First Point of Decision . . . . .	262
D.4. Phases of the Flight II - Last Point of Decision . . . . .	268
D.5. Time Series Analysis I - Correlation Dimension . . . . .	273
D.6. Time Series Analysis II - Largest Lyapunov Exponent . . . . .	277
<b>Bibliography</b>	<b>281</b>
<b>Lebenslauf</b>	<b>293</b>



# **1. Introduction**

## **1.1. General Scope**

While birds are able to cover vast distances and possess the ability to home in on a very specific goal, be it the breeding site of a migratory bird or the loft of a homing pigeon (*Columba livia f. domestica*), some of us seem to require the aid of GPS just to find the next supermarket (Hofmann-Wellenhof *et al.*, 1992). The birds' ability is not only impressive, but also of great general interest. With the knowledge about the process that allows birds to perform this task satellite-independent navigation would be possible. An experience based GPS that could cut the cost of satellite maintenance and also allow position determination in areas, where satellite coverage is bad due to rough vegetation or high buildings, is not only of great scientific, but also of civilian interest.

## **1.2. Basic Mechanisms of Orientation in Birds**

Current assumptions about bird-navigation evolve around the map and compass system, as described by Kramer (1957). According to his theory bird-navigation is a two step process, a compass step and a map step. During the compass step birds either use their innate magnetic compass (Wiltschko, 1968; Keeton, 1971) or one of several other compass systems, they have learned in their youth (Sun compass: Schmidt-König (1958); Kramer (1959); Star Compass: Sauer (1957)), to specify the compass directions. In the map step they use a learned map to determine their current position. With these two types of information,

## 1. Introduction

the birds are then able to set a course towards their goal. The basic principles of the compass step are pretty clear and therefore the discussion mainly evolves around the magnetic compass and its implementation in a living being. The basic principles of the map step, on the other hand, are still unknown and there are considerable discussions going on about the general structure of such a navigational map. It is mostly accepted that there must be at least two different types of maps, a map for navigation close to the goal, the so-called mosaic map, and another for long range navigation that also allows the birds to determine their home course from unknown places, the so-called gradient map (Wiltschko & Wiltschko, 1999). The mosaic map is supposed to be a mental representation of visual cues, so-called landmarks, and other non-visual cues, as well as their relative position to each other and their relative position to the goal (Wallraff, 1974). The mosaic map therefore requires a lot of information in order to allow effective navigation and its scale must be limited. Estimations about the size of the mosaic map are mainly based on direct observations of pigeons returning to their home loft (Michener & Walcott, 1967; Braithwaite, 1993), but there are also first approaches to calculate the scale of the mosaic map from tracking data (Schiffner *et al.*, 2006). It is currently assumed that the mosaic map's size is somewhere between 6 and 10 km. The gradient map must consist of at least two different natural gradients that also allow extrapolation beyond the birds' familiar area. It is assumed that one of these gradients is the intensity of the earth's magnetic field (Wiltschko & Wiltschko, 1999) - a factor that could provide the birds with information on whether they are north or south of their goal. Other factors that have been considered to be potential navigational factors are the earth's gravitational field (Lednor & Walcott, 1984), infrasound (Hagstrum, 2001) and also olfactory cues (Papi *et al.*, 1971; Papi & Wallraff, 1982). However, experiments testing the involvement of either of these factors in the navigational process have not yet produced consistent results. It is also

not clear whether infrasound could be used as a map factor at all or whether it could serve as yet another directional sense. Olfactory cues are more likely to form patches of gradients, which would be difficult to extrapolate beyond a certain area and therefore could not explain long range navigation (Becker & van Raden, 1986; Waldvogel, 1987). While the mosaic map must be limited in size, the gradient map must be limited in resolution, as it is improbable that the natural gradients can be resolved with unlimited precision. Therefore the scale of the mosaic map has implicit effects on the resolution of the gradient map and vice versa. This means, the resolution of the gradient map must be precise enough to allow navigation until the birds have reached the area of the mosaic map; and in turn the size of the mosaic map must cover the area, where the change in gradient factors is below the detectable threshold. Yet, experiments with pigeons wearing frosted lenses (Schmidt-König & Schlichte, 1972) imply that at least some pigeons can return home without the aid of visual cues. Thus suggesting that there might be considerable overlap between the mosaic map and the gradient map.

### **1.3. A Model Organism**

Most of what we know about navigation in birds comes from studies focusing on the homing behavior of pigeons. The pigeon therefore can already be considered a model organism for navigation in birds, although it seems not everyone shares this point of view. Their ability to home from distances up to 1000 km is as impressive as the distances birds cover during migration (for example the Eurasian coot or the black-headed gull; Rüppell & Schifferli, 1939). Furthermore, the basic principles of navigation are considered to be the same in all bird species (Wiltschko & Wiltschko, 2003a) and therefore selection of a species for research should only be based on practical considerations.

## 1. Introduction

The pigeon has some considerable advantages when performing tracking studies: Recovery rates are almost 100%, because the experimenter always knows where to find the pigeon after the experiment. In addition the pigeon's urge to return to its loft is present throughout the whole year, therefore experiments are not restricted to a specific season. Through domestication, with extreme focus on loft loyalty in order to compete in pigeon races, this urge is even higher than in any wild bird. All in all, not only is the pigeon extremely reliable, but also always properly motivated to perform the task of homing.

Most reservations towards pigeons come from studies indicating that domesticated animals suffer from brain size reduction (e.g. in ducks Ebinger, 1995); however, a recent study indicates that a general regression of brain size can not be observed in pigeons (Rehkämper *et al.*, 2007). While the size of certain portions of the brain are indeed reduced, the hippocampus, which is considered to play an important role in navigation (Bingman *et al.*, 2003), has an increased size (for a concise review see Mehlhorn & Rehkämper, 2009).

### 1.4. Tracking Animals

Traditional behavioral studies of pigeons were limited to recording the initial behavior of pigeons as they leave a site and orient towards their home loft, as well as to homing speed and recovery rates. The information gained from such studies is limited and naturally it has always been of great interest to devise methods that allow tracking the animals behavior over an extended period of time, in order to gain insight into the actual homing process.

Today there are many different approaches that allow researchers to track animals, ranging from the still most popular method of radio telemetry to more expensive approaches, where the animal is followed by plane (Griffin, 1952a; Hitchcock, 1952) or helicopter (Wagner, 1970). While radio telemetry has the

advantage of being extremely cost-effective, it also has the disadvantage that it requires a rather complicated antenna setup. In order to achieve acceptable accuracy and continuous recording it is necessary to either have a vast array of antennas set up along the most probable route or follow the bird with a vehicle or airplane (Michener & Walcott, 1967). Though, even under optimal conditions accuracy of radio telemetry still is limited. Before commercial GPS was available the only alternative were bird-borne direction recorders (Bramanti *et al.*, 1988). While being cost-effective and light weighted enough to be carried by birds, reconstruction of the actual flight path was complex and therefore the method has probably not received the attention it would have deserved.

For quite some time now miniaturized GPS recorders are available for scientific purposes and allow direct recording of the birds' flight paths with high accuracy and acceptable additional weight load on the birds. The GPS recorders that are currently used in research of pigeon homing have been originally developed independently by two different workgroups (von Hünenbein *et al.*, 2000; Steiner *et al.*, 2000), but are both quite similar in weight, size and general set-up. Currently the only limiting factor for GPS studies is the receiver's operating time, due to high energy consumption and the limited capacity of modern batteries.

### **1.5. Analyzing Tracking Data**

So far analysis of tracking data is still mostly limited to variables that are equivalent to those recorded during traditional releases. Although there are several studies that have employed more sophisticated methods, the knowledge gained from the data that is now available from tracks recorded with GPS devices is still rather limited. In light of these circumstances I felt the need to develop new methods that would pay tribute to the increased number of data points and thus give deeper insight into the pigeons' homing process.

## *1. Introduction*

One aspect of particular interest is the influence of experience and how certain parts of the tracks are affected by it. Another aspect is the point of decision (Schiffner & Wiltschko, 2009), the point after which the pigeons have decided to fly home, and the meaning of the preceding initial phase, in which the birds seem to stray around the release site. Although there is no evidence that the pigeons look for navigational factors during that time, evidence contradicting such a hypothesis is also very weak.

### **1.6. Dynamic Systems Theory**

Beyond these comparatively simple calculations I decided to introduce methods from the field of dynamic systems theory to the field of behavioral research. These methods could help to characterize the underlying mechanisms of the pigeons' homing process. The approach I used is based on the method of time lag embedding (Takens, 1980), which allows reconstruction of the underlying process from an one dimensional time series, e.g. the tracks recorded during the homing flight of the pigeons. By applying this method it is possible to analyze dynamic systems, such as the navigational process, without any a priori knowledge about the number of factors involved in these processes and their interactions.

Dynamic systems can display either deterministic, stochastic or chaotic behavior and as it has been shown in a previous study the behavior of the pigeons is of chaotic nature (Nehmzow, 2006). At first this may sound confusing, as chaos is commonly associated with stochastic behavior, but unlike stochastic processes, chaotic processes are basically deterministic and are by no means random. While deterministic processes have clear points of attraction, so-called attractors, to which they return repeatedly in specific patterns, chaotic processes are characterized by so-called strange attractors and while being attracted to these points, they never actually reach these points of attraction and

do so in a seemingly random pattern. Determinism and stochasticity are merely theoretical concepts that serve the purpose of characterizing the behavior of different systems. The concepts I am going to introduce in this study allow me to measure directly the stochasticity within a system, as well as the complexity of a system. The basic principles of this idea evolved from the discovery of the so-called butterfly effect and the sensitive dependency on initial conditions. This effect was discovered by Edward Lorenz (1963) during his study of fluid convection in the atmosphere which is also governed by the principles of chaos. Another popular system that displays chaotic behavior is the so-called logistic map, which is commonly used as a simple population growth model. Chaotic behavior has been described in a multitude of different systems in a wide variety of fields (e.g. Medicine: Lai *et al.* (2002); Miyata *et al.* (2004); Robotics: Nehmzow (2006); Turbulence Convection: Castillo & Hoover (1998); and many more).

### 1.7. Characterization of the Navigational Process

The primary goal of this study is to define the characteristic properties of the navigational process. Individual abilities of pigeons may limit access to certain navigational factors and in turn force each individual to apply different navigational strategies. Access to certain navigational factors may also depend on previous experience and familiarity with a site. Hence, experience may enable pigeons to use specific navigational factors and thus allow application of different navigational strategies. Therefore I analyze the results for dependence on abilities of individual pigeons, as well as for dependence on the pigeons' experience.

The secondary goal is to identify transitions between different navigational strategies, with the focus on separating navigational from non-navigational phases and assessing the precision with which the pigeon can determine its

## *1. Introduction*

home course. While this may not tell us how precise the individual components, the map and the compass, are, this estimate may allow setting more precise boundaries for simulation experiments (Wiltschko & Nehmzow, 2005).



## **2. Tracking and Experimental Procedure**

### **2.1. GPS Tracking**

The Global Positioning System or in short GPS is a satellite supported positioning system and was originally developed by the U.S. Department of Defense. Its purpose is to determine the position and velocity of objects on the earth's surface. Like radio tracking the system is a sender receiver system, but unlike radio tracking, where one transmitter is used together with several receivers, the system is comprised of 24 satellites acting as transmitters. These satellites are deployed in earth's orbit and constantly transmit radio signals, ensuring that position determination is possible around the clock. The signal emitted by each satellite contains information about the time when the message was sent, the precise orbital location of the satellite, the so-called ephemeris, and information about the health of the system, including rough estimates about the current orbits of all other satellites, the so-called almanac. By measuring the transit time of the signals received from at least three or more satellites a GPS-receiver can then theoretically determine its current position through trilateration. Trilateration is a position determination process similar to triangulation, but positions are derived from distances instead of angles. Although three satellites are theoretically sufficient to determine the receivers position, even small errors in the internal clock of the satellites already yield very large errors in position. This is due to the fact that the radio signals travel at the speed of light, so that even minor discrepancies in time can have such a dev-

## 2. Tracking and Experimental Procedure

**Table 2.1.** – GPS receiver specifications for the two types used in the current study

<b>Sensitivity</b>	<b>UP300</b>	<b>UP500</b>
Acquisition	143dBm	146dBm
Navigation	158dBm	159dBm
Tracking	158dBm	159dBm

The table includes the Acquisition sensitivity, i.e. the minimum signal power level at which the GPS receiver can autonomously acquire satellites, the Navigation sensitivity, i.e. the minimum signal power level at which the GPS receiver can continue taking position fixes without having to rely on the ephemeris and the Tracking sensitivity, i.e. the minimum signal power level at which the GPS receiver will keep track of at least one satellite. The reference value for dBm is 1 mW. An increase of 1dBm roughly equals a 25% increase in sensitivity

astating impact. Therefore usually four or more satellite signals are used for a valid positional fix.

All GPS recorders used in this study were based on the prototype developed by von Hünenbein *et al.* (2000) which later was modified by H. Hamann in order to increase reliability and precision, while at the same time decreasing the weight of the device. The actual receiver modules of the GPS recorders were either of type Fasttrax up300 or up500, both allowing a precision of  $\pm 1.8$  m for the determination of the current position and  $\pm 0.1$  m/s for the determination of the current velocity (for details see Table 2.1). Additional components were a data logger and an embedded patch antenna.

The dimensions of the GPS recorder were roughly 50\*50\*10 mm. The weight, not including the battery, was 12 g. The pigeons were equipped with a harness made from about 85 cm Teflon tape (Bally Ribon Mills) and two epoxy resin plates (20\*60 mm ventral, 25\*85 mm dorsal), altogether weighing 5 g. The flight recorder was wrapped in anti electrostatic plastic, ensuring shielding from water and electrostatic discharges that could have damaged the flight recorders. In order to allow access to satellite signals a window equal to the size of the patch antenna, was left open and covered with normal plastic foil. Aside from shielding the device from external influences, the anti electrostatic

## *2. Tracking and Experimental Procedure*

plastic also shielded the pigeons from any possible influence from the device. The coating added 2-3 g of weight. Immediately before release, the recorder was attached to the dorsal plate of the harness and fixed with Velcro and additional sticky tape.

The recorder was set to take a positional fix every second. Each fix was based on the RMC line (Recommended Minimum Specific GPS Data), including date, time, geographic longitude and latitude and speed over ground. The settings allowed operation for 5 to 7 hours, limited only by the capacity of the battery. Three different types of batteries were used during the course of the experiments. Due to bottlenecks in delivery of batteries of suitable size and capacity in the early stages of the study, the first two batches were handmade, from bigger batteries, resulting in higher variability of weight. The first batch weighed between 8 and 9 g, and the second batch 11 g. Both types roughly had the same dimensions (50\*30\*5 mm). The third and final batch were industrial manufactured batteries of the type Kokam SLPB 20C, with slightly increased dimensions (50\*35\*5 mm) and a weight of 11 g. Besides these differences all batteries roughly had the same size as the GPS recorder itself, were lithium polymer accumulators and had the same voltage of 4.2 V and current output of 350 mAh and therefore allowed equal operating times.

Although I always made sure that the GPS receiver was properly working and had satellite contact before it was wrapped in the coating, technical difficulties with the GPS receiver (satellite loss, battery failure, etc.), occasionally led to incomplete or otherwise non-evaluable tracks. On other occasions, pigeons landed before they had reached home and took pauses that lasted longer than the operating time of the recorders, also resulting in incomplete tracks.

The components sum up to a maximum additional load of 31 g. Considering that a pigeon weighs between 350 g and 450 g, the setup easily exceeds the recommended 5% of body mass. Yet these 5% are just a rule of thumb

## 2. Tracking and Experimental Procedure

and studies have shown that the additional weight has no influence on the flying abilities of pigeons (Gessaman & Nagy, 1988) or birds in general (Barron *et al.*, 2010). However, according to these studies an increase in energy cost is observed, which is considered to be related to the additional drag and not to the weight itself. This notion has just recently been confirmed by a wind tunnel study, which showed that drag from even smaller tracking devices already results in 10% increase of metabolic cost (Bowlin *et al.*, 2010). As the increased metabolic cost from carrying transmitters is estimated to be roughly as high as during molt I decided to abstain from performing tracking experiments during that period.

### 2.2. Experimental Birds and Training

The experimental birds were adult pigeons from the loft at the J. W. Goethe University in Frankfurt (50°08'N, 8°40'E). They were at least one year old and in their first year of life they had participated in a standard training program, with releases up to 40 km in all cardinal compass directions. Additionally, they had completed several training flights each spring and some, but not all, had participated in previous experiments, the number of such flights increasing with age. The normal training regime in spring included training releases of all pigeons at least twice a week, up to 30 km and additional trainings up to 20 km with dummy weights. The pigeons taking part in each series of releases were all born in the same year. There were two groups, the first born in 2007 and the second born in 2008. The first group consisted of a total of 27 individuals, with 9 male pigeons, 11 female pigeons and 7 pigeons of undetermined sex. The second group consisted of 15 individuals, with only 2 male pigeons, 8 female pigeons and 5 pigeons of undetermined sex. Pigeons need to be sexed by observation of courtship or copulation. Due to the fact that the pigeons were quite young when I conducted these experiments and some of them were

lost before they had been observed during such activities it was unfortunately impossible to determine the sex of all individuals.

### 2.3. The Release Sites

Release sites (for details see Table 2.2 and Figure 2.1) were selected 30 km away from the loft, in directions close to the cardinal compass directions north and south. The study was restricted to releases from more distant sites in order to ensure a sufficient number of data points were available for analysis. In addition, release sites in 60 km distance from the loft were selected roughly in the same directions, so that pigeons flying from these locations would presumably fly over the area around the closer release sites and thus over familiar terrain. Due to the mountain ridges in the west and the extended forests in the east these areas were not suited for the present study. In addition to the previously mentioned sites I also selected two more: NE40 which is located in the magnetically anomalous region of the Vogelsberg and had served as an experimental site in previous studies (Wiltschko *et al.*, 2009a, 2010) and a control site, SW40, from the same study, located 40 km west of the Frankfurt loft. Pigeons released from these two additional sites included pigeons from the two series, as well as six additional pigeons that were born in 2005.

**Table 2.2.** – Names and information on each release site used in the present study.

Name	Longitude	Latitude	Direction	Distance
N30	50°24'N	8°43'E	189°	30.7 km
N60	50°36'N	8°51'E	194°	54.5 km
S30	49°52'N	8°34'E	13°	28.8 km
S60	49°36'N	8°28'E	14°	58.9 km
NE40	50°24'n	9°06'E	225°	44.8 km
SW40	49°47'N	8°08'E	61°	42.2 km

The table includes the abbreviations for each release site, as they are used in the main text, the longitude and latitude and the direction and distance to the pigeons' home loft.

## 2. Tracking and Experimental Procedure

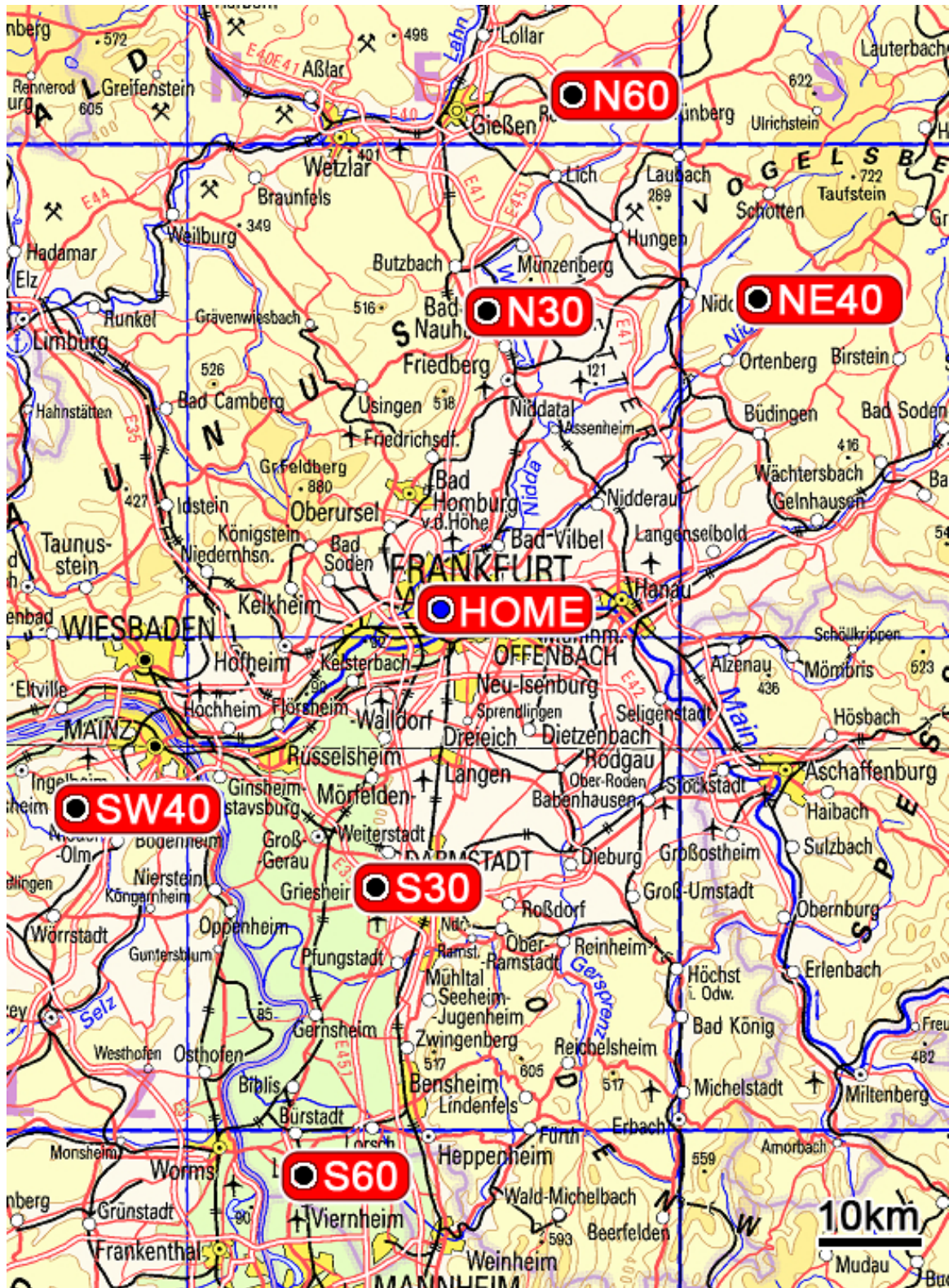


Figure 2.1. – Locations of the six release sites plotted on a Ordnance Survey map of the area around Frankfurt.

## 2.4. Release Procedure

The experiments were conducted in a fixed sequence of recorded and unrecorded releases with altogether 12 releases, 30 km from home, and one additional release, 60 km from home. Only every fourth flight was recorded with the help of the GPS receiver, meaning the first, fourth, eighth, and twelfth release were recorded and henceforth I will refer to these as F1, F4 and so on. Between those releases the pigeons flew from the same release site, but without GPS receivers, ensuring each individual would get more and more familiar with the region in the course of the study. Pigeons were released singly on these training flights, so they were forced to find their way home alone and could not just follow other pigeons. On these flights, the pigeons flew only with the harness and only when additional training seemed necessary, i.e. when the birds had returned late, weights were added. Before I released the pigeons at the sites N60 and S60, additional training flights in 60 km distance from the loft with and without weight were conducted. These training flights took place either from a site in the opposite direction or from a site located northwest of the loft. The additional training flights were necessary to ensure that the pigeons would be able to home with the additional load over these distances.

The first series of releases (N30) started on June 16th, 2008 and ended on August 5th, 2008. When the 12th release from 30 km distance was conducted, the experiments were forced to a halt due to extremely hot weather conditions and an unusually long period of molting. Therefore the additional flight from N60 could not be performed within the same year. The series was then restarted on May 4th, 2009 and came to conclusion on May 20th, 2009, adding another four flights to the series, during which the birds had to get reacquainted with the site. The flight from N60 was performed on June 5th, 2009. All pigeons taking part in this first series were born in 2007.

## 2. Tracking and Experimental Procedure

The second series (S30) took place from June 29th, 2009 to August 5th, 2009 and the release from S60 was conducted two weeks later on August 18th, 2009. The first flight from S30 took place under anomalous conditions, due to a severe magnetic storm. This resulted in unusually long return times, with some pigeons returning as late as the next day and only one complete track. Therefore I decided to record the pigeons' second flight, too, adding another recorded release to the series. All pigeons taking part in this second series were born in 2008.

The additional single releases at NE40 and SW40 took place on August 23rd, 2009 (NE40) and on June 29th, July 7th and 20th, 2010 (SW40), with a group of pigeons comprised of individuals from both series plus 6 additional pigeons that were born in 2005.

### 2.5. Track Analysis

The analysis of the tracks is separated into three distinctively different chapters, where each chapter is loosely based on the preceding and will introduce methods that get increasingly more complex. In the chapter "Traditional Analysis" I focus on parameters that are commonly calculated and analyzed in current scientific publications (Wiltschko *et al.*, 2007). In the chapter "Phases of the Flight" I utilize a new method, developed by myself, to separate the flight paths of the pigeons into distinctively different phases (Schiffner & Wiltschko, 2009). In the final chapter "Time Series Analysis" I introduce methods from the field of dynamic systems theory to the field of behavioral research to analyze the individual phases in view of characteristic properties of the pigeons' homing process. Due to the complexity of the different methods, they will be introduced in the corresponding chapter, yet there are some similarities that I will explain at this point. All programs used in this study, with a few exceptions which will be mentioned accordingly, have been developed by myself. The tracking data recorded



## *2. Tracking and Experimental Procedure*

by the GPS which were originally stored as geographic coordinates (longitude and latitude), were transformed to the Universal Transverse Mercator (UTM) projection, a 2-dimensional Cartesian coordinate system, to allow calculation of distances and angles. The beginning of each flight was counted right from the moment when the bird's speed had increased beyond 5 km/h, based on the assumption that a pigeon is hardly able to move faster than 5 km/h without flying. Therefore portions of the track with a speed below 5 km/h were considered to be pauses and were consequently ignored during all calculations. The end of the flight was counted right from the moment the pigeon had entered the home area, defined as the area within a radius of 100 m around the loft. All track data within this area were also ignored during all calculations in order to avoid problems with pigeons flying over their home loft for an extended period before landing. It is quite obvious that such behavior is no longer part of the navigational process and thus it is reasonable to ignore it. Over the course of the experiments I recorded a total of 167 tracks from 48 individual pigeons, yet due to the varying requirements the number of evaluable tracks differs between each method of analysis. A detailed overview of all calculated variables for each track can be found in appendix D.

The programs for the statistical analysis have also been developed by myself, but are all based on well known statistical tests. All directional data was tested for preferences in directional choices using the Rayleigh test, including corresponding confidence limits for the directional choices. All comparisons on an individual level, i.e. between individual pigeons, were performed using the Wilcoxon signed rank test for matched pairs. Differences between different individuals were established using the Watson-Williams test for directional data and the Mann-Whitney U-test for all others. All tests for randomness of spatial distributions were performed using Hotelling's one sample test. All correlation coefficients and corresponding significance levels were determined using Spear-

## *2. Tracking and Experimental Procedure*

man's rank correlation. Details on all statistical tests applied in this study can be found in Batschelet's (1981) "Circular Statistics in Biology". Test statistics are given for all statistical test including significance levels. Significance levels given in tables are indicated by asterisks after the test statistic, with \*  $p \leq 0.05$ , \*\*  $p \leq 0.01$  and \*\*\*  $p \leq 0.001$ , all test statistics without asterisks are not significant, with  $p > 0.05$ .

## **3. Traditional Analysis**

### **3.1. Introduction**

In this chapter I am going to analyze the tracks on a level that is equivalent to the observations made during traditional releases without GPS. This means, I am going to derive variables from the tracks that are equivalent to those gathered during traditional experiments, where the pigeons are observed only with binoculars. Of course, such a use of the data would be very limited and therefore additional variables are introduced describing the behavior of the pigeons after they have left the immediate vicinity of the release site.

### **3.2. Analysis and Evaluation**

As means to describe the pigeon's behavior close to the release site I calculate so-called virtual bearings for the pigeon's position relative to the release site. One of these bearings is based on the position 1 minute after the pigeon took flight and the other is based on the position when the pigeon has reached a distance of 2.5 km from the release site. I chose a distance of 2.5 km as this distance corresponds to the distance a skilled observer can manage to follow a pigeon using binoculars. These values, therefore, roughly correspond to the bearings after one minute and the vanishing bearings that are recorded during traditional releases. Additionally the time when the pigeon took flight until it reached the point where the 2.5 km bearing is calculated was taken. This variable then is equivalent to the traditional vanishing interval. In order

### 3. *Traditional Analysis*

to discriminate these variables from the traditional ones I will refer to these variables as bearings after one minute, as well as 2.5 km bearings and intervals.

In traditional experiments the flight path of the pigeon after vanishing is not accessible. The only value that could be recorded is the homing time. Yet the homing time strongly depends on how many pauses a pigeon makes on its way home and how fast it flies. Therefore, this variable is not very useful to describe the pigeons' behavior during homing. GPS now allows us to exclude times where the pigeon is not flying, but still homing times strongly depend on the pigeons' flying speed, therefore earlier publications have introduced the efficiency of the track as a value that is independent of speed and pauses (Biro *et al.*, 2002). The efficiency of the flight is defined as the true length of the track divided by the direct distance from starting point to the end. It is usually given as an index value, with a value of 1.00 indicating that a pigeon took the most direct route and lower values indicating increased length of the path taken. I calculated the efficiency for all complete tracks as the total efficiency, but in order to get some useful efficiency estimates from incomplete tracks I also calculated so-called 2.5 km efficiencies, i.e. the efficiency until the pigeon had reached a point 2.5 km away from the release site. In order to get an assessment of the efficiency of a bird's flight, where the initial flying over the release site is excluded, I calculate so-called overland efficiency, defined as the efficiency from the first point 2.5 km away from the release site to the first point 1 km away from the home loft (Wiltschko *et al.*, 2007). Here the area 1 km around the home loft has been excluded to eliminate influences from possible changes in the pigeon's behavior as it approaches the loft.

For the analysis of the effect of experience on the flights of individuals I calculated so-called partial efficiencies. However, in order to calculate partial efficiencies a reference point is required. Theoretically partial efficiencies can either be calculated in reference to the release site or in reference to the home

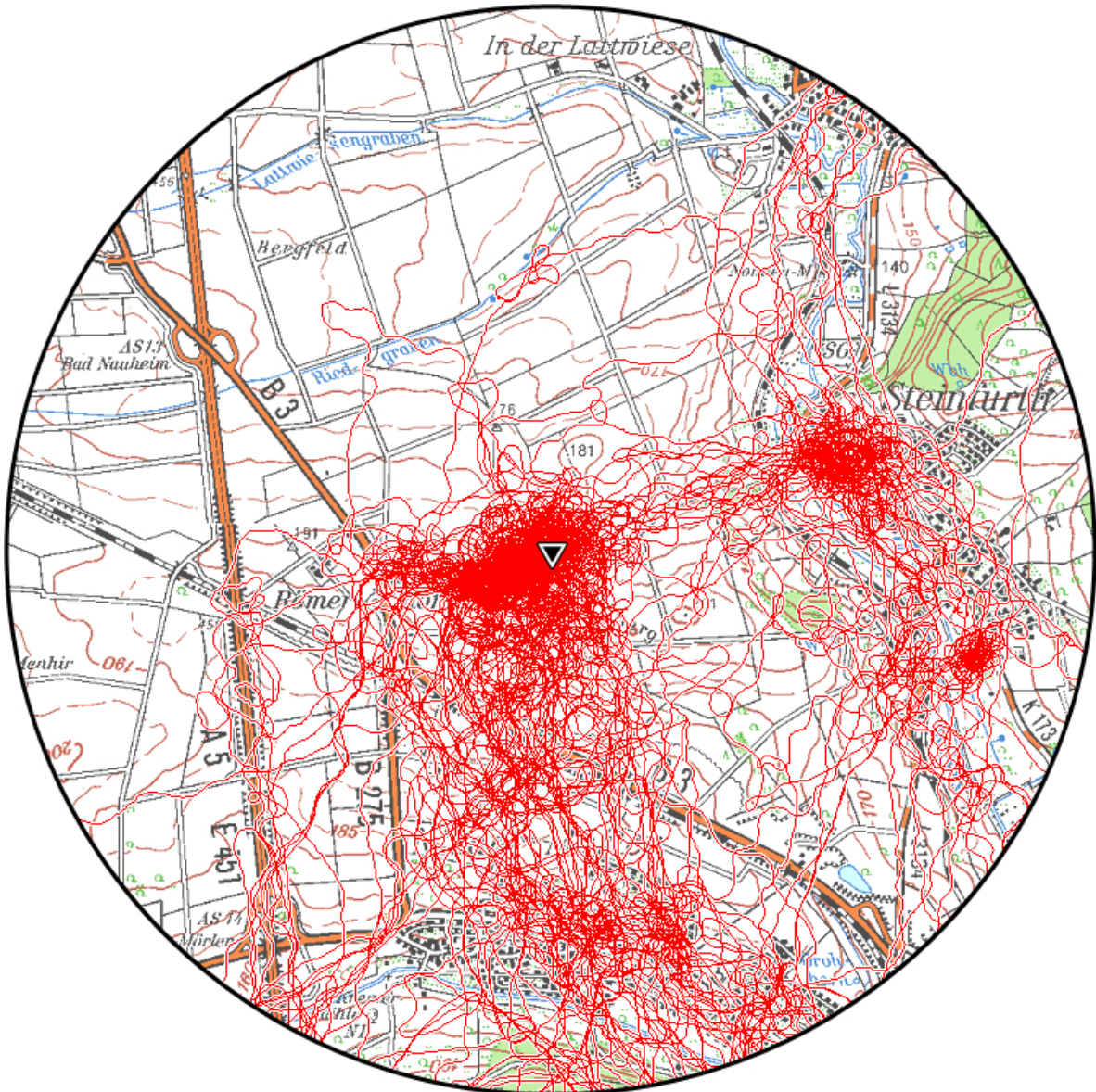
loft. These partial efficiencies are then calculated in reference to segments with increasing radii centered around one of these reference points. While using the release site as a reference point tells us how efficient a pigeon is moving away from the release site, using the home loft as a reference point on the other hand tells us how efficient the pigeon is flying towards home. I choose to calculate these partial efficiencies in fixed intervals of 500 m in reference to the home loft instead of the release site to allow comparison between different sites. Each segment's partial efficiency is then calculated based on the first fix within the next segment. Assuming a pigeon travels on average with a speed of about 16 m/s (60 km/h), this point may lie up to 16 m farther away from the exact interval distance. In cases where a pigeon enters a new segment and then flies back to the previous, the additional distance traveled is still attributed to the current segment. The efficiency of a segment is considered not to be evaluable in cases where the track ends before the next segment or when more than 5% of the data points are missing due to satellite loss. Efficiencies calculated for the final step are based only on the first 400 m, as the home area 100 m around the home loft, as mentioned before, is generally excluded from all calculations.

### **3.3. The Tracks**

Before I begin with the actual analysis of the tracks, I do a simple visual inspection. The visualization is realized by conversion of the original GPS data to the Geo-grid ".ovl" format. These ".ovl" files are then plotted on an ordnance survey map of the area around Frankfurt using the program TOP 50 Hessen (2005). In the beginning of the flight from release site N30, as shown in Figure 3.1, the pigeons tend to fly to one of two villages in the immediate vicinity of the release site. In almost all cases their flights continue (see Figures 3.2 to 3.6) on a course slightly left of the home direction, which leads them over a series of villages. After roughly 8 km, the pigeons' behavior changes and the tracks

### 3. Traditional Analysis

diverge. From this point some pigeons head out into directions that lead them to an area 12 km away and almost exactly north of their home loft. Others choose a more direct route, immediately correcting their initial deviation, and yet others continue on their previous path until they are also roughly 12 km away from the home loft, when they adjust their flight path and head home on a more or less straight route.



**Figure 3.1.** – All flights (colored lines) from release site N30 (black triangle), depicted is the immediate area 2.5 km around the release site.



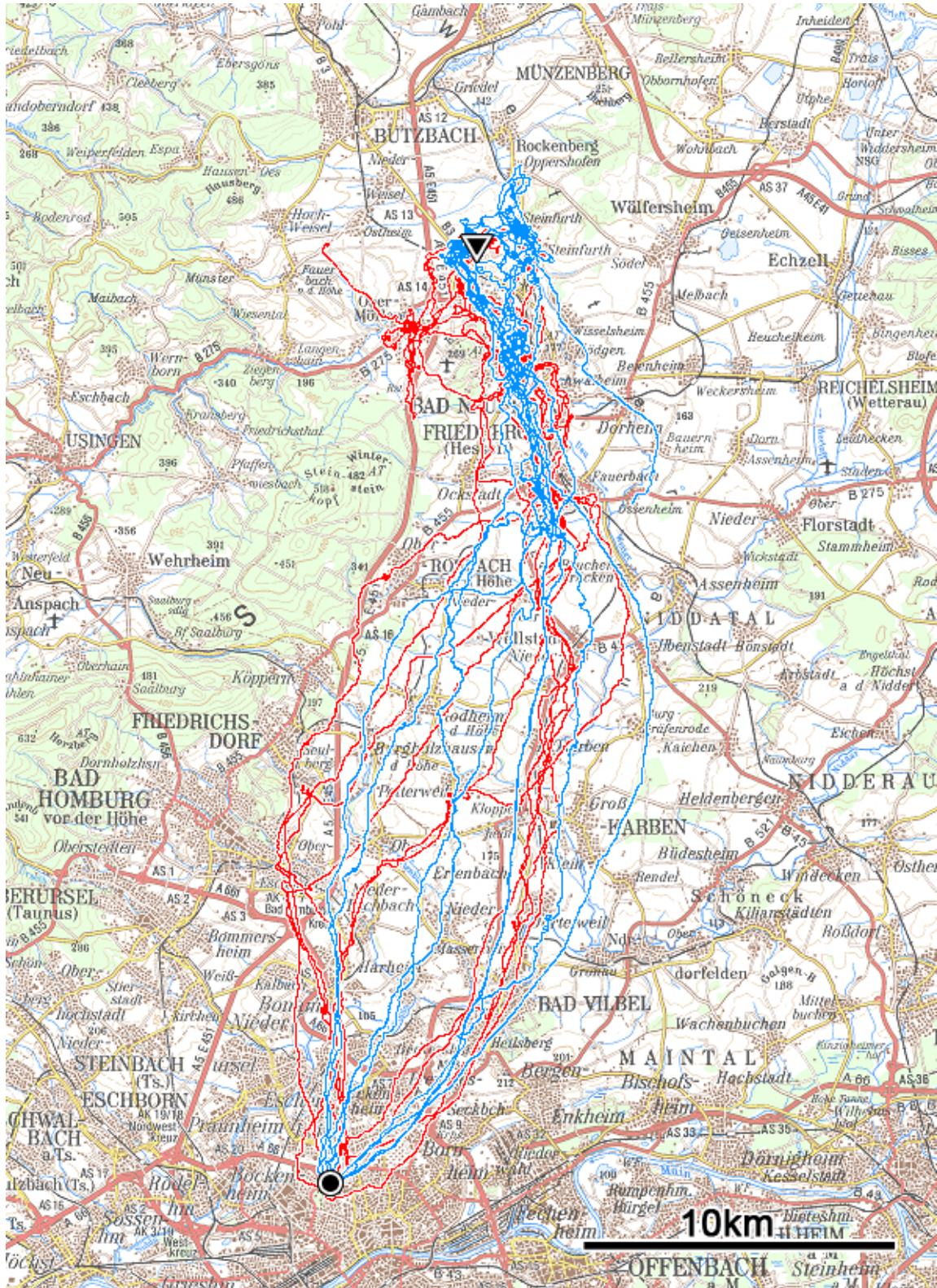


Figure 3.2. – Flights F1 (red) and F4 (blue) from release site N30 (black triangle) to the pigeons' home loft (black circle).



### 3. Traditional Analysis

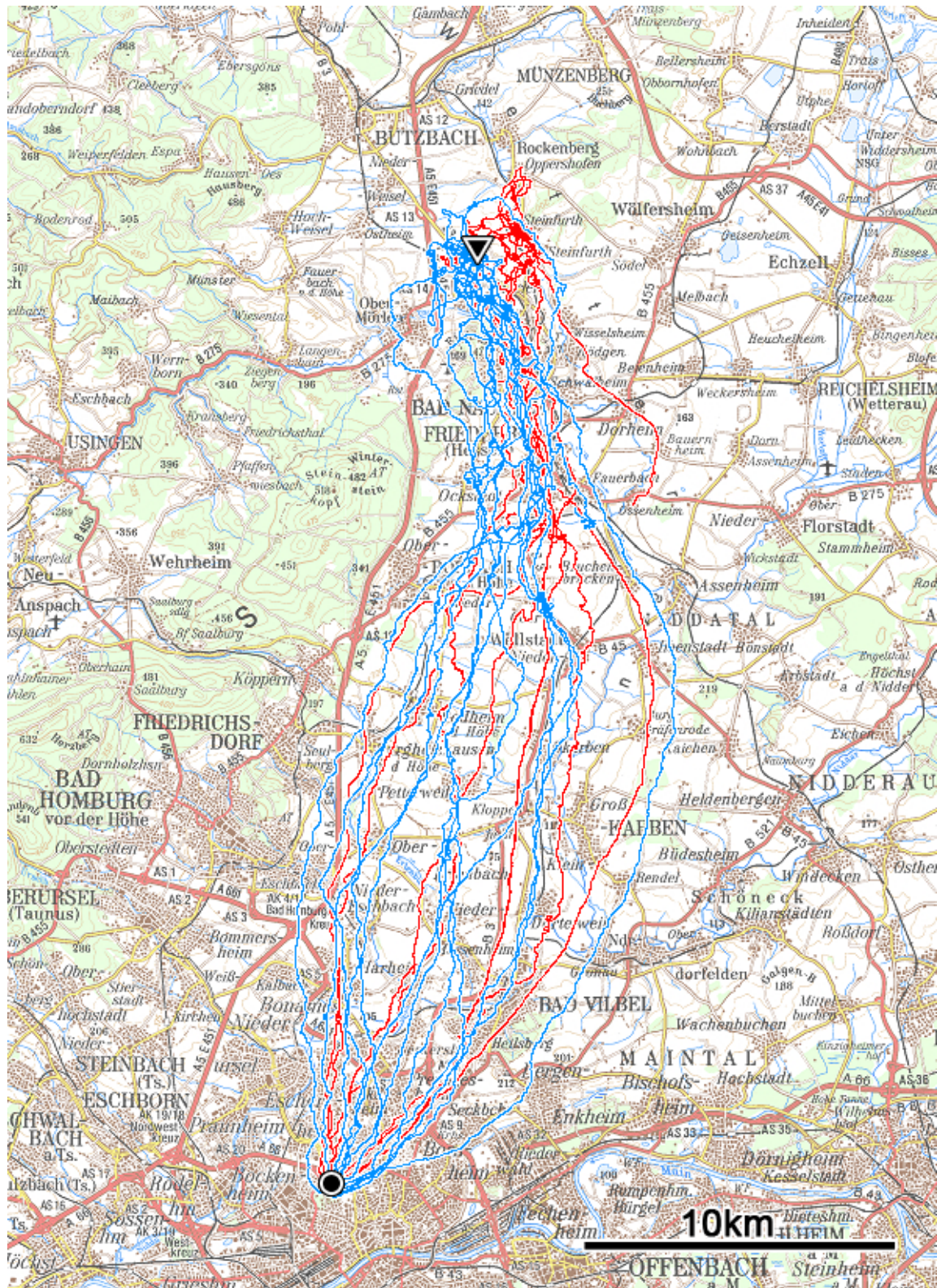


Figure 3.3. – Flights F4 (red) and F8 (blue) from release site N30 (black triangle) to the pigeons' home loft (black circle).



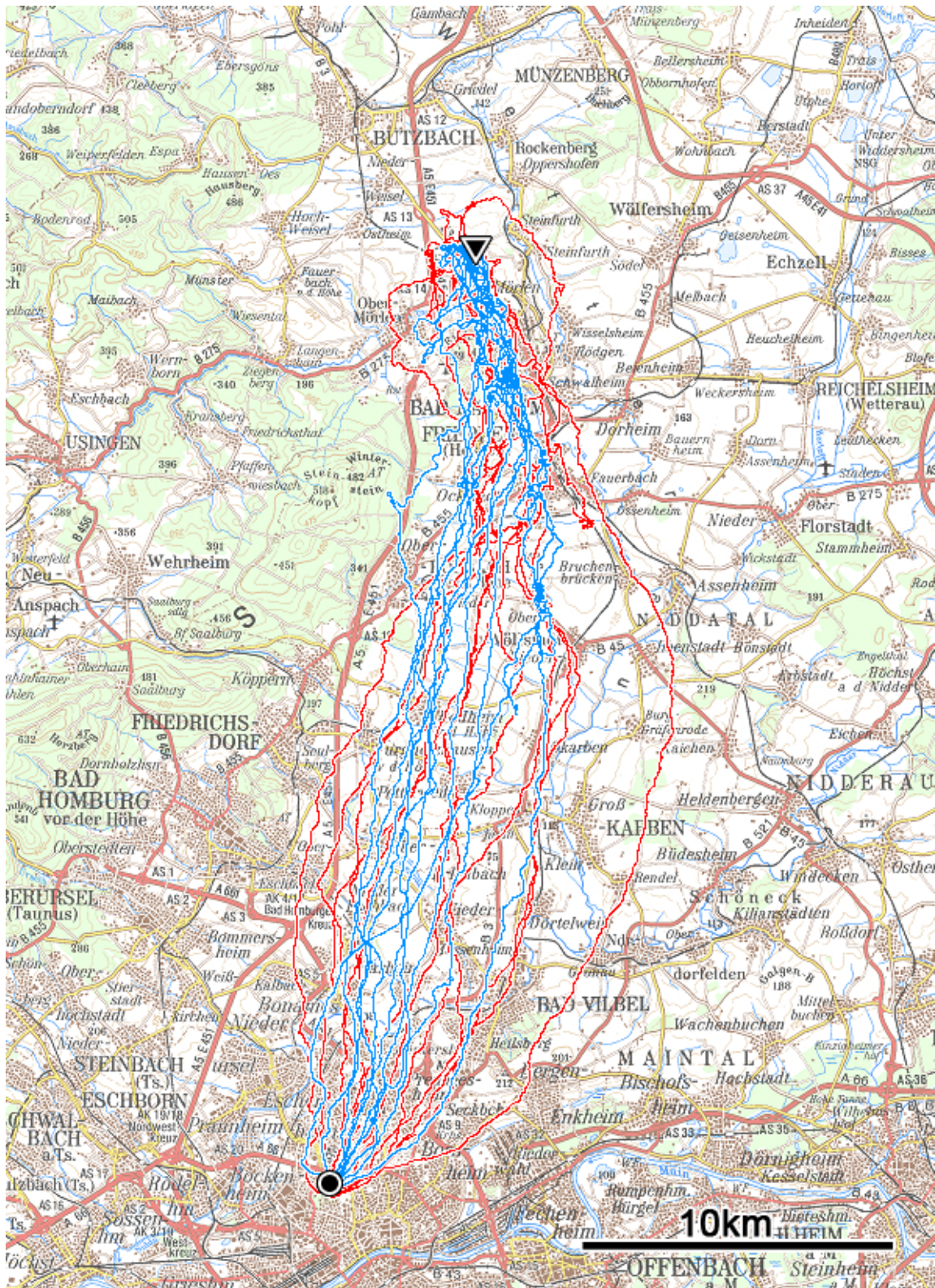


Figure 3.4. – Flights F8 (red) and F12 (blue) from release site N30 (black triangle) to the pigeons' home loft (black circle).



### 3. Traditional Analysis

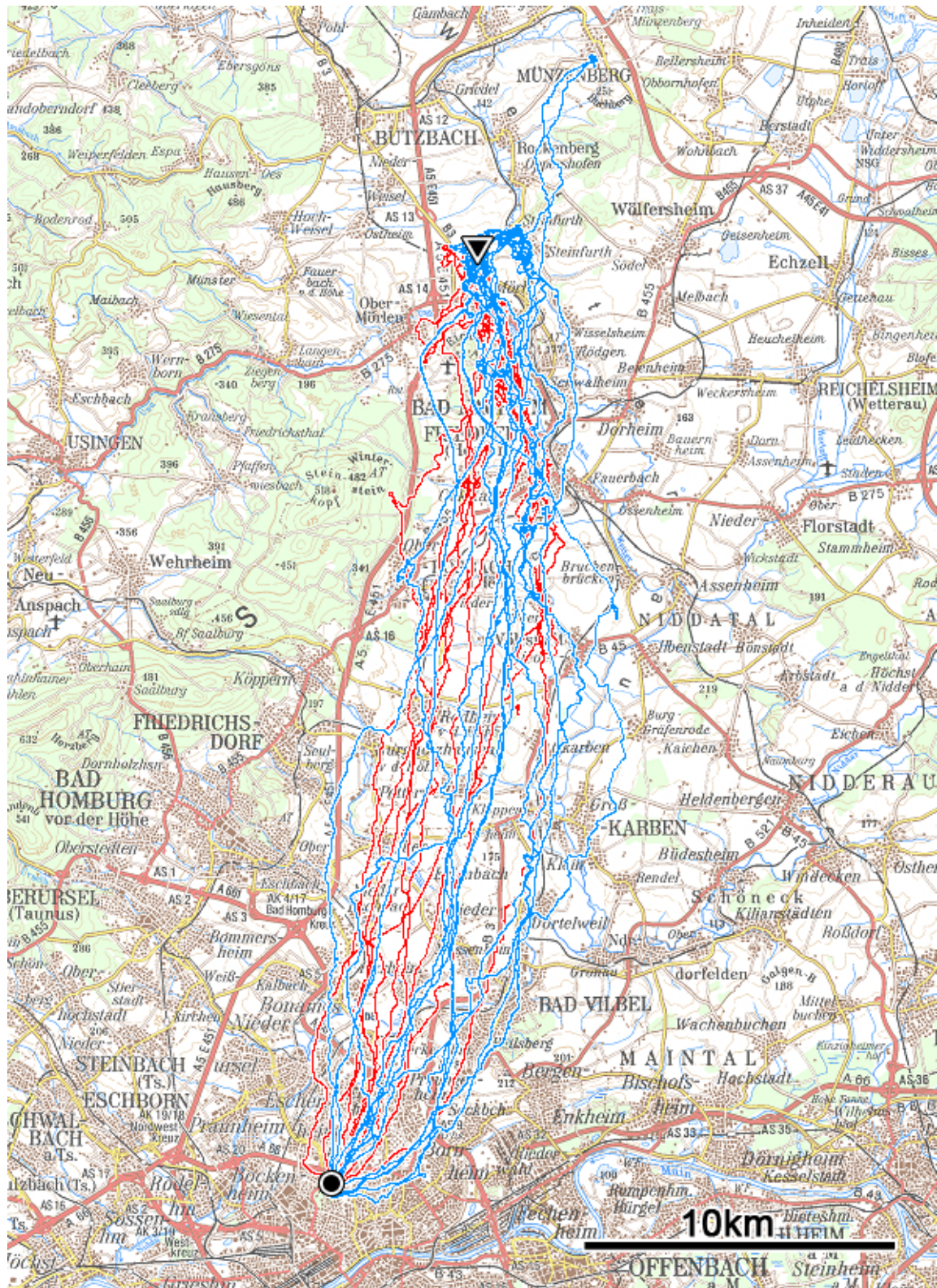


Figure 3.5. – Flights F12 (red) and F13 (blue) from release site N30 (black triangle) to the pigeons' home loft (black circle).



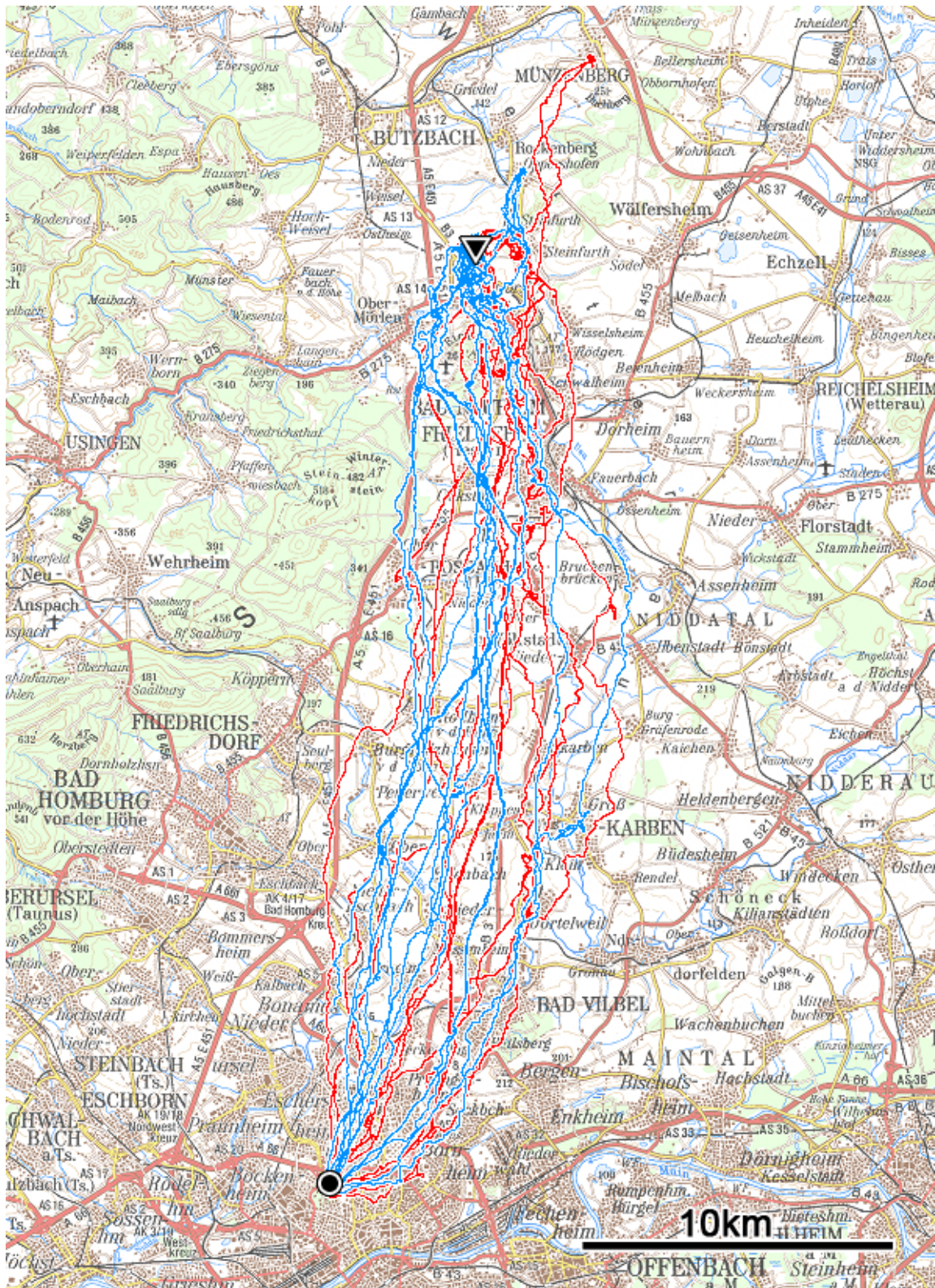


Figure 3.6. – Flights F13 (red) and F16 (blue) from release site N30 (black triangle) to the pigeons' home loft (black circle).

### *3. Traditional Analysis*

The same tendencies, for flight paths to converge over villages and for pigeons to fly towards the closest village can be observed during the S30 series. This is shown in Figure 3.7 and Figures 3.8 to 3.11. During the earlier releases of the series most pigeons head out on a westerly course; but later during the series the pigeons take a route that leads them away from the release site on a northerly heading - thus conveying the impression of two very distinctive flight corridors. The pigeons choosing the westerly course show a rather abrupt change in heading approximately 20 km away from their home loft, when they fly over the city of Rüsselsheim. The pigeons heading out north from the release site also adjust their flight paths at a similar distance from the home loft, at a distance of approximately 18 km. Yet some pigeons do not adjust their course until their current flight paths coincide with those of the westerly corridor, but interestingly no pigeon flies beyond this very point.







### 3. Traditional Analysis



Figure 3.8. – Flights F1 (red) and F2 (blue) from release site S30 (black triangle) to the pigeons' home loft (black circle).





Figure 3.9. – Flights F2 (red) and F4 (blue) from release site S30 (black triangle) to the pigeons' home loft (black circle).



### 3. Traditional Analysis



Figure 3.10. – Flights F4 (red) and F8 (blue) from release site S30 (black triangle) to the pigeons' home loft (black circle).





Figure 3.11. – Flights F8 (red) and F12 (blue) from release site S30 (black triangle) to the pigeons' home loft (black circle).

### *3. Traditional Analysis*

When looking at the releases from the two more distant sites N60 and S60, as shown in Figures 3.12 and 3.13, the same tendency to head towards the closest village immediately after release can be observed. Yet again the flight paths converge over villages and cities in the initial parts of the flight (see Figures 3.14 and 3.15). Interestingly, some individuals show an increased tendency to depart further from the home direction and occasionally visit bigger cities that lie in directions nowhere close to the home direction. As the pigeons approach the previous release sites they continue on paths that roughly coincide with those observed at the respective release sites. This behavior seems to be independent of whether the individual pigeon flies over the release site or only close to it. During the flight of the pigeons from S60 it was also possible to observe several pigeons circling above the previous release site (see Figure 3.16).



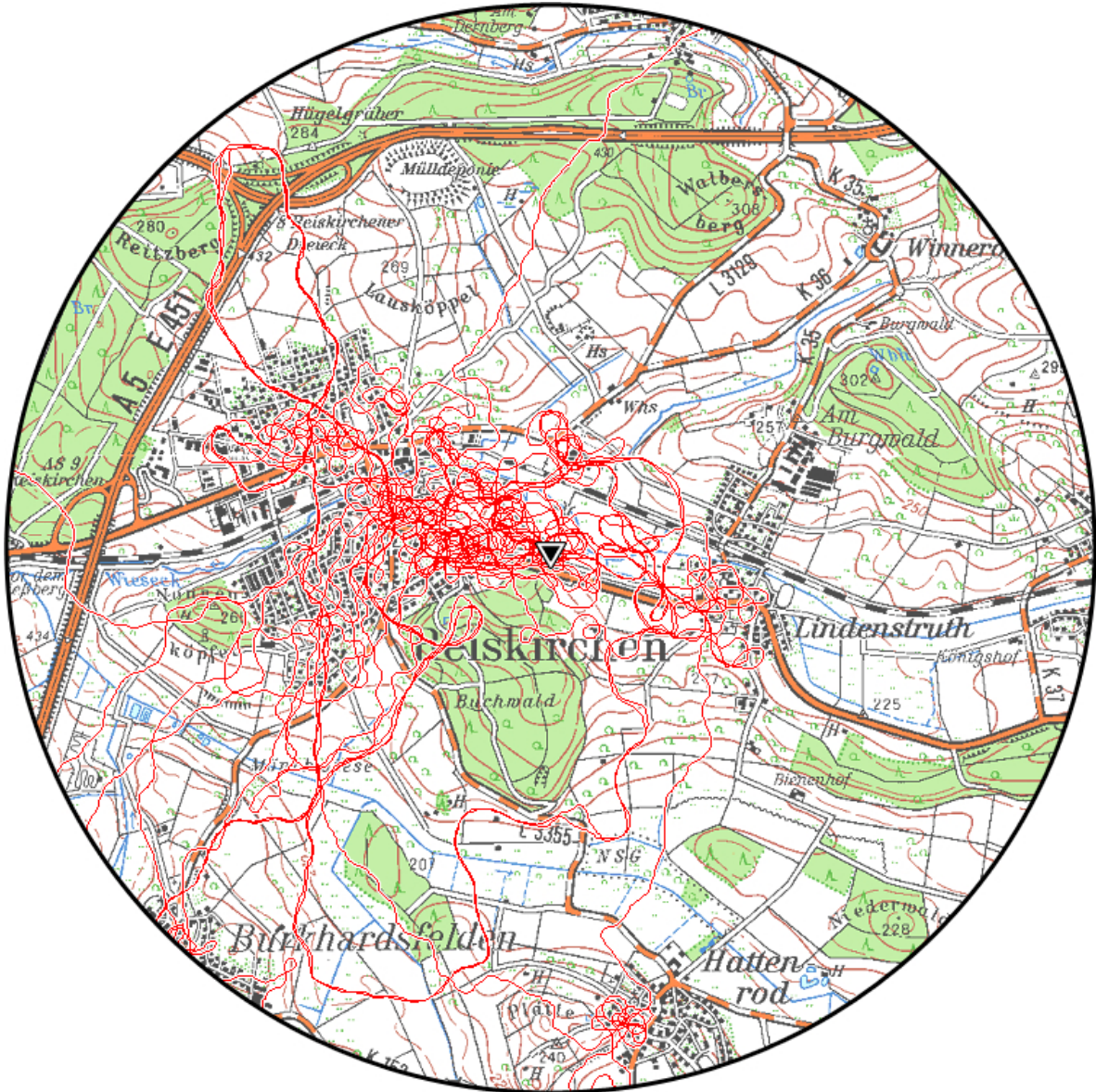
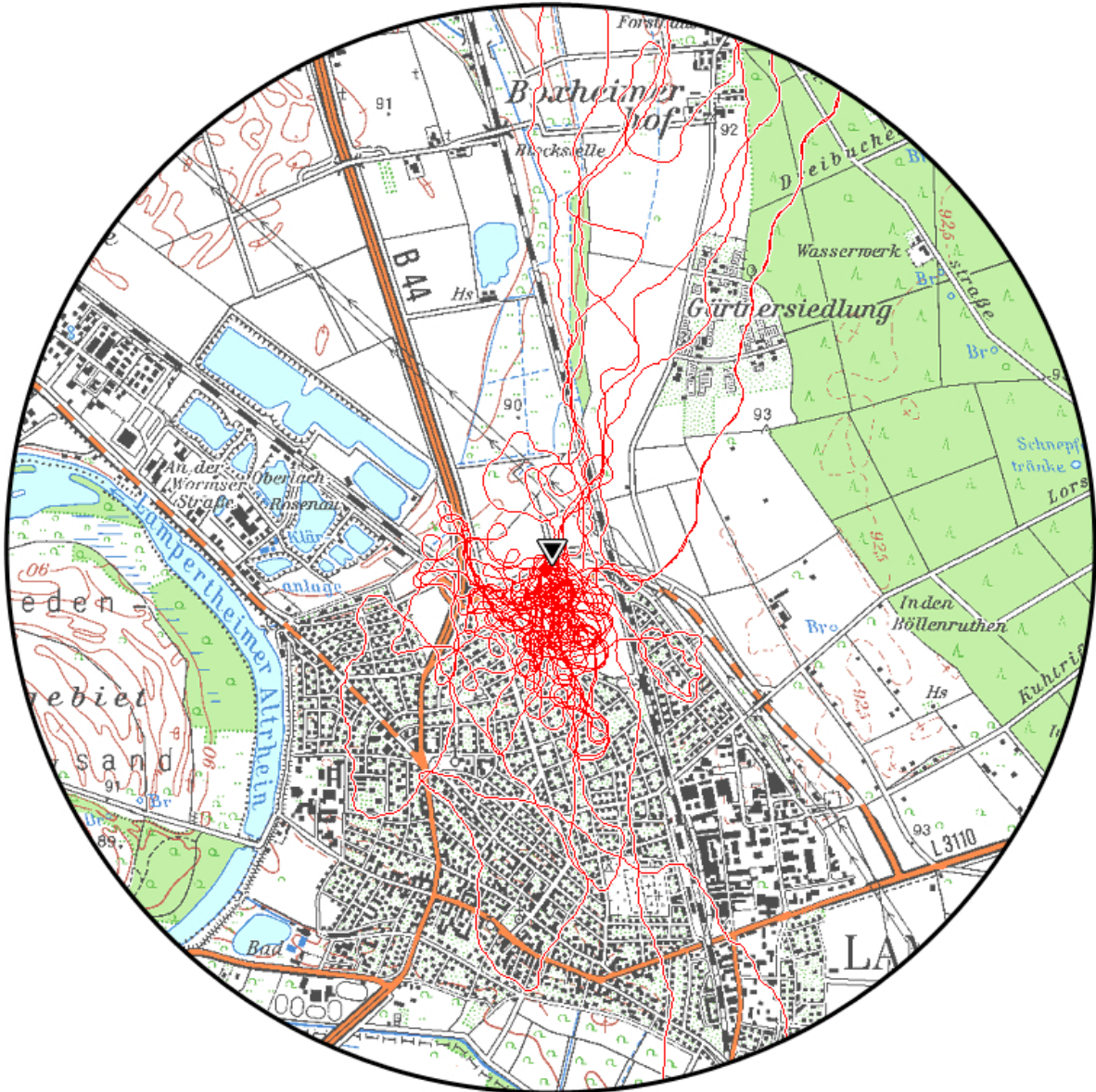


Figure 3.12. – All flights (colored lines) from release site N60 (black triangle), depicted is the immediate area 2.5 km around the release site.

### 3. Traditional Analysis



**Figure 3.13.** – All flights (colored lines) from release site S60 (black triangle), depicted is the immediate area 2.5 km around the release site.



### 3. Traditional Analysis

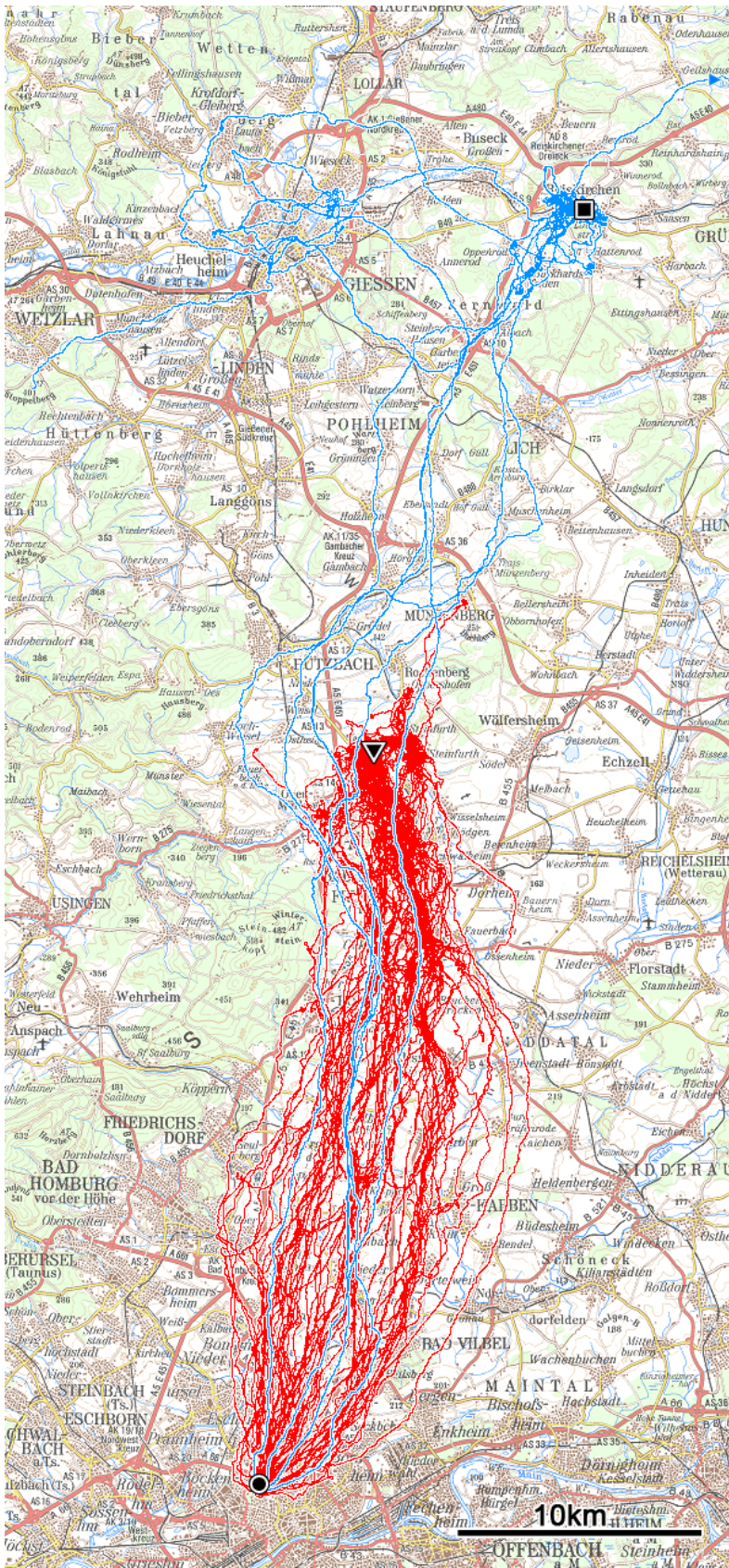


Figure 3.14. – All flights (red lines) from release site N30 (black triangle) and all flights (blue lines) from release site N60 (black square) to the pigeons' home loft (black circle). One pigeon 07-393 exits (filled blue triangle) the displayed area of the map; for a complete representation of the track see appendix C.



### 3. Traditional Analysis

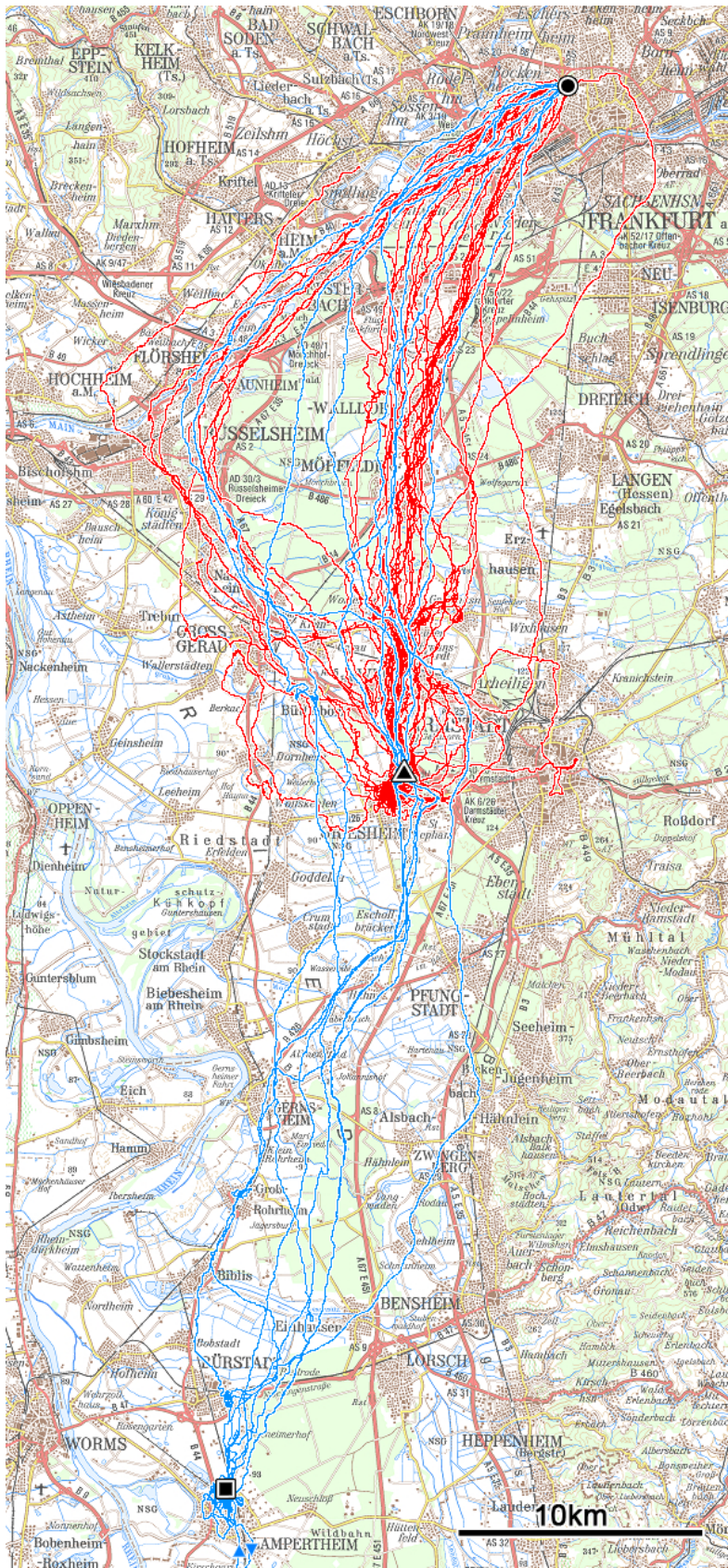


Figure 3.15. – All flights (red lines) from release site S30 (black triangle) and all flights (blue lines) from release site S60 (black square) to the pigeons' home loft (black circle). One pigeon 08-778 exits (filled blue triangle) and re-enters (open blue triangle) the displayed area of the map; for a complete representation of the track see appendix C.



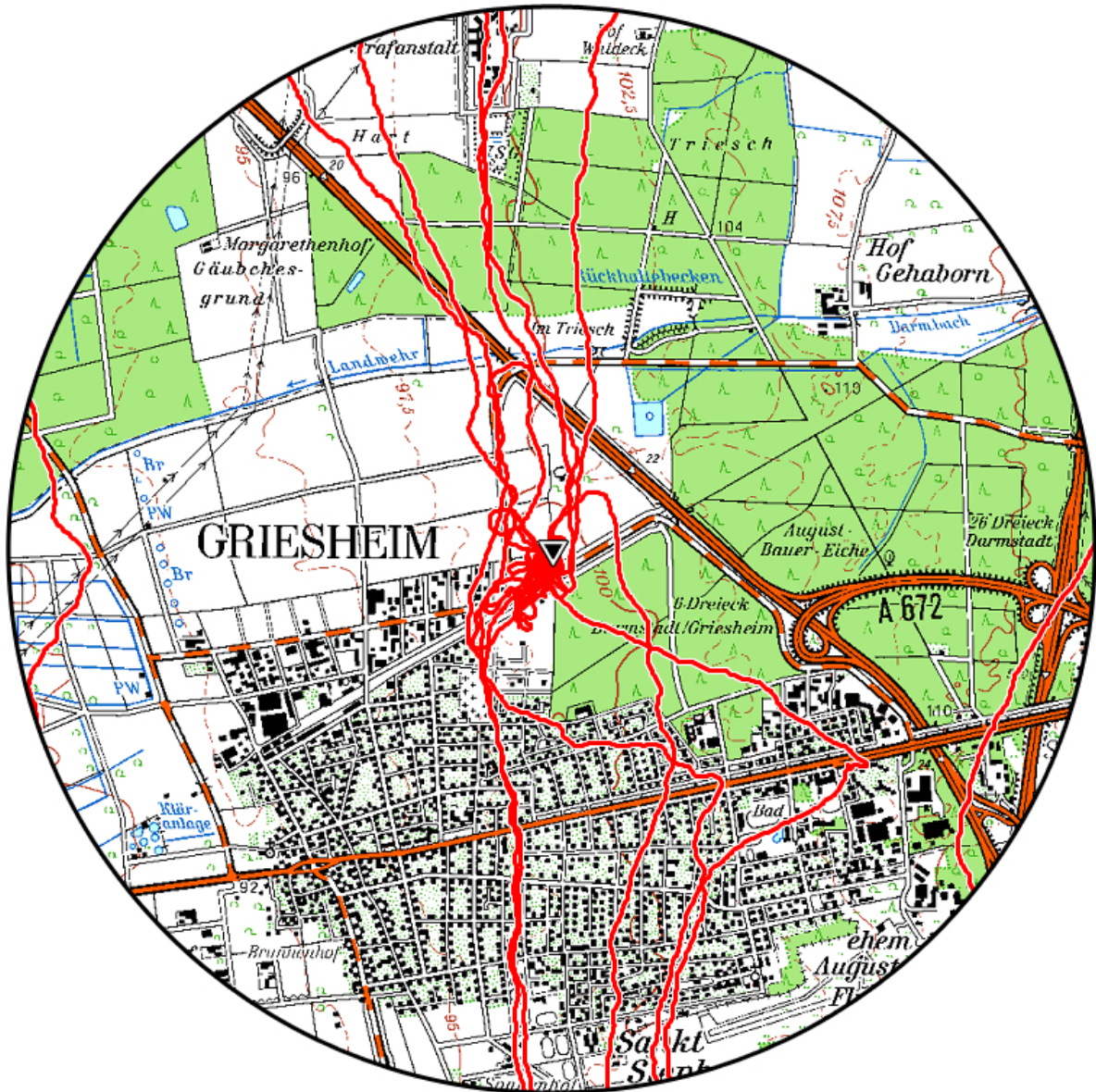


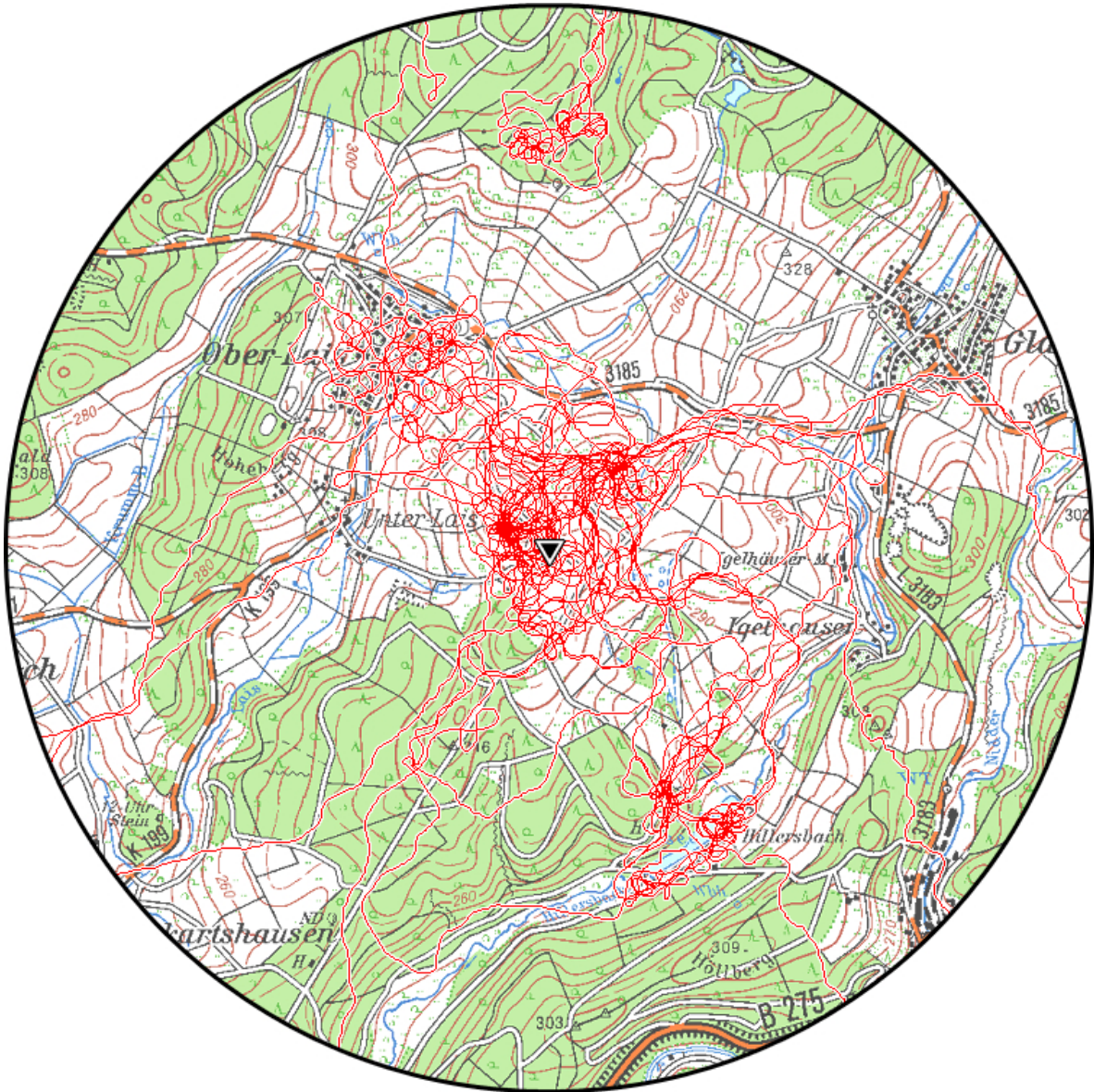
Figure 3.16. – Flights of pigeons (red lines) released at S60 as the pigeons approach S30 (black triangle).

### *3. Traditional Analysis*

The additional releases from NE40 and SW40 are shown in Figures 3.19 and 3.20. Close ups of the immediate area 2.5 km around the release site can be found in Figures 3.17 and 3.18. Like in all previous releases, the flights immediately after release show increased concentration over the village closest to the release sites. Yet the flights from NE40 seem to be a bit more erratic and circling behavior can also be observed over non-built-up areas. While the initial phase of the flight seems to be more erratic, the pigeons' flights become fairly straight after they have left the area of the Vogelsberg's magnetic anomaly. All except one pigeon choose routes left of the home direction and continue on those routes until they are roughly 15 km away from the home loft.

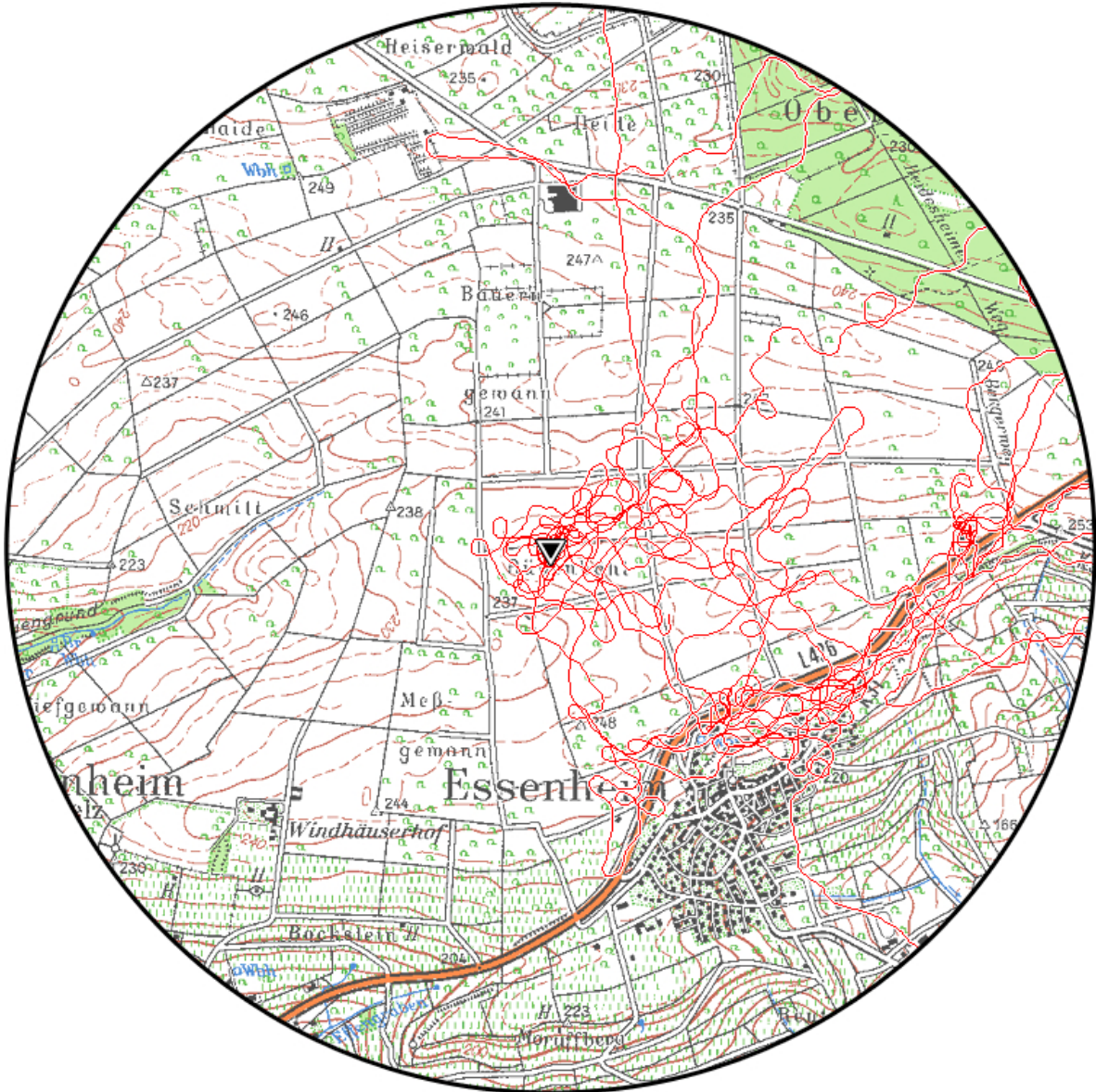
The pigeons released at SW40 also leave the site on a heading left of the home direction, yet their initially very straight routes change as they reach the city of Mainz. It seems as if the pigeons hesitate to cross the river Rhein and prefer to do so close to bridges. Some even make long detours and head towards the city of Wiesbaden before they attempt to cross the river (see Figure 3.21). After they have crossed the river the pigeons mostly continue on their previous heading, where some of the pigeons fly along the same corridor observed during the releases at the sites S30 and S60. Others choose more northerly routes crossing the city of Wiesbaden. Regardless of the path the pigeons had taken, they all finally adjust their course at a distance of roughly 25 km from the home loft. On both of these additional releases the pigeons show an increased tendency to correct for the displacement on the north-south axis during the initial portion of the flight and adjust their flight paths only as they are almost exactly east or west of their home loft.





**Figure 3.17.** – All flights (red lines) from release site NE40 (black triangle), depicted is the immediate area 2.5 km around the release site.

### 3. Traditional Analysis



**Figure 3.18.** – All flights (red lines) from release site SW40 (black triangle), depicted is the immediate area 2.5 km around the release site.



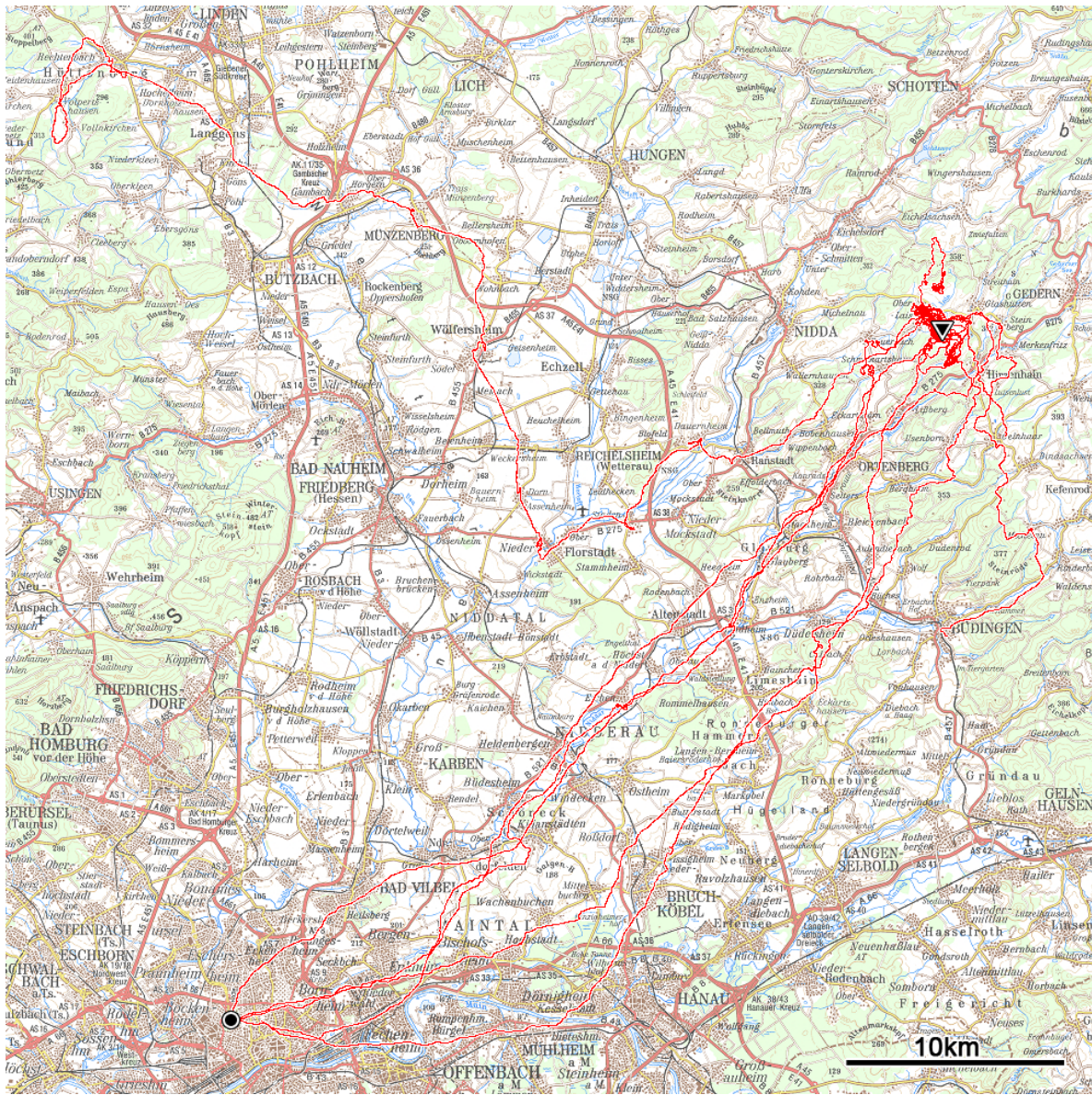


Figure 3.19. – All flights (red lines) from release site NE40 (black triangle) to the pigeons' home loft (black circle).



### 3. Traditional Analysis

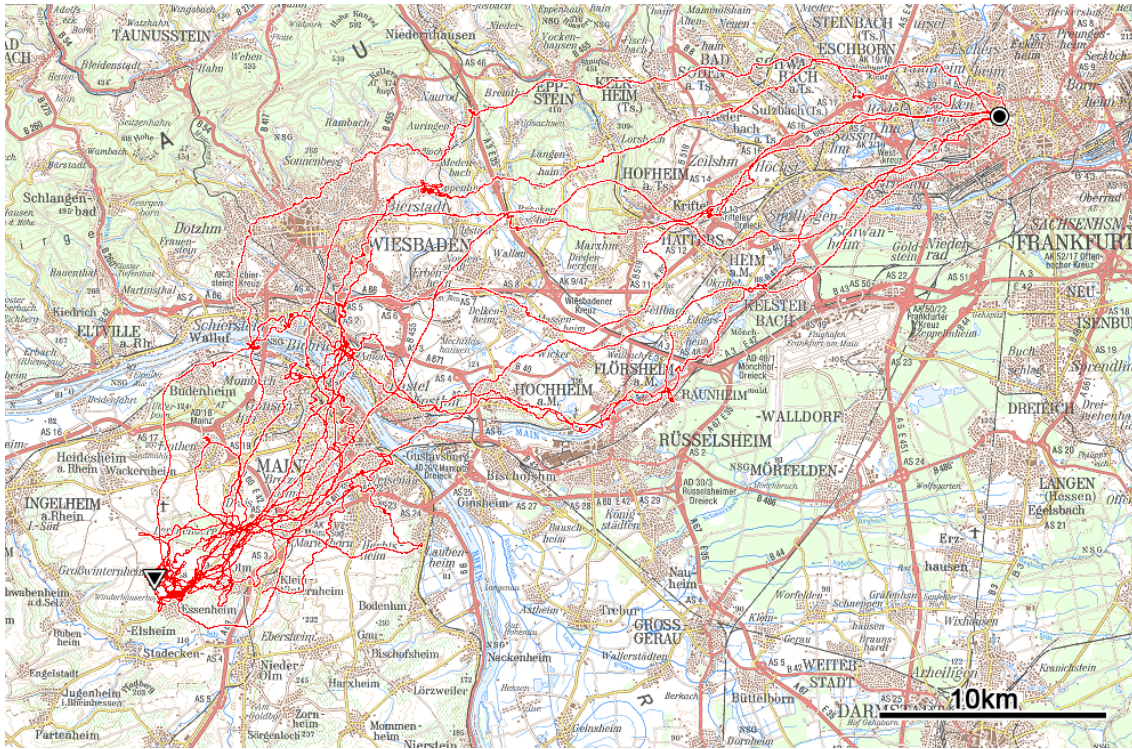


Figure 3.20. – All flights (red lines) from release site SW40 (black triangle) to the pigeons' home loft (black circle).

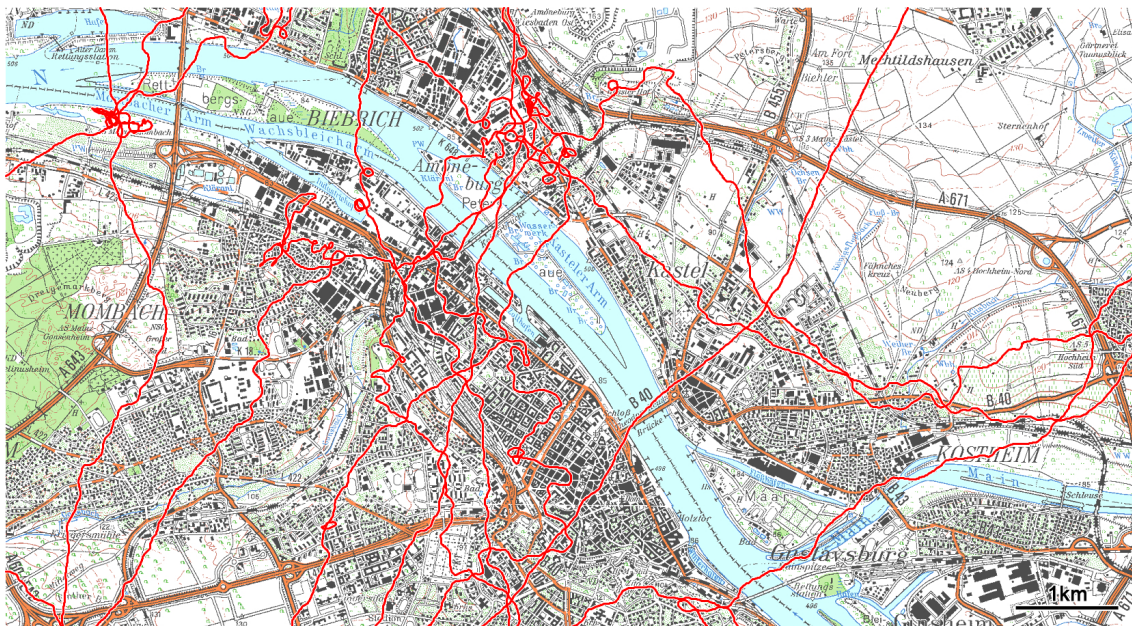


Figure 3.21. – Flights of pigeons (red lines) released at SW40 as the pigeons cross the river Rhein.

### 3.4. Bearings and Efficiencies

When looking at the bearings after one minute (see Table 3.1), I find significant vector lengths in 3 out of 6 releases of the N30 series, in 2 out of 5 releases of the S30 series and in 2 of the single releases. Yet in each case where agreement after one minute can be observed, the directions in which the pigeons had flown are significantly different from the home direction. These directions closely coincide with the direction of the village or town closest to the release site.

**Table 3.1.** – Behavior after one minute.

R. No.	N	Bias?	$\Delta h_{min}$	$r_{min}$	Sign.?
N30-F1	13	n.s.	76	0.25	n.s.
N30-F4	11	n.s.	136	0.26	n.s.
N30-F8	13	*	46	0.54	*
N30-F12	11	**	46	0.75	***
N30-F13	14	n.s.	-64	0.32	n.s.
N30-F16	12	**	60	0.80	***
S30-F1	7	n<8	-157	0.64	n.s.
S30-F2	10	**	-154	0.78	***
S30-F4	11	**	-153	0.77	***
S30-F8	10	n.s.	-98	0.26	n.s.
S30-F12	8	n.s.	-81	0.36	n.s.
N60	9	**	119	0.68	*
S60	9	**	164	0.74	**
NE40	9	*	85	0.49	n.s.
SW40	10	n.s.	74	0.32	n.s.

Table shows the deviation from the home direction after one minute  $\Delta h_{min}$  and the corresponding vector length  $r_{min}$  for all releases, included are also the sample size N as well as the significance levels for the deviation from the home direction defined by the confidence interval Bias? and for directional preferences by the Rayleigh Test Sign.?.

A comparison between both series reveals a significant difference in the direction of the bearings after one minute (see Table 3.2). This is in accordance with the observation that, while the bearings from N30 show a clockwise deviation in all but one case, those from S30 series show a counter-clockwise deviation from the home direction, meaning that both groups initially deviate towards the west. There are no differences when comparing the releases from N60 and S60, yet a significant difference after one minute can be found when

### 3. Traditional Analysis

comparing the releases from NE40 and SW40, indicating that pigeons released at NE40 show considerably more scatter after one minute.

**Table 3.2.** – Comparison of behavior after one minute.

Site1	N1	Site2	N2	$\Delta h_{min}$	$r_{min}$
N30	6	S30	5	19.64**	11.5
N60	9	S60	9	2.96	31.0
NE40	9	SW40	10	0.05	10.5**

Table includes the abbreviations of the release sites that are being compared, the sample sizes N1 and N2 and the test statistics. All tests involving comparisons between directions have been performed using the Watson-Williams test and are based on the deviation from the home direction. All test statistics for the other comparisons have been determined using the Mann-Whitney U-test. The comparison between the releases at N30 and S30 is a second order comparison and is based on the mean and median values of the single releases. The other two are first order comparisons and are based on the data from individual pigeons. Please refer to the previous table for details on the variables that are compared.

The 2.5 km bearings, as shown in Table 3.3, are in all releases from N30 significantly different from random and with the exception of the first release, they are also significantly different from random for the S30 series. The vanishing bearings at the two most distant sites, as well as from SW40, are also significantly different from random, but not from within the magnetic anomaly at release site NE40. Release site biases can be observed only occasionally during the N30 series (2 out of 6), but in all 4 releases from S30 where vector lengths differ significantly from random (4 out of 4).

After 2.5 km no significant difference can be observed any longer between the bearings of the two series and the corresponding intervals also do not differ significantly (see Table 3.4). This is in accordance with the observation that the mean bearings after 2.5 km show a counter-clockwise deviation from the home direction in both series, meaning that the pigeons released from N30 now fly east of the beeline. There is also no significant difference in 2.5 km bearings and intervals between the releases from N60 and S60. However, when comparing the release at NE40 with the release at SW40 there is a significant difference between the vector lengths of the bearings at 2.5 km and also a significant difference in the intervals. That is the pigeons released from NE40 take

considerably longer to reach a distance of 2.5 km and do so with considerably more scatter.

**Table 3.3.** – Behavior after 2.5 km.

R. No.	N	Bias?	$\Delta h_{2.5}$	$r_{2.5}$	Sign.?	$i_{2.5}$
N30-F1	13	n.s.	-18	0.86	***	327
N30-F4	11	**	-35	0.94	***	479
N30-F8	14	n.s.	-15	0.88	***	372
N30-F12	11	n.s.	-8	0.95	***	455
N30-F13	14-16	**	-35	0.82	***	592
N30-F16	12	n.s.	-8	0.79	***	393
S30-F1	7	n<8	-6	0.27	n.s.	1141
S30-F2	10	*	-33	0.76	**	689
S30-F4	11	*	-27	0.92	***	768
S30-F8	10-11	**	-22	0.98	***	345
S30-F12	8	*	-22	0.98	***	497
N60	9	*	41	0.70	**	850
S60	9	n.s.	12	0.80	**	565
NE40	9	n.s.	-44	0.31	n.s.	746
SW40	12	n.s.	10	0.84	***	417

Table shows the deviation from the home direction after 2.5 km  $\Delta h_{2.5}$  and the respective vector length  $r_{2.5}$  and time interval  $i_{2.5}$  for all releases, included are also the sample size N as well as the significance levels for the deviation from the home direction defined by the confidence interval Bias? and for directional preferences by the Rayleigh Test Sign.?.

**Table 3.4.** – Comparison of behavior after 2.5 km.

Site1	N1	Site2	N2	$\Delta h_{2.5}$	$r_{2.5}$	$i_{2.5}$
N30	6	S30	5	0.10	14.0	6.0
N60	9	S60	9	1.55	28.0	25.0
NE40	9	SW40	12	2.18	13.5**	20.0*

Table includes the abbreviations of the release sites that are being compared, the sample sizes N1 and N2 and the test statistics. All tests involving comparisons between directions have been performed using the Watson-Williams test and are based on the deviation from the home direction. All test statistics for the other comparisons have been determined using the Mann-Whitney U-test. The comparison between the releases at N30 and S30 is a second order comparison and is based on the mean and median values of the single releases. The other two are first order comparisons and are based on the data from individual pigeons. Please refer to the previous table for details on the variables that are compared.

As can be expected from the previous observations, there is also no significant difference in 2.5 km efficiencies between the two series (see Tables 3.5 and 3.6) and the two single releases at N60 and S60, but when comparing the releases from NE40 and SW40, indicating that the flight of the pigeons released from NE40, within the magnetic anomaly, is less efficient during the first 2.5

### 3. Traditional Analysis

km. What is more surprising is that there are also no significant differences between the overland and total efficiencies between both series, the two releases from N60 and S60, as well as between the two releases from NE40 and SW40.

**Table 3.5.** – Efficiency of the flight.

R. No.	N	$e_{2.5}$	N	$e_{ovl}$	N	$e_{tot}$
N30-F1	13	0.50	11	0.71	11	0.62
N30-F4	11	0.33	9	0.76	9	0.69
N30-F8	13	0.44	13	0.82	12	0.74
N30-F12	11	0.36	10	0.89	10	0.76
N30-F13	12	0.26	13	0.84	11	0.72
N30-F16	12	0.44	9	0.89	9	0.72
S30-F1	7	0.14	7	0.66	1	0.39
S30-F2	9	0.26	6	0.71	6	0.63
S30-F4	11	0.19	9	0.85	9	0.68
S30-F8	10	0.47	11	0.87	10	0.76
S30-F12	8	0.34	7	0.91	7	0.80
N60	9	0.17	6	0.70	6	0.59
S60	9	0.29	8	0.78	8	0.70
NE40	9	0.22	4	0.81	4	0.72
SW40	10	0.39	7	0.72	6	0.69

Table shows the median of the 2.5 km  $e_{2.5}$ , overland  $e_{ovl}$  and total  $e_{tot}$  efficiencies of each release and the respective sample sizes N.

**Table 3.6.** – Comparison of the efficiency of the flight.

Site1	N1	Site2	N2	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
N30	6	S30	5	7.5	14.5	13.5
N60	-	S60	-	22.5	17.0	14.5
NE40	-	SW40	-	16.5*	6.0	9.5

Table includes the abbreviations of the release sites that are being compared, the sample sizes N1 and N2 and the test statistics. All tests have been performed using the Mann-Whitney U-test. The comparison between the releases at N30 and S30 is a second order comparison and is based on the mean and median values of the single releases. The other two are first order comparisons and are based on the data from individual pigeons, as the sample sizes are highly variable please refer to the previous table for details on the sample sizes and the meaning of the variables that are compared.

### 3.5. Differences between Individuals

The repeated releases of the same pigeons from the same site offer the possibility for an in-depth analysis of individual behavior. Still, the sample size on a level of individual pigeons is, due to GPS failure, because pigeons did not



### 3. *Traditional Analysis*

return home within the operating time of the GPS or were lost in the course of the experiments, rather small and therefore all results should be viewed with caution. Due to the amount of single individuals involved in the experiments, it is, however, still not possible to show all tracks of each individual in this section. Therefore I will focus on giving some of the more prominent examples of individual behavior; a complete overview of all tracks of individuals can be found in appendix C. The individuals shown here, as well as those in the appendix, cover only individuals where at least 2 tracks from the same site are available and where each of these tracks cover at least 50% of the distance release site - home. The tracks in blue are the first flights from the respective site and the tracks in red are the last flights, all flights in between are in black.

### 3. Traditional Analysis



Figure 3.22. – All flights of pigeon 07-366 from release site N30 (black triangle) to its home loft (black circle).



### 3. Traditional Analysis



Figure 3.23. – All flights of pigeon 07-386 from release site N30 (black triangle) and N60 (black square) to its home loft (black circle).

### 3. *Traditional Analysis*

Figure 3.22 shows all flights of pigeon 07-366 from release site N30. The repeated choices of the pigeon's route coincide mainly in the beginning of its journey. Although several portions of the individual routes are similar, the first and 12th flight vary greatly. The flights of pigeon 07-386 are shown in Figure 3.23. Compared to pigeon 07-366 there is more variability in the beginning of the flight from release site N30. Again major portions of the individual routes coincide with each other, yet the routes are never exactly the same. During the early phase of the series the pigeon chooses routes that lie more to the east, but later during the series the pigeon chooses more westerly routes. When released at N60 the pigeon initially follows these westerly routes, but in the final parts of the journey it flies along a route that does roughly coincide with those it took in the early phase of the series. Pigeon 08-785 mostly chooses similar routes, leaving the release site S30, on northerly headings (see Figure 3.24) and chooses the same route, when released from S60. Although the routes are quite similar, they are also never exactly the same and seldom overlap. On one of the releases in the middle of the series the pigeon also completely abandons this northerly course and leaves the site on a westerly heading, flying towards the city of Rüsselsheim, from where it heads towards Frankfurt. Pigeon 08-797 is one of the most efficient pigeons, yet shows the highest variability in its choice of individual routes, as is shown in Figure 3.25. It initially chooses westerly routes towards home, which it later abandons, following a northerly course towards home. Yet when released from S60 it returns to the westerly course.



### 3. Traditional Analysis

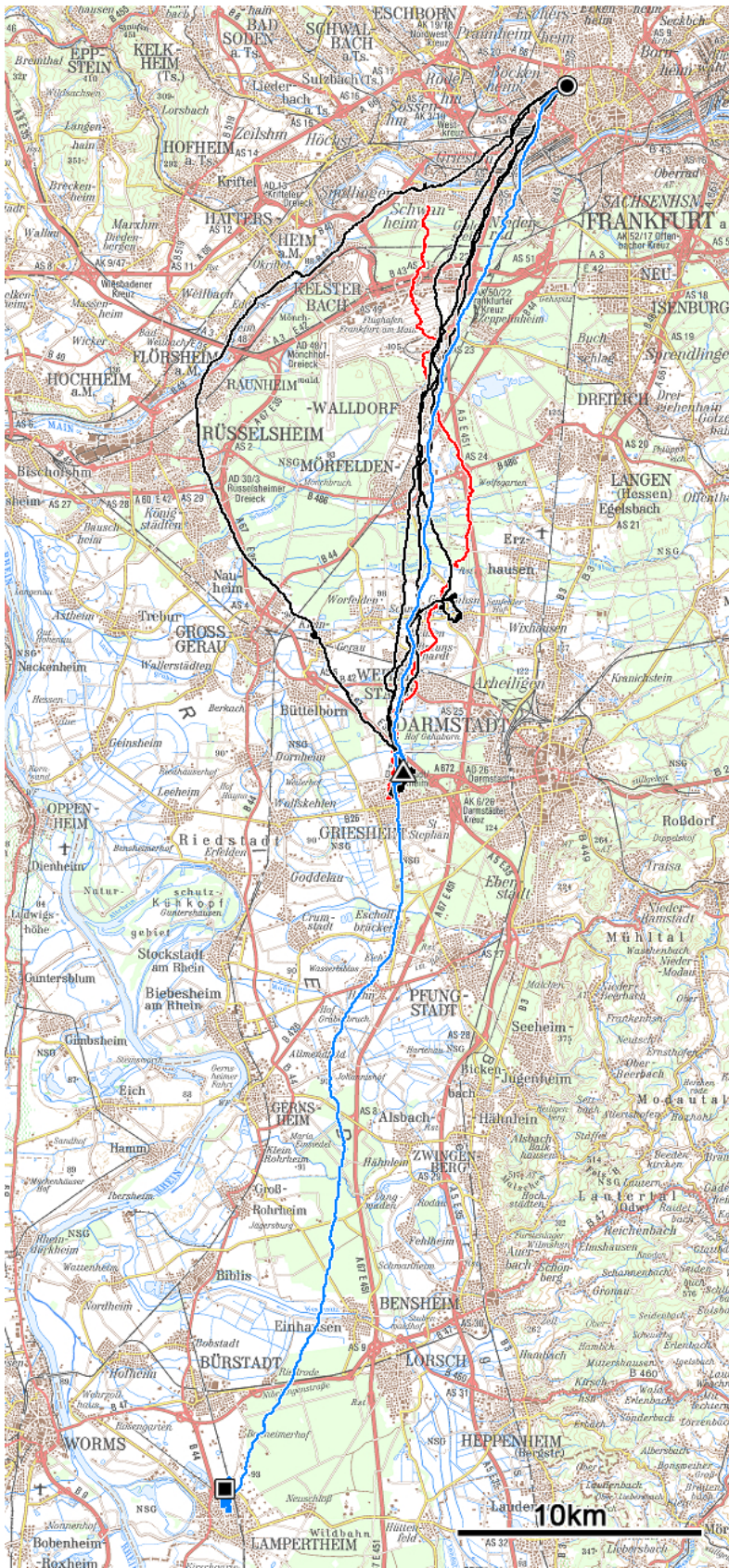


Figure 3.24. – All flights of pigeon 08-785 from release site S30 (black triangle) and S60 (black square) to its home loft (black circle).



### 3. Traditional Analysis

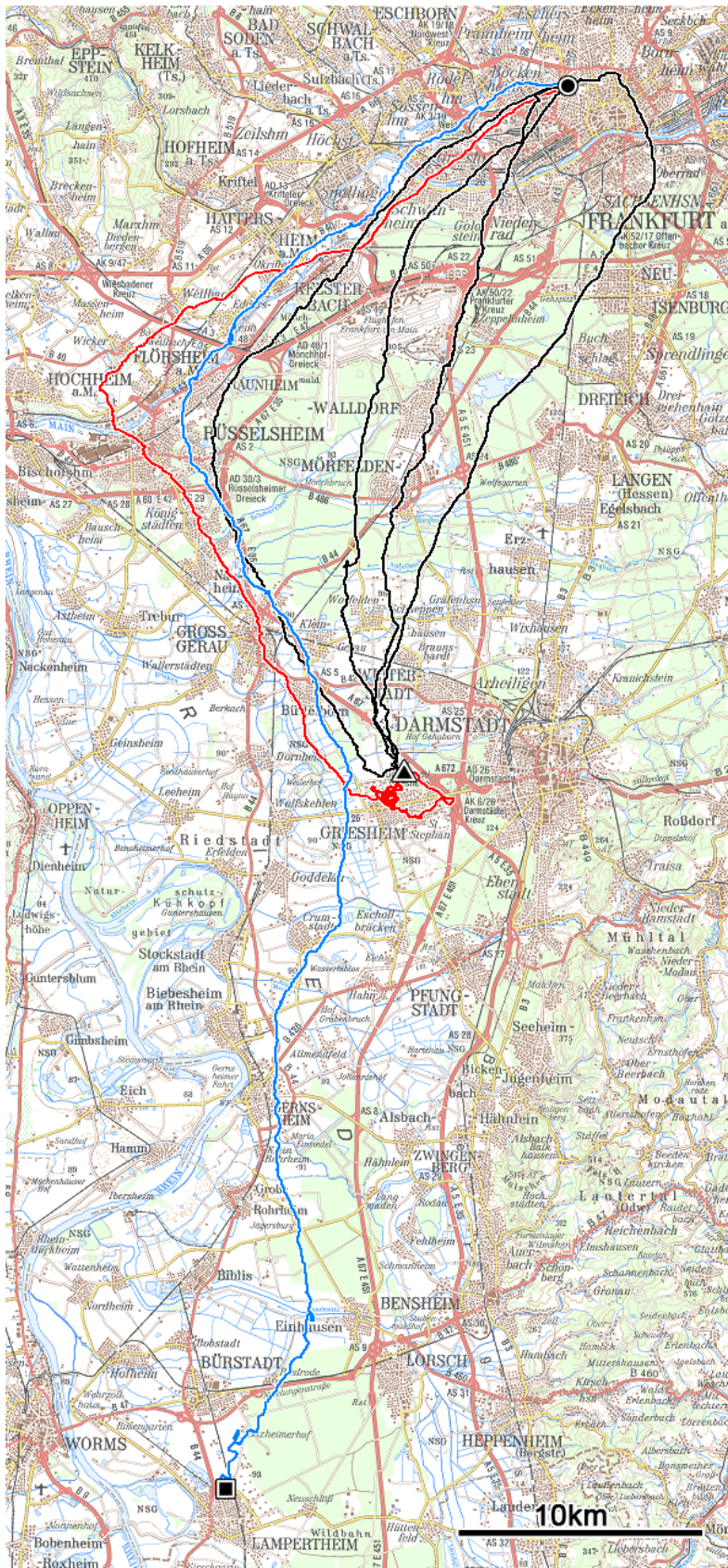


Figure 3.25. – All flights of pigeon 08-797 from release site S30 (black triangle) and S60 (black square) to its home loft (black circle).

**Table 3.7.** – Behavior after one minute.

ID No.	N	$\Delta h_{min}$	$r_{min}$	Sign.?
<b>N30</b>				
07-354	5	157	0.36	n.s.
07-366	4	35	0.39	n.s.
07-382	4	-7	0.94	*
07-392	4	64	0.99	**
07-393	4	112	0.61	n.s.
07-399	4	-2	0.79	n.s.
07-410	5	28	0.54	n.s.
<b>S30</b>				
08-785	4	-148	0.82	n.s.
08-797	5	-70	0.28	n.s.

Table shows the deviation from the home direction after one minute  $\Delta h_{min}$  and the corresponding vector length  $r_{min}$  for all individuals released from N30 and S30, included are also the sample size N as well as the significance levels for directional preferences defined by the Rayleigh test Sign?.

Although it was not possible to identify biases in the repeated choices of the individual pigeons, due to the limited sample size, it may be of particular interest that, while agreement after one minute can only be observed for two pigeons (see Table 3.7), the 2.5 km bearings show significant agreement for all pigeons, with the lowest vector length being 0.88 (see Table 3.8).

**Table 3.8.** – Behavior after 2.5 km.

ID No.	N	$\Delta h_{2.5}$	$r_{2.5}$	Sign.?	$i_{2.5}$
<b>N30</b>					
07-354	5	-12	0.86	*	626
07-366	4	-33	0.99	**	472
07-382	4	-32	1.00	**	300
07-392	4	-6	0.97	*	424
07-393	4	-21	0.99	**	481
07-399	4	-1	0.92	*	325
07-410	5	-11	0.95	n.s.	255
<b>S30</b>					
08-785	4	-29	0.98	**	991
08-797	5	-57	0.88	*	197

Table shows the deviation from the home direction after 2.5 km  $\Delta h_{2.5}$  and the respective vector length  $r_{2.5}$  and time interval  $i_{2.5}$  for all individuals released from N30 and S30, included are also the sample size N as well as the significance levels for directional preferences defined by the Rayleigh test Sign?.

### 3. Traditional Analysis

While the 2.5 km intervals as well as the 2.5 km efficiencies vary greatly, the overland and total efficiencies, although not considerably good, are much more similar for all birds (see Table 3.9).

**Table 3.9.** – Efficiency of the flight.

ID No.	N	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
<b>N30</b>				
07-354	5	0.24	0.87	0.67
07-366	4	0.33	0.79	0.70
07-382	4	0.53	0.61	0.60
07-392	4	0.39	0.91	0.81
07-393	4	0.37	0.87	0.77
07-399	4	0.49	0.72	0.71
07-410	5	0.58	0.66	0.65
<b>S30</b>				
08-785	4	0.17	0.84	0.62
08-797	5	0.72	0.85	0.79

Table shows the median of the 2.5 km  $e_{2.5}$ , overland  $e_{ovl}$  and total  $e_{tot}$  efficiencies of each release and the respective sample sizes N.

In order to analyze the differences between individual pigeons in more detail I compare all variables irrespective of the influence of experience, using the Watson-Williams test for comparisons of directional data and the Mann-Whitney U-test for all other. I then count the number of significant differences, with  $p \leq 0.05$ , disregarding the actual significance level. Positive values indicating that the median of a variable of a certain individual is higher than that of the pigeon I compare it to and negative values the opposite. I then give significance levels for each variable and individual based on the Sign-test (Baschelet, 1981), where only significant differences are counted and all non-significant differences are ignored. The results of this cross-comparison for the N30 series is shown in Table 3.10. While this cross-comparison reveals several significant differences between individuals, no evident pattern emerges. Noteworthy is only pigeon 07-354, whose bearings after one minute and after 2.5 km are significantly more scattered compared to others.



**Table 3.10.** – Number of significant differences in behavior between the individuals of the N30 series.

Variable	354	366	382	392	393	399	410
$\Delta h_{min}$	2	0	3	2	2	3	0
$r_{min}$	-5*	-1	2	4	2/-2	1	1/-2
$\Delta h_{2.5}$	0	1	1	2	0	0	0
$r_{2.5}$	-5*	2	3	1	2/-1	1/-3	0
$i_{2.5}$	2	2	-1	0	0	-2	-1
$e_{2.5}$	-3	-2	2	0	0	2	1
$e_{ovl}$	2	1/-1	-2	3	1	-4	0
$e_{tot}$	-2	-1	-1	4	1	-1	0

For reference of the variables see previous tables. Significance for the differences in directions have been established using the Watson-Williams test and for all others using the Mann-Whitney U-test. Overall significance levels have been determined using the Sign test.

The individuals show high variability in their behavior, yet the choices of individual routes are quite similar. Their initial behavior is mostly erratic, but show high agreement in their repeated directional choices after 2.5 km. Although their behavior during the overland flight remains variable there are no indications that some individuals are generally more or generally less efficient than others.

### 3.6. Influence of Experience

In order to identify trends for improvement of the directional choices and the efficiency with increasing experience, I perform correlations between the number of releases and the respective variables of all releases from both series. I exclude the releases N30-F13 and F16, as the extended time span between these and the previous releases could obscure such trends. The correlations, as shown in Table 3.11, show that the deviations after one minute do not decrease and that the corresponding vector lengths do not increase as the pigeons get more familiar with the respective site.

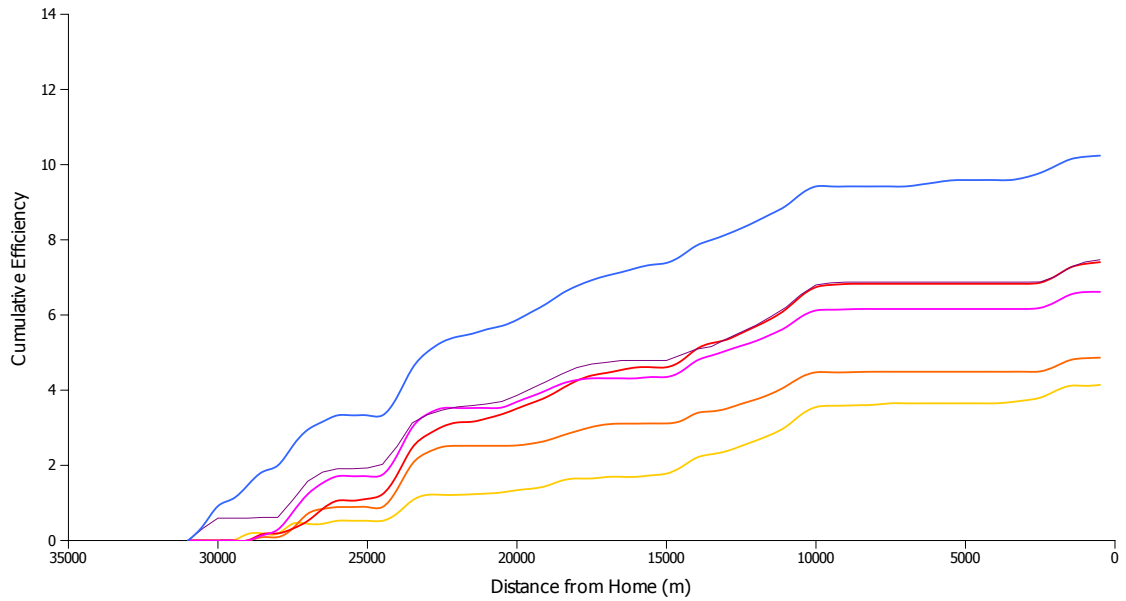
### 3. Traditional Analysis

**Table 3.11.** – Influence of increasing familiarity on the pigeons' behavior. Significance levels and correlation coefficients are given by Spearman's rank correlation. The sample size N is 9 for all variables. For explanation of the variables see previous tables.

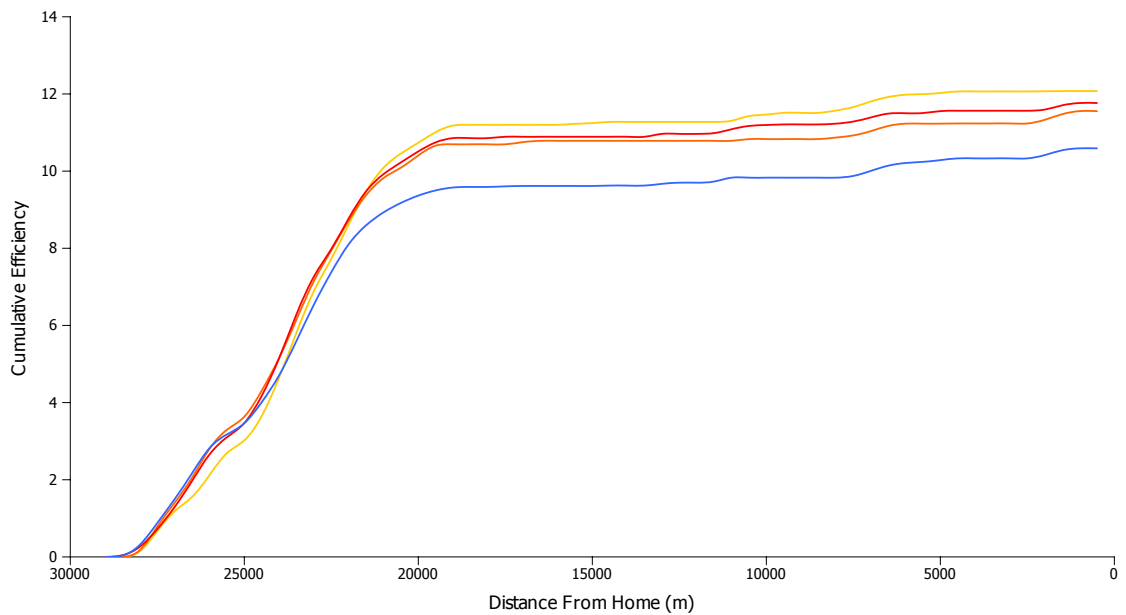
Variable	$r_{sp}$
$\Delta h_{min}$	-0.571
$r_{min}$	0.054
$\Delta h_{2.5}$	-0.021
$r_{2.5}$	0.846**
$i_{2.5}$	-0.200
$e_{2.5}$	0.300
$e_{ovl}$	0.942***
$e_{tot}$	0.971***

While the same is true for the deviations after 2.5 km and the respective interval, there is a clear increase in vector length. While the 2.5 km efficiency does also not change, the overland and the total efficiency increase as the pigeons get more familiar with the site. Concerning the 2.5 km efficiencies it may also be noteworthy that the highest efficiency from release site N30 was observed on the pigeons very first flight from that site.

In order to analyze the influence on experience in more detail I calculate the homing efficiencies for each 500 m segment of each flight, form averages for each release and calculate the increase or decrease in efficiency for each segment compared to the efficiency in the corresponding segment on the first flight; in case of the S30 series I use the second release, because only one track of the first release was complete. In a last step I then calculate the cumulative increase in efficiency by summing up all increases in efficiency for each distance step, whereas decreases in efficiency are ignored as the pigeons had already shown that they are able to fly more efficient in the corresponding segments. Portions of this curve with high increases then indicate areas where the pigeons became more efficient and portions with no or only little increase indicate areas where they did not improve. The results of this analysis are shown in Figures 3.26 and 3.27.



**Figure 3.26.** – Cumulative increase in efficiency of each flight from release site N30, as well as from N60 relative to the first flight from N30. The cumulative increase in efficiency is given for each 500 m step from the home loft, with the colored functions indicating the cumulative increase on flights F4 (yellow), F8 (orange) F12 (red) F13 (pink), F16 (violet) and N60 (Blue).



**Figure 3.27.** – Cumulative increase in efficiency of each flight from release site S30, as well as from S60 relative to the second flight from S30. The cumulative increase in efficiency is given for each 500 m step from the home loft, with the colored functions indicating the cumulative increase on flights F4 (yellow), F8 (orange) F12 (red) and S60 (Blue).



### *3. Traditional Analysis*

The pigeons released at N30 show initial increases in efficiency which are interrupted sporadically by short segments where cumulative efficiency remains at a steady level. Only small increases can be observed during the first 5 km of the pigeons' journey. At approximately 24 km from home I observe the highest increases, which last for about 1 km. These increases are directly followed by other more subtle, but steady increases, lasting until the pigeons are roughly 10 km away from their home loft. From here on no further increases can be observed until the pigeons are 2 km away from home. Interestingly, I then observe further increases in efficiency. There is a clear tendency for increase in efficiency over the course of the first 12 releases, while the efficiencies of the releases F13 and F16 that were performed in the following year are very similar to those of release F12. Of particular interest is that the efficiencies of the pigeons released from the much more distant site N60 are higher in the area the pigeons knew from the previous flights than during the releases from the site itself.

From S30 I also observe increases in efficiency in the beginning of the pigeons' flight, also including a small plateau like region at roughly 25 km from the home loft. The increases are much steeper, but also much shorter, as those observed in the N30 series. They end roughly 20 km away from the home loft and are followed by an extended phase where only minor or no increases in efficiency can be observed. Yet again small increases occur in 2 km distance from the home loft. A general increase in efficiency, between the consecutive releases, can not be observed. Unlike the previously observed higher cumulative efficiencies when flying from the more distant site, the cumulative increase in efficiency of the pigeons flying from S60 is slightly lower than those of the pigeons flying from S30.

### 3.7. Influence of Abiotic Factors

In order to assess the influence of abiotic factors on the performance of the pigeons I correlate weather data gathered on the field, as well as planetary estimates of the daily variations in magnetic intensity, with the data from each release. The respective data can be found in appendix D. Weather data include cloud cover, wind speed, wind direction and temperature, which were recorded during each release at the release site. The measured wind directions are transformed into directions relative to the pigeons assumed goal, the home loft, and therefore can be considered a measure of the head and tail winds which the pigeons experienced on their way home.

The planetary estimate of the daily variation in magnetic intensity is a worldwide estimate of these variations and was acquired from the space weather prediction center of the National Oceanic and Atmospheric Administration in form of the so-called K-index. The K-index quantifies the disturbance in the horizontal component of earth's magnetic field observed on a magnetometer during a three-hour interval. In previous studies the K-index itself has been used to identify possible influences of such magnetic variations on the animals' behavior (Keeton *et al.*, 1974; Larkin & Keeton, 1976; Kowalski *et al.*, 1988). Yet the K-index depends only on the maximum fluctuation, where these deviations may occur any time during the 3-hour period. Therefore this variable alone does not reflect whether these variations occur often or only sporadically over the measurement period and therefore is a less suitable variable for such an analysis (Skiles, 1985). In order to derive a useful variable I calculate the standard deviation of those planetary estimates over a period of 12 hours including the time of release. By calculating the deviation of the K-index, over a specific time interval, a rough estimate of the actual variability of the earth's magnetic field during that period can be acquired. In cases where releases spanned more than one day, average values are used accordingly.

### 3. Traditional Analysis

For this analysis I restrict the data set to tracks recorded from the sites N30 and S30 to avoid possible effects from the increased distance at the sites N60, S60 and SW40, as well as possible influences of the anomalous magnetic conditions at NE40. The results of this analysis are shown in Table 3.12.

**Table 3.12.** – Influence of abiotic factors on pigeons' behavior.

<b>Variable</b>	<b>Cloud Cover</b>	<b>Wind Speed</b>	<b>Wind Dir.</b>	<b>Temp.</b>	<b>Mag. Var.</b>
N	11	11	7	11	11
$\Delta h_{min}$	-0.218	-0.357	-0.188	0.434	0.416
$r_{min}$	-0.261	-0.102	0.223	0.375	0.507
$\Delta h_{2.5}$	0.402	0.450	-0.161	-0.355	0.043
$r_{2.5}$	0.066	0.068	-0.071	-0.259	-0.711**
$i_{2.5}$	-0.130	-0.100	-0.571	0.470	0.627*
$e_{2.5}$	0.064	0.045	0.536	-0.398	-0.659*
$e_{ovl}$	-0.150	0.007	0.580	-0.236	-0.559
$e_{tot}$	-0.195	0.291	0.393	-0.359	-0.677**

For the correlations between the individual variables and the wind direction, tracks from releases where no wind was measurable are ignored and absolute values are used for all correlations except for correlations between directional data and wind direction. Significance levels are given by Spearman's rank correlation. Also shown is the sample size N. For explanation of the variables see previous tables.

The analysis shows that there is no significant influence of cloud cover or wind speed on either the behavior at the release site, nor the efficiency. Although the relationship between wind directions and the efficiency is not significant, there are indications for an increase in efficiency when the pigeons experience tail-winds.

The only significant relationships, however, are associated with the variation of the earth's magnetic field, with high variations leading to more scattered bearings after 2.5 km and increased time until the pigeons reach this distance. The 2.5 km efficiency, as well as the total efficiency are also negatively affected by high variations in the earth's magnetic field, yet the overland phase is not significantly influenced.



### 3.8. General Behavior

By correlating all the variables I have calculated so far with each other it is possible to identify some general properties of the pigeon's behavior. As the purpose of this analysis is to identify general properties of the pigeon's behavior all releases are included in this analysis. The results of this analysis are shown in Tables 3.13 and 3.14. As shown the deviation from the home direction after one minute and the 2.5 km interval seem to depend on each other, indicating that smaller initial deviations lead to reduced time until the pigeon leaves the site. There is also a tendency for more efficient flight the closer the pigeon departs to the home direction after one minute. This relationship is not only significant for the efficiency after 2.5 km, but also for the total efficiency. Furthermore, there are also indications that short 2.5 km intervals result in longer vectors, as well as increased efficiency during the first 2.5 km of the journey.

**Table 3.13.** – Interdependency of behavior at the release site.

Variables	$r_{min}$	$\Delta h_{2.5}$	$r_{2.5}$	$i_{2.5}$
$\Delta h_{min}$	0.140	0.215	-0.321	0.599**
$r_{min}$		-0.234	-0.359	0.416
$\Delta h_{2.5}$			-0.064	0.340
$r_{2.5}$				-0.578**

Table shows the coefficients for Spearman's rank correlation between different variables describing the pigeon's behavior near the release site. Variables included are the deviation from the home direction after one minute  $\Delta h_{min}$  and the corresponding vector length  $r_{min}$ , as well as the deviation from the home direction after 2.5 km  $\Delta h_{2.5}$  and the respective vector length  $r_{2.5}$  and time interval  $i_{2.5}$ . The sample size for all correlations was N=15.

Considering these observations it may not be surprising that there is also a tendency for more efficient flight the more the pigeons agree in their choices of bearings after 2.5 km. For obvious reasons I did not perform correlations between the partial and the total efficiencies, as the total efficiency depends more strongly on the overland efficiency than on the efficiency over the first 2.5 km. Yet the two partial efficiencies do not significantly depend on each other (Spearman's rank correlation:  $R_{sp} = 0.389$ ;  $p > 0.05$ ).

### 3. Traditional Analysis

**Table 3.14.** – Dependency between behavior at the release site and the efficiency of the flight.

Variable	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
$\Delta h_{min}$	-0.591**	-0.498	-0.555*
$r_{min}$	-0.369	0.134	-0.088
$\Delta h_{2.5}$	-0.356	-0.110	-0.066
$r_{2.5}$	0.576**	0.638**	0.620**
$i_{2.5}$	-0.991***	-0.355	-0.462

Table shows the coefficients for Spearman's rank correlation between different variables describing the pigeon's behavior. Variables included are the deviation from the home direction after one minute  $\Delta h_{min}$  and the corresponding vector length  $r_{min}$ , as well as the deviation from the home direction after 2.5 km  $\Delta h_{2.5}$ , the respective vector length  $r_{2.5}$  and time interval  $i_{2.5}$ . These variables are correlated with the 2.5 km  $e_{2.5}$ , overland  $e_{ovl}$  and total  $e_{tot}$  efficiencies. The sample size for all correlations was N=15.

## 3.9. Discussion

### 3.9.1. Attraction of Villages

Right after being released, the pigeons tend to fly towards nearby villages and towns. Irrespective of whether these settlements lie in directions that coincide with the home direction or not, this initial behavior always leads the pigeons to the town or village closest to the release site. An attractiveness of towns near the release site has been described before (Kiepenheuer, 1993). Analysis of data from two lofts seemed to suggest that the influence of towns does usually not grossly mislead the pigeons, but appear to be attractive features mainly when they lie on the route pigeons intend to fly (Wallraff, 1994). While this may be true for the observed tendency to fly along series of towns, the initial behavior to fly towards the closest town appears to be quite different. However, the pigeons used in the current study may have been less familiar with the region around the release site, which could have made those towns more attractive and a detour more acceptable.

As already mentioned the behavior to fly over built-up areas is not limited to this early phase of the flight. When released from N30 the pigeons seem to follow a series of villages that roughly coincide with the home direction and

from release site S30 they initially follow a series of villages that lie in a direction almost 90° left of the home direction. There are several possible reasons for this behavior; the Frankfurt pigeons, born in a loft that lies within a major city, surrounded by tall buildings may be attracted to built-up areas in general. This attraction may then be caused by a general urge for exploration, the need to fly over familiar terrain or just because attacks of predators are less likely and the terrain could offer shelter in case of such attacks. However, as this behavior can still be observed during the latter parts of the pigeons' journey and also after repeated releases, it can be assumed that the behavior is not induced by simple curiosity. Although a general aversion of open terrain, like open fields and forests, cannot be observed, it is intriguing that pigeons never linger around open fields, except at the release site itself, while they do regularly interrupt their journey or fly less steady when over villages. Thus, it is possible that the chosen flight paths are the result of a conflict, where the pigeons have to choose between the safer, but probably longer, route along a series of villages or the quicker, but probably more dangerous, route over open fields.

Another possibility is that these villages are used in the sense of landmarks, which allow the pigeons to leave the site towards home. In previous studies it has been argued that the reduction in the effect of clock-shift treatment that can be observed at familiar sites hints at such a use (e.g. Gagliardo *et al.*, 2005). Yet, the differences in behavior observed in such studies could also be explained by differences in experience of the experimental groups, a problem that has been conclusively addressed in another study (Wiltschko *et al.*, 2005). In this study pigeons with equal experience were used and no significant reduction in the effect of the clock shift treatment could be observed. A study with pigeons that had a bar magnet attached to their back, showed that pigeons treated this way would show the expected deviation from the controls (Wiltschko & Wiltschko, 2001). These findings indicate that the effect of the reduced clock-shift can

### 3. *Traditional Analysis*

probably be explained as a compromise between the two compass systems, the magnetic and the sun compass. A view that has just recently received support by a similar study using GPS loggers. In this study no significant differences were found in virtual vanishing bearings of the two groups, yet the tracks of the clock-shifted birds bearing magnets displayed a greater deviation throughout the whole journey compared to those of the magnetically un-manipulated clock-shifted pigeons (Gagliardo *et al.*, 2009). This study therefore also explains the seemingly contradictory results of a previous study, where no differences in vanishing bearings had been found (Ialò *et al.*, 2006). Aside from these observations it has been shown that pigeons in general are able to home without the aid of any visual cues at all, as is indicated by several studies of pigeons wearing frosted lenses (Schmidt-König & Schlichte, 1972; Schmidt-König & Walcott, 1978; Benvenuti & Fiaschi, 1983). Other findings like the effect of daily variation of the magnetic field on the pigeons initial orientation also provide further evidence against the use of static cues like landmarks as means to guide the pigeons towards their home loft (Keeton *et al.*, 1974; Larkin & Keeton, 1976; Kowalski *et al.*, 1988). Evidence against the use of landmarks at the release sites can also be found in the current study and comes from the observation that increasing familiarity does not lead to an increase in efficiency in the immediate vicinity of the release site. Therefore the improvement that can be observed in pigeons released from familiar sites (Kowalski & Wiltschko, 1987) is unlikely due to the use of familiar landmarks at the release site.

In view of such findings it is more likely that the behavior to fly over towns is not related to the use of familiar landmarks and that the direction in which the pigeons depart from a release site is determined by other non-visual navigational cues. The tendency to fly in directions that deviate from the home direction over such prolonged distances, however, indicates that biases (Kramer, 1957) that can be observed at almost any site are not short-living phenomena. This



supports the idea that biases could indicate the use of a gradient based map, as suggested by Keeton (1973). The extreme bias that can be observed at S30 is also in accordance with the general behavior in the area south of Frankfurt and can also be observed at several other release sites in the vicinity, hence indicating that the phenomenon is not limited to this specific release site but rather a regional phenomenon (Wiltschko & Wiltschko, 2003b). The finding that the pigeons released from S60 seem to recognize the previous release site, may suggest an importance of landmarks for site recognition, although it can not be excluded that the pigeons were able to recognize the site by other non-visual means.

#### **3.9.2. Influence of Familiarity**

The behavior to fly over villages is mostly limited to the first half of the flights from N30 and S30. While the tendency to linger around over these villages decreases with increasing familiarity with the release site, the pigeons still choose the same routes along the same series of villages. At first glance, these findings might give the impression that such behavior could be limited to the first half of a journey in general, but when released from the sites N60 and S60 the pigeons still show the same tendency to fly over the same set of villages. Although it seems unlikely that these villages are used as navigational cues themselves, as discussed before, they may serve as stabilizing or directing features that happen to coincide with course indicated by other navigational cues. Hence these villages probably act in the sense of so-called "Leitlinien", linear features that help the pigeons to maintain a straight course towards their goal. The behavior to follow such linear features was first described for migrating birds (von Schweppenburg, 1933), but an extensive study of GPS tracked pigeons showed that pigeons also tend to follow linear features, like highways and roads, as long as they roughly coincide with the direction of the true home course (Lipp

### 3. *Traditional Analysis*

*et al.*, 2004). If the pigeons' flight from N30 and S30 is indeed directed by these features it may not be surprising that they do not depart closer to the home direction or fly more efficient in the initial portions of the flight, with increasing familiarity. That these linear features do not serve as navigational cues themselves is also indicated by the observation that the pigeons did not follow the highway A5, which would be a linear feature much closer to the home direction and could have guided the pigeons home from 4 of the 6 release sites.

An overall trend for increasing efficiency can be observed during the over-land phase. The analysis of the cumulative increase in efficiency, however, indicates that this increase remains mostly limited to the first half of the pigeons' journey, excluding the immediate area around the release site. Irrespective of the pigeons' actual flight path there seems to be a specific distance from the home loft where final course corrections are made. While these distances can already be made out from the tracks overlayed on an ordnance survey map, these observations closely coincide with those areas where no cumulative increases in efficiency can be observed for an extended portion of the flight. In these specific regions the pigeons already fly as efficient as possible during their first release from either site. It seems that the pigeons do enter some sort of familiar area. This area seems to expand 20 km to the south and 10 km to the north and ends in both cases 2 km before the pigeons reach their home loft. The differences in expansion of this area seem strange, especially as the pigeons received equal training in all cardinal compass directions. Yet, the highest increase in efficiency can be observed between the first two recorded releases of the N30 series and therefore it is probable that the differences between the two series are due to the fact that the first release from S30 could not be used for this analysis. Compared to this initial increase in efficiency the following improvements are comparatively small, but while the improvements after the 4th flight from S30 are almost negligible, the homing efficiency of the pigeons

released from N30 keeps increasing until the 12th release. Therefore another viable explanation for the increased size of the familiar area to the south may be that the distribution of the navigational factors differ between the two regions.

Irrespective of whether such a difference in the distribution of the navigational factors exists, the results in general suggest that the navigational strategy does not change after the pigeons have entered this familiar area. The area seems to end only 2 km away from the home loft, as is indicated by the slight but undeniable increase in efficiency at that specific distance. It seems unlikely that the pigeons used familiar landmarks for navigation during the preceding portion of the journey. This is indicated by observations from previous experiments with pigeons from the Frankfurt loft (Schmidt-König & Schlichte, 1972). During these experiments the pigeons had to wear frosted lenses and therefore were deprived of the ability to perceive landmarks. Despite this impairment the pigeons were still able to approach their home loft, where those that did not return were later found at distances of about 2 km from the home loft. It is also highly unlikely that a mental representation of landmarks could span up to 20 km. Therefore the most probable explanation is that within this familiar area the pigeons still use a gradient based map for navigation. The daily variation in the factors then could lead to situations where the pigeons have to readjust their flight path when these factors are no longer available and have to switch to different means of navigation. The results therefore could indicate that the Frankfurt pigeons' mosaic map (Wallraff, 1974) is either limited to the last 2 km, does not exist at all, or that there is considerable overlap between the gradient map and mosaic map. As the assumed switch in navigational strategy occurs at a distance where the pigeons should be able to see their goal or at least the buildings of the institute next to their home loft, simple beacon homing, i.e. flying directly towards the goal, would suffice to lead the pigeons home. Although previous findings from clock-shift experiments suggest that pi-

### 3. *Traditional Analysis*

geons do not use beacon homing even at such short distances, such experiments have not yet been conducted with the pigeons in Frankfurt (Graue, 1963). The tracks of pigeons from Oxford show that pigeons highly familiar with a region can indeed use piloting, i.e. navigation by landmarks (Griffin, 1952b), which is simply a more complex form of beacon homing (Biro *et al.*, 2004; Meade *et al.*, 2005; Biro *et al.*, 2007; Mann *et al.*, 2010), hence it can not be excluded that the Frankfurt pigeons use this simple strategy to fly towards the building of the institute.

#### **3.9.3. Flight Corridors**

The flight paths of the pigeons flying from S30, as well as from N30, lead to the impression of distinctive flight corridors. Even when released from more distant sites the pigeons from Frankfurt still reenter the same corridors irrespective of whether they actually fly close to the previous site or are several km away. The westerly corridor that can be observed at S30 has also been used by a different group of pigeons on their flight from another site roughly 10 km due south (Wiltschko *et al.* 2010 in prep.) In this study the pigeons have additionally been released at two other sites along this corridor. Irrespective of the release site they again reentered the same corridor. As the distribution of the biases in the region south of Frankfurt all point at a westerly tendency it is thinkable that the flights of the pigeons in this area are mostly channeled through this specific corridor (Wiltschko & Wiltschko, 2003b). A different corridor, not observed in the current study, may be indicated by the finding that pigeons released at a site 10 km west of Frankfurt show a tendency to fly south of the actual beeline (Wiltschko *et al.*, 2007). A similar, but yet unmistakably different behavior, the so called route loyalty, has been observed in pigeons from Oxford (Biro *et al.*, 2004; Meade *et al.*, 2005; Biro *et al.*, 2007; Mann *et al.*, 2010). In these studies individual pigeons have been found to follow idiosyncratic



routes after extensive training. Unlike these routes which are specific for each individual, the Frankfurt pigeons all fly along the same corridors, do so from the very first release and show high variability in their individual choices of routes. While route loyalty suggests some sort of visually guided navigation, i.e. piloting (Griffin, 1952b), where pigeons follow a series of landmarks, the corridors on the other hand strongly support the idea of navigation based on natural gradients. The observed variability within each corridor is most likely the result of daily fluctuations in the availability of these gradients. Data from previous experiments already indicates that release site biases are a regional loft specific phenomenon and are not necessarily characteristics of a specific release site (see Schmidt-König, 1963; Windsor, 1975; Walcott, 1996); more diagrams of the distribution of biases at other lofts and some discussions can be found in Papi & Wallraff (1982). The corridors observed in the current study and the fact that pigeons released from more distant sites reenter the same corridors, are in accordance with the theory that biases are a regional phenomenon and support Keeton's (1973) theory that biases are the result of the distribution of navigational factors.

The differences in behavior between the pigeons from Frankfurt and Oxford may be related to the fact that the pigeons from Oxford are born in a more rural region. The environment around Oxford may offer less useful natural gradients where the landmarks would be their only option to find their way home. Yet, the rural area, where less, but probably more unique landmarks, are available may also be more suited for visual guided navigation, whereas the region around Frankfurt with its multitude of possible landmarks may simply be too confusing to support such behavior (Mann *et al.*, 2010). That the importance of landmarks differs between lofts is already indicated by the finding that, unlike pigeons from Frankfurt, pigeons from other lofts are able to approach the loft, but do not find the loft itself, if they are deprived of visual cues (Schmidt-König

### 3. *Traditional Analysis*

& Walcott, 1978). Landmarks are by no means the only factor were regional differences have been reported. That the importance of individual navigational factors does differ between lofts is also supported by the different effects of olfactory deprivation in different regions. A comparative study in three different countries indicates that olfactory cues are more important in the Pisa region, than in the region around Frankfurt or in upstate New York (Wiltschko *et al.*, 1987). The same might be also true for magnetic information, as is indicated by differences in the effect of magnetic anomalies on pigeons from different lofts (see for comparison Walcott, 1978; Lednor & Walcott, 1988; Wiltschko *et al.*, 2009a, 2010). These difference, however, seem not to be caused by genetic differences, but seem to depend on the type of loft that is used or the early experience of the birds. This is indicated by studies analyzing the differences in behavior of siblings raised in different lofts (e.g. Wiltschko, 1992; Braithwaite & Guilford, 1995), as well as experiments with pigeons from lofts in close vicinity (Schmidt-König, 1963).

#### **3.9.4. Navigational Factors**

The results so far strongly indicate that the pigeons from Frankfurt use natural gradients for navigation. The nature of these gradients, however, is mostly unclear, which is mainly due to the fact that data on such gradients is generally sparse. Yet, one of the possible navigational factors is the earth's magnetic field and information on the earth's magnetic field can be obtained relatively easy. Its involvement in the navigational process has been successfully shown in previous studies (Wiltschko *et al.*, 2009a, 2010). These studies showed that there is a clear effect of the magnetic anomaly on the pigeons' behavior, especially on the vanishing interval and the vector lengths. The same effects can also be found in the current study as indicated by the increased 2.5 km intervals and the decreased efficiency and vector length after 2.5 km of the flights of

pigeons released from within the magnetic anomaly (NE40) compared to flights of pigeons released from outside the anomaly (SW40). The result that there is no difference in overland efficiency between those two release sites, as well as the previous finding that pigeons with anesthetized beaks (Wiltschko *et al.*, 2010) are very well able to find their way home, may indicate that the pigeons are able to cope with the situation and can use other factors to determine their course towards home. As the release site used in the current study is located at the periphery of the anomaly the current results may, however, also be related to the relatively short period during which the pigeons have to experience anomalous conditions.

Similar effects can be observed when looking at the influence of the daily variation of the earth's magnetic field on the pigeons' behavior. High variations seem to result in larger scatter of the 2.5 km bearings as well as increased time until this distance is reached. The vanishing efficiency is likewise affected and although a significant effect can be observed for the total efficiency, the effect is not significant for the overland efficiency. Although such effects had been shown before, it was only possible to find such influence on the behavior on vanishing and also only for the sum of the K-index of the 12 hour period ending with the last release, therefore not including the actual time of the homing flight (Keeton *et al.*, 1974; Larkin & Keeton, 1976; Kowalski *et al.*, 1988). These previous results, are however not invalidated by these new findings. The 12 hour period before each release may very well be important for the pigeons. The magnetic field is much more stable during the night, which is usually included in this 12 hour period, as releases are normally conducted in the morning. Therefore the previous result could indicate that pigeons do calibrate their magnetic sense during the night.

### **3.10. Conclusion**

The results so far strongly suggest that the pigeons use natural gradients to determine their course towards home. The involvement of landmarks in the navigational process seems to be limited to certain areas and are more likely to act as stabilizing or directing features. The availability and distribution of natural gradients, however, seems to differ in certain areas around Frankfurt. One of these gradients is, as is indicated by the results, the geomagnetic field. Yet, the behavior to fly along distinctively different corridors indicates that this factor may just be one among several others and can probably be easily replaced if necessary. The availability and reliability of these factors, as well as the pigeons ability to determine differences in these factors, seem to be sufficient enough for the pigeons to approach their home loft up to 2 km. Although I have put considerable effort into analyzing all possible aspect of the pigeons' behavior the knowledge gained from this analysis does not reveal anything that could be considered particularly new. Therefore supporting my initial statement that the traditional analysis methods are by no means sufficient enough to analyze the tracks of pigeons.



## **4. Phases of the Flight**

### **4.1. Introduction**

A common problem in behavioral research is to get the animal to perform a specific task or to display the desired behavior in order to study it. In many cases the only solution to this problem is extensive training or conditioning. Fortunately, the pigeon's motivation to return home can be considered to be exceptionally high. Yet, there are situations where the pigeon's motivation to return to its loft may not be as high as one would wish. Tracking experiments with pigeons are usually performed when there are no young, and without food deprivation to avoid additional stress. This may inadvertently result in situations where the pigeons may not be in a hurry to return to their loft and delay their decision to fly home. Analyzing the track as a whole or even parts defined by external references can not solve this problem and therefore the results of purely traditional analysis will always include non-navigational behavior.

As the pigeons do return sooner or later, there must be a moment where the pigeons make a decision to finally fly home. While GPS has the advantage of being able to get data from the complete flight, the experimenter needs to be constantly aware that although he may be able to monitor the behavior throughout the complete experiment, there are many things a GPS track can not tell him; for example, whether the pigeon is flying alone or with con-specifics from another loft. It also remains difficult to assess why a pigeon chooses to fly in a specific direction. In most cases directions that significantly differ from

#### 4. *Phases of the Flight*

the home direction are considered to be navigational errors, yet it is possible that the pigeon's choice is neither random nor the result of a navigational error, but intentional. Even pigeons that made up their mind and are already on their way home may encounter situations en route that may lead to a interruption of the homing flight.

### 4.2. **Analysis and Evaluation**

In sight of these problems I developed a method that makes it possible to calculate when such a change in behavior has occurred. The method itself is based on the observation that pigeons that have made up their mind and are ready to leave the release site, change their flying behavior, i.e. they pick up speed and fly more steadily.

Consequently I calculate the following variables:

1. The cumulative velocity, defined as the bird's current distance from the release site divided by the time that has passed since its release. This variable remains low as long as the pigeon flies around at the release site and will increase steadily, approaching the bird's actual flying speed, once it leaves the site. It may decrease again, when the pigeon changes its heading and flies tangential to the release site or even attempts to return to it.
2. The steadiness of the flight, defined as the vector length of successive headings, with heading being defined as the angle between two consecutive positional fixes. Steadiness approaches a value of 1.00 when the pigeon flies steadily in one direction and decreases the more there are changes in direction. Steadiness is calculated as a sliding mean for every 15 seconds over a period of 60 seconds. This specific time interval is selected to avoid

chance variations and ensure that calculations are based on a sufficient number of data points.

Based on the cumulative velocity, the tracks are split into phases of either increasing or decreasing cumulative velocity. Each such phase is comprised of at least 5 successive steps of either increasing or decreasing cumulative velocity. In order to ensure that separation into phases could succeed, even when cumulative velocity is extremely low, successive steps are allowed to be interrupted by steps with no change in cumulative velocity. Each phase ends after 5 successive steps, showing the opposite trend. Thus, each track consists of several subsets where each phase with decreasing cumulative velocity is immediately followed by a phase of increasing cumulative velocity, until the end of the track is reached. Normally, each track starts out with a phase of decreasing cumulative velocity, unless the pigeon flies away from the release site without hesitation on a straight line. Therefore, the separation into phases already allows a rough estimation of the points of decision, where each end of a phase with decreasing cumulative velocity marks such a decision. Yet the cumulative velocity does not allow a very precise estimate of the exact time and location of this decision. Especially, when pigeons are still close to the release site and head into opposite directions during the two phases of each subset, one will inadvertently observe a prolonged phase of decreasing cumulative velocity and the cumulative velocity will increase only after the true moment of decision has long passed.

As the steadiness depends on the determination of the individual to head out in a specific direction, it is more suitable for the purpose of determining the exact point of decision. I therefore calculated the point of decision of each subset as the highest increase of steadiness between two consecutive steps. In order to avoid chance variations this point had to lie within the period showing the highest increase of steadiness over 60 seconds (4+1 steps, thus also explaining why each phase had to consist of at least 5 steps).

#### 4. *Phases of the Flight*

After the true point of decision had been defined, mean headings (relative to home), steadiness and average flying speed for each phase are calculated. The flight of the pigeon can usually be separated into an initial phase of flying about, a departure phase and/or final homing phase, but in more complex cases a multitude of intermediary phases can be defined too. For this study I focused on three distinctive phases of the pigeons' flight. The phase until the first point decision, the initial phase, the phase following the first point of decision, the departure phase and the phase after the last point of decision, the final homing phase. For the final homing phase only those cases are considered where the track is complete. This is to ensure that this phase was really the phase that lead the pigeon to its home loft. In cases where there is only one point of decision the final homing phase and the departure phase are the same, so there may be a certain amount of overlap.

#### **4.3. The First Decision**

The behavior before and after the first point of decision for all releases is summarized in Tables 4.1 to 4.4. In 8 of the 15 releases I can already observe significant orientation in initial heading (see Table 4.1). This agreement in initial heading coincides with 4 of the 5 cases where I find no agreement in departure heading. In 3 of these cases, the pigeons also headed out into directions significantly different from the home direction.

When comparing the behavior during the initial phases at the different sites, it can be found that in all cases there are significant differences in the initial headings (see Table 4.2). The flight of the pigeons released at N30 also is significantly more steady, but also significantly slower than the flight of the pigeons released at S30. A difference in the initial steadiness can also be observed between the release within (NE40) and outside the magnetic anomaly (SW40). In all cases, however, there are no significant differences in the time



until the first point of decision and the vector length. The results therefore suggest that the time until the first point of decision is independent of the direction of displacement and that the deviation from the home direction during this initially phase is different for each site.

**Table 4.1.** – Behavior during the initial phase until the first point of decision.

R. No.	N	$t_{ini}$	Bias?	$\Delta h_{ini}$	$r_{ini}$	Sign.?	$s_{ini}$	$v_{ini}$
N30-F1	14	128	n.s.	-25	0.30	n.s.	0.32	54
N30-F4	13	195	n.s.	52	0.55	*	0.27	52
N30-F8	13	150	n.s.	-21	0.76	***	0.14	52
N30-F12	11	270	n.s.	24	0.55	*	0.24	52
N30-F13	12	173	n.s.	0	0.37	n.s.	0.36	51
N30-F16	12	308	n.s.	-5	0.27	n.s.	0.24	54
S30-F1	8	240	n.s.	-172	0.21	n.s.	0.11	53
S30-F2	9	210	n.s.	-76	0.24	n.s.	0.11	48
S30-F4	12	165	***	-146	0.82	***	0.17	51
S30-F8	9	135	n.s.	-103	0.37	n.s.	0.14	50
S30-F12	8	300	n.s.	-10	0.95	***	0.16	51
N60	9	420	***	97	0.76	**	0.17	51
S60	9	330	n.s.	-22	0.25	n.s.	0.09	51
NE40	9	270	***	-169	0.63	*	0.16	52
SW40	10	143	n.s.	40	0.57	*	0.35	52

Variables used to describe the pigeons' behavior include the duration of the phase  $t_{ini}$  in seconds, the mean heading in relation to the home direction  $\Delta h_{ini}$ , the corresponding vector length  $r_{ini}$ , the median steadiness  $s_{ini}$  and the median speed  $v_{ini}$  in km/h. Significance levels are given for the deviation from the home direction defined by the confidence interval Bias? and for directional preferences by the Rayleigh test Sign.?.

**Table 4.2.** – Comparison of behavior during the initial phase.

Site1	N1	Site2	N2	$t_{ini}$	$\Delta h_{ini}$	$r_{ini}$	$s_{ini}$	$v_{ini}$
N30	6	S30	5	14.0	10.42*	14.5	2.5*	5.0*
N60	9	S60	9	35.5	5.35*	24.5	25.5	40.0
NE40	9	SW40	10	24.5	18.91***	35.0	23.0*	40.0

Table includes the abbreviations of the release sites that are being compared, the sample sizes N1 and N2 and the test statistics. All tests involving comparisons between directional data have been performed using the Watson-Williams test and are based on the deviation from the home direction. All test statistics for the other comparisons have been determined using the Mann-Whitney U-test. The comparison between the releases at N30 and S30 is a second order comparison and is based on the mean and median values of the single releases. The other two are first order comparisons and are based on the data from individual pigeons. Please refer to the previous table for details on the variables that are compared.

The points of decision are in most cases randomly distributed around the release sites. Spatial distributions that are significantly different from random

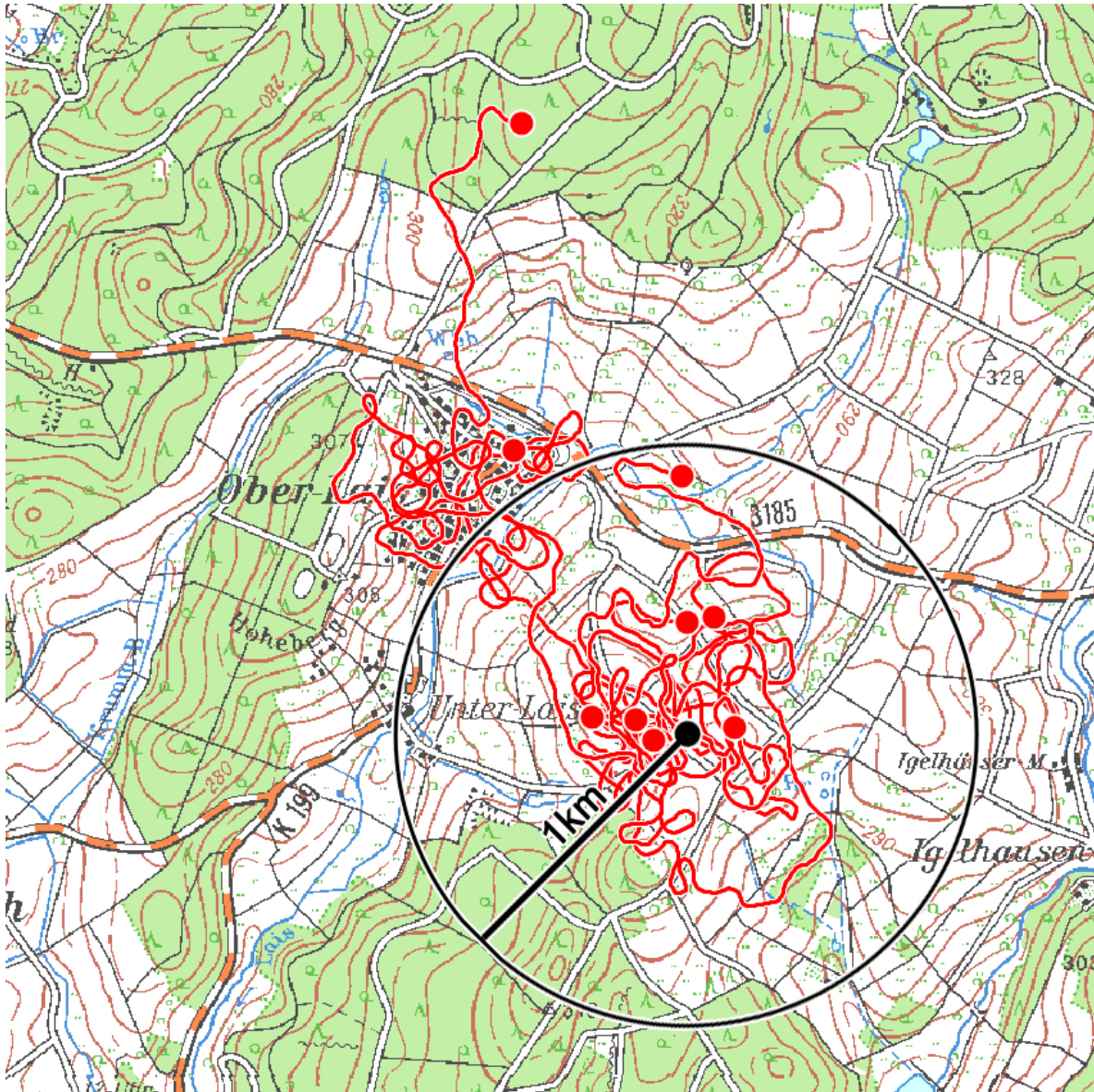
#### 4. Phases of the Flight

can be observed only during 4 of the 15 releases and only during such releases where the pigeons already headed out in specific directions during the initial phase. Details for this analysis are shown in Table 4.3, samples of the distributions of points of decisions are given in Figures 4.1 and 4.2 for the two release sites NE40 and SW40. Furthermore, it seems spatial distributions significantly different from random can only, but not always, be observed at sites familiar to the birds. On a group level, including all releases, the distribution of the points of decision of the N30 series is different from random ( $-13^\circ$ ; 647 m; Hotelling's one sample test:  $F = 135.96$ ;  $p \leq 0.01$ ), but the distribution of those of the S30 series is not ( $-81^\circ$ ; 128 m; Hotelling's one sample test:  $F = 9.97$ ;  $p > 0.05$ ).

**Table 4.3.** – Spatial distribution of the first points of decision.

R. No.	N	$PoD_{\Delta h}$	$PoD_{\Delta d}$	Sign.?
N30-F1	14	-28	1074	5.92
N30-F4	13	42	239	1.79
N30-F8	13	29	274	24.68**
N30-F12	11	-13	818	18.34**
N30-F13	12	-23	1117	2.91
N30-F16	12	-5	592	5.75
S30-F1	8	178	384	10.06
S30-F2	9	-147	94	6.47
S30-F4	12	-163	336	17.95**
S30-F8	9	-19	278	1.26
S30-F12	8	-33	743	17.94*
N60	9	78	473	5.82
S60	9	115	126	2.16
NE40	9	120	666	6.17
SW40	10	29	547	8.50

Distributions are given as the direction of the center of the distribution from the release site in relation to the home direction  $PoD_{\Delta h}$  as well as the respective distance from the release site  $PoD_{\Delta d}$ . Included are also the sample size N as well as significance levels for distributions that differ from random as determined by Hotelling's one sample test Sign.?.



**Figure 4.1.** – Points of decision (red dots) for all tracks (red lines) of pigeons released from NE40 (black circle). The scale (1km) points in home direction.

4. Phases of the Flight

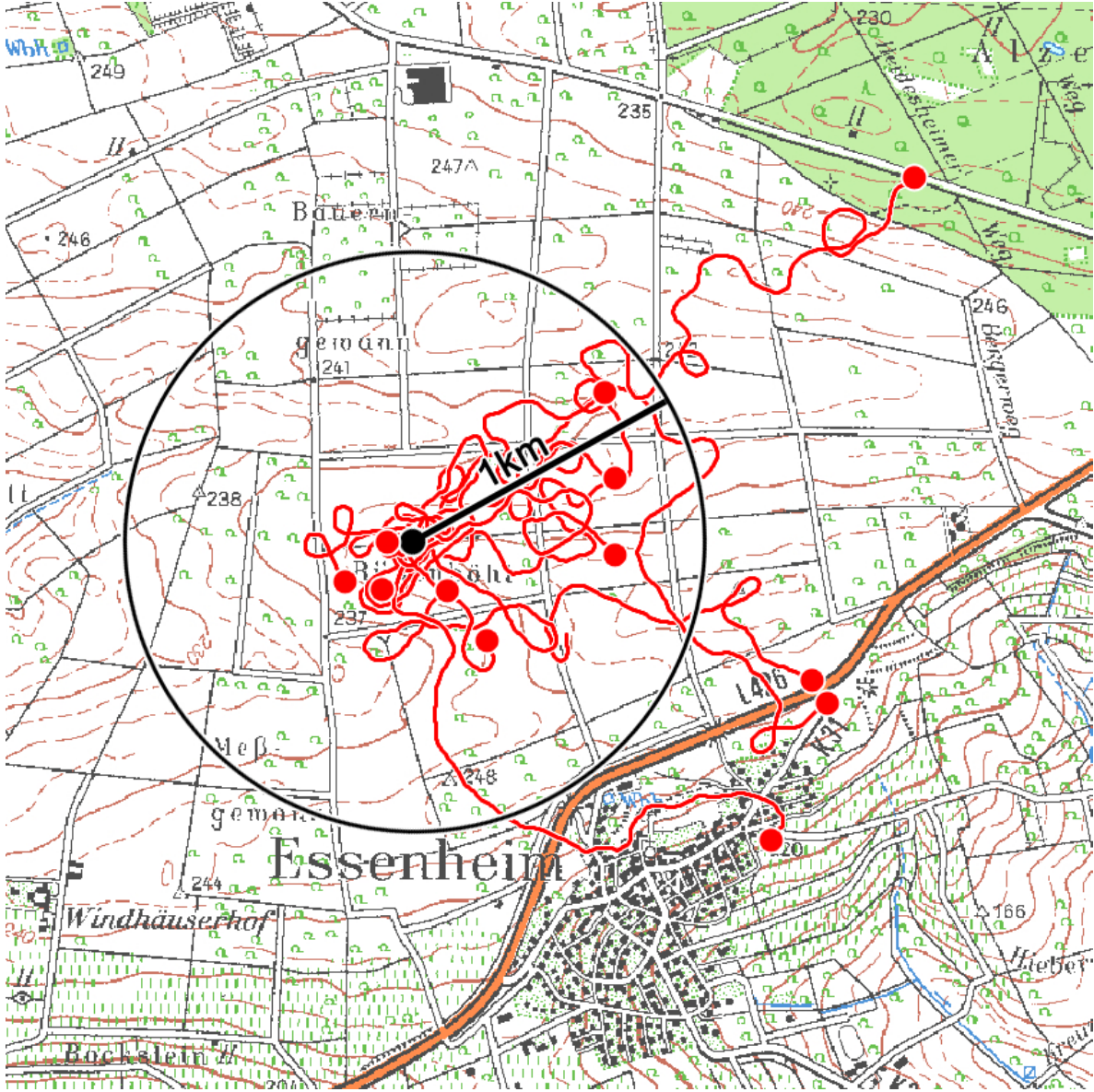


Figure 4.2. – Points of decision (red dots) for all tracks (red lines) of pigeons released from SW40 (black circle). The scale (1km) points in home direction.



Although not always homeward oriented, vector lengths after the first point of decision are in most cases significantly different from random (10 out of 15 releases; see Table 4.4 ). In only four of these cases a significant bias can be observed, two in the N30 and two in the S30 series, where during each series one of these biases is much more pronounced and lead the pigeons into a direction clearly different from the home direction. These pronounced biases occurred in the early stages of either of each series (N30-F4 and S30-F1). The biases observed later in the series are much closer to the home direction and occurred in both cases on the 12th release from either site. In none of the releases from the two more distant sites, N60 and S60, as well as from NE40, agreement in the headings on departure can be observed. Yet from SW40 the pigeons do agree significantly in their headings on departure.

A comparison between the departure phases of the releases from S30 and N30 reveals no significant differences (see Table 4.5). While a comparison between the releases from N60 and S60 does also reveal no difference in the deviation from the home direction and vector length, the pigeons released at N60 fly faster, but also less steady compared to the pigeons released at S60. In addition to these differences the pigeons released at N60 do not fly in the departure direction for very long and soon make a new decision. Interestingly there are also no significant differences between the departure phase of the pigeons released in the magnetic anomaly at NE40 and those released in the magnetically quiet region at SW40. It might however be worth mentioning that the difference in vector length may still be indicated by the results, as the test statistic is very close to significance  $p \leq 0.10$ .

#### 4. Phases of the Flight

**Table 4.4.** – Behavior during the departure phase, after the first point of decision.

R. No.	N	$t_{dep}$	Bias?	$\Delta h_{dep}$	$r_{dep}$	Sign.?	$s_{dep}$	$v_{dep}$
N30-F1	14	135	n.s.	-30	0.62	**	0.84	62
N30-F4	13	165	**	-43	0.84	***	0.78	62
N30-F8	13	405	n.s.	-9	0.67	n.s.	0.80	57
N30-F12	11	645	*	-12	0.97	***	0.83	60
N30-F13	12	158	n.s.	-48	0.55	*	0.75	58
N30-F16	12	240	n.s.	-13	0.79	***	0.81	62
S30-F1	8	68	**	160	0.67	*	0.66	59
S30-F2	9	315	n.s.	-59	0.57	*	0.86	55
S30-F4	12	90	n.s.	-158	0.26	n.s.	0.73	59
S30-F8	9	495	n.s.	-27	0.62	*	0.89	63
S30-F12	8	533	***	-19	0.99	***	0.90	56
N60	9	285	n.s.	36	0.26	n.s.	0.78	60
S60	9	2235	n.s.	-1	0.55	n.s.	0.88	53
NE40	9	420	n.s.	38	0.08	n.s.	0.69	62
SW40	10	293	n.s.	14	0.71	**	0.80	52

Variables used to describe the pigeons' behavior include the duration of the phase  $t_{dep}$  in seconds, the mean heading in relation to the home direction  $\Delta h_{dep}$ , the corresponding vector length  $r_{dep}$ , the median steadiness  $s_{dep}$  and the median speed  $v_{dep}$  in km/h. Significance levels are given for the deviation from the home direction defined by the confidence interval Bias? and for directional preferences by the Rayleigh test Sign?.

**Table 4.5.** – Comparison of behavior during the departure phase.

Site1	N1	Site2	N2	$t_{dep}$	$\Delta h_{dep}$	$r_{dep}$	$s_{dep}$	$v_{dep}$
N30	6	S30	5	14.0	1.18	11.0	12.0	10.0
N60	9	S60	9	16.0*	0.51	35.0	6.0***	16.5*
NE40	9	SW40	10	34.0	1.37	28.0	33.5	29.0

Table includes the abbreviations of the release sites that are being compared, the sample sizes N1 and N2 and the test statistics. All tests involving comparisons between directional data have been performed using the Watson-Williams test and are based on the deviation from the home direction. All test statistics for the other comparisons have been determined using the Mann-Whitney U-test. The comparison between the releases at N30 and S30 is a second order comparison and is based on the mean and median values of the single releases. The other two are first order comparisons and are based on the data from individual pigeons. Please refer to the previous table for details on the variables that are compared.

After the first point of decision there clearly is a change in behavior, yet there are only three cases where the headings after the decision are closer to the home direction than during the initial phase (see Table 4.6). Still, during all releases a significant increase in steadiness, as well as, in all but one release, a significant increase in speed can be observed.

**Table 4.6.** – Change in behavior after the first points of decision.

R. No.	N	$\Delta h$	$s$	$v$
N30-F1	14	29.0	0.0**	0.0**
N30-F4	13	30.0	1.0**	3.0**
N30-F8	13	32.0	0.0**	5.0**
N30-F12	11	21.0	0.0**	2.0**
N30-F13	12	34.0	0.0**	4.0**
N30-F16	12	21.5	0.0**	0.0**
S30-F1	8	9.0	0.0**	2.0*
S30-F2	9	22.0	0.0**	0.0**
S30-F4	12	23.0	0.0**	0.0**
S30-F8	11	3.5**	0.0**	1.0**
S30-F12	8	12.0	0.0**	0.0**
N60	9	17.0	0.0**	0.0**
S60	9	13.0	0.0**	9.0
NE40	9	6.0*	0.0**	1.0**
SW40	10	6.0*	0.0**	7.0*

The table includes the test statistic and the significance levels for the change in directness of the mean headings  $\Delta h$ , the steadiness  $s$  and speed  $v$  as given by the Wilcoxon signed rank test.

#### 4.4. The Final Homing Phase

The distributions of the last points of decision are shown in Table 4.7. The spatial distributions for these last points of decision are unlike the first points of decision significantly different from random in 9 out of the 14 evaluable releases (i.e. the first flight from S30 was excluded because only one pigeon returned home within the operating time of the GPS), with all of them, even the non-significant ones, more or less in home direction. It is quite striking that in the final releases of each series, the distributions do no longer differ from random and tend to be closer to the release site. The distribution of the last

#### 4. Phases of the Flight

points of decision on a second order level is significantly different from random only for the N30 series (Hotelling's one sample test:  $F = 57.98$ ;  $p \leq 0.01$ ) where I also observe the most significant first order distributions, but not for the S30 series (Hotelling's one sample test:  $F = 10.97$ ;  $p > 0.05$ ).

After the final decision vector lengths of the headings are in all releases significantly different from random (see Table 4.8) and range from 0.96 to 1.00. Although the birds' mean deviation from the home direction for the complete N30 series is only  $-9^\circ$  and  $-12^\circ$  for the complete S30 series, significant biases can be observed in 10 out of the 14 evaluable releases. The median steadiness during homing is also very high during all releases and ranges from 0.83 to 0.90.

**Table 4.7.** – Spatial distribution of the last points of decision.

R. No.	N	PoD's	$PoD_{\Delta h}$	$PoD_{\Delta d}$	Sign.?
N30-F1	11	3	-7	11950	25.24**
N30-F4	9	3	-18	8504	15.57*
N30-F8	13	2	-5	8976	12.32*
N30-F12	11	2	-13	5849	12.24*
N30-F13	13	2	-14	4810	13.45*
N30-F16	9	2	-16	4418	3.96
S30-F2	6	2	-26	16863	33.16*
S30-F4	9	2	-16	1016	18.55*
S30-F8	11	2	-12	7623	8.12
S30-F12	7	2	-9	9512	5.51
N60	6	4	24	16643	39.15*
S60	8	2	-5	32200	73.34***
NE40	4	3	-11	11021	2.44
SW40	7	3	-9	21634	37.75**

Distributions are given as the direction of the center of the distribution from the release site in relation to the home direction  $PoD_{\Delta h}$  as well as the respective distance from the release site  $PoD_{\Delta d}$ . Included are also the sample size N as well as significance levels for distributions that differ from random as determined by Hotelling's one sample test Sign?. Also included are the total number of points of decision PoD's.

There are no significant differences in the behavior of the pigeons during this final homing phase between the two major series (see Table 4.9). The same is mostly true for the comparison between the four other releases, however the pigeons released from N60 produced slightly but significantly longer vectors and flew significantly faster than those released from S60 and the pigeons



released at NE40 flew faster than those released at SW40. Therefore besides some differences in speed the behavior during the final homing phase is mostly similar during all releases.

**Table 4.8.** – Behavior during the final homing phase, after the last point of decision.

R. No.	N	$t_{home}$	Bias?	$\Delta h_{home}$	$r_{home}$	Sign.?	$s_{home}$	$v_{home}$
N30-F1	11	1245	n.s.	-6	0.97	***	0.85	65
N30-F4	9	1665	n.s.	-5	0.98	***	0.86	57
N30-F8	13	1710	**	-13	0.98	***	0.85	59
N30-F12	11	1665	n.s.	-5	0.99	***	0.90	61
N30-F13	13	1635	***	-11	0.99	***	0.87	67
N30-F16	9	1755	**	-11	0.99	***	0.89	62
S30-F2	6	1095	***	-4	1.00	***	0.90	52
S30-F4	9	1725	*	-15	0.96	***	0.83	64
S30-F8	11	1470	***	-19	0.99	***	0.90	65
S30-F12	7	1905	***	-11	1.00	***	0.90	54
N60	6	3480	***	-11	1.00	***	0.86	62
S60	8	2055	**	-23	0.97	***	0.83	52
NE40	4	2528	*	-16	0.99	**	0.84	62
SW40	7	1395	n.s.	-8	0.99	***	0.88	56

Variables used to describe the pigeons' behavior include the duration of the phase  $t_{home}$  in seconds, the mean heading in relation to the home direction  $\Delta h_{home}$ , the corresponding vector length  $r_{home}$ , the median steadiness  $s_{home}$  and the median speed  $v_{home}$  in km/h. Significance levels are given for the deviation from the home direction defined by the confidence interval Bias? and for directional preferences by the Rayleigh test Sign.?.

**Table 4.9.** – Comparison of behavior during the final homing phase.

Site1	N1	Site2	N2	$t_{home}$	$\Delta h_{home}$	$r_{home}$	$s_{home}$	$v_{home}$
N30	6	S30	4	12.0	1.45	7.5	7.5	8.5
N60	6	S60	8	16.0	2.78	10.0*	20.5	5.5**
NE40	4	SW40	7	6.0	1.55	14.0	8.0	0.5**

Table includes the abbreviations of the release sites that are being compared, the sample sizes N1 and N2 and the test statistics. All tests involving comparisons between directional data have been performed using the Watson-Williams test and are based on the deviation from the home direction. All test statistics for the other comparisons have been determined using the Mann-Whitney U-test. The comparison between the releases at N30 and S30 is a second order comparison and is based on the mean and median values of the single releases. The other two are first order comparisons and are based on the data from individual pigeons. Please refer to the previous table for details on the variables that are compared.

#### 4.5. Differences between Individuals

For the analysis of the behavior of individual pigeons I selected only those pigeons where variables could be calculated for at least four flights of the same individual from the same release site. Behavior during the initial phase, as shown in Table 4.10, seems to be quite random and no discernible pattern is detectable. The individual's initial headings show no preferences for specific directions.

A second order analysis reveals that the directional choices during the initial phases differ significantly between both series (Watson-Williams test:  $F = 12.72$ ;  $p \leq 0.01$ ). There are, however, no significant differences in the time until the first point of decision (Mann-Whitney U-test:  $U = 21.0$ ;  $p > 0.05$ ), vector length (Mann-Whitney U-test:  $U = 20.0$ ;  $p > 0.05$ ), steadiness (Mann-Whitney U-test:  $U = 13.5$ ;  $p > 0.05$ ) and speed (Mann-Whitney U-test:  $U = 13.0$ ;  $p > 0.05$ ) between the two groups.

The distribution of the points of decision of the individuals, as shown in Table 4.11, are in most cases not different from random. In each series there is only one pigeon whose distribution of the points of decision does differ significantly from random. While on a group level the distribution of the points of decision of the N30 series is different from random (Hotelling's one sample test:  $F = 48.86$ ;  $p \leq 0.01$ ), the distribution of those of the S30 series is not (Hotelling's one sample test:  $F = 12.67$ ;  $p > 0.05$ ). This is in accordance with the analysis of the data by release number.

When looking at the departure phase at an individual level, there is a striking difference between the two series, N30 and S30. The behavior of the individual pigeons during the N30 series is fairly similar throughout the entire series, whereas the behavior of the pigeons during the S30 series seems to be somewhat more erratic. There is considerably more agreement between

**Table 4.10.** – Individual behavior during the initial phase, until the first point of decision.

ID No.	N	$t_{ini}$	Bias?	$\Delta h_{ini}$	$r_{ini}$	Sign.?	$s_{ini}$	$v_{ini}$
<b>N30</b>								
07-354	5	465	n.s.	-17	0.14	n.s.	0.18	54
07-364	4	158	n.s.	23	0.59	n.s.	0.25	54
07-366	4	293	n.s.	1	0.86	*	0.24	56
07-382	5	255	*	-22	0.98	**	0.61	54
07-392	5	195	*	72	0.84	*	0.17	47
07-393	4	158	n.s.	75	0.48	n.s.	0.32	46
07-399	4	105	n.s.	-6	0.87	*	0.41	53
07-402	5	315	n.s.	52	0.26	n.s.	0.18	53
07-410	5	75	n.s.	31	0.72	n.s.	0.29	48
<b>S30</b>								
08-752	5	150	n.s.	-150	0.19	n.s.	0.12	49
08-765	4	165	n.s.	-98	0.30	n.s.	0.04	46
08-771	4	218	n.s.	-32	0.52	n.s.	0.36	51
08-785	4	578	n.s.	-72	0.16	n.s.	0.12	48
08-797	5	90	n.s.	-30	0.86	*	0.32	53

Variables used to describe the pigeon's behavior include the duration of the phase  $t_{ini}$  in seconds, the mean heading in relation to the home direction  $\Delta h_{ini}$ , the corresponding vector length  $r_{ini}$ , the median steadiness  $s_{ini}$  and the median speed  $v_{ini}$  in km/h. Significance levels are given for the deviation from the home direction defined by the confidence interval Bias? and for directional preferences by the Rayleigh test Sign.?.

**Table 4.11.** – Spatial distribution of the first points of decision of individual pigeons.

R. No.	N	$PoD_{\Delta h}$	$PoD_{\Delta d}$	Sign.?
<b>N30</b>				
07-354	5	-21	1713	1.35
07-364	4	47	417	33.50
07-366	4	-16	1856	104.70*
07-382	5	-29	2102	19.37
07-392	5	39	404	7.60
07-393	4	81	140	1.65
07-399	4	-13	776	11.13
07-402	5	79	287	6.55
07-410	5	11	340	10.33
<b>S30</b>				
08-752	5	-21	216	1.00
08-765	4	-169	139	95.94*
08-771	4	-35	462	2.04
08-785	4	-156	357	27.57
08-797	5	-49	362	3.64

Distributions are given as the direction of the center of the distribution from the release site in relation to the home direction  $PoD_{\Delta h}$  as well as the respective distance from the release site  $PoD_{\Delta d}$ . Included are also the sample size N as well as significance levels for distributions that differ from random as determined by Hotelling's one sample test Sign.?.

#### 4. *Phases of the Flight*

the repeated choices of departure heading in the N30 series, with 6 out of 9 pigeons showing vector lengths significantly different from random (see Table 4.12). In the S30 series, no such agreement can be observed and none of the five evaluable pigeons show vector lengths significantly different from random. In consequence biases can only be observed during the N30 series, with two pigeons showing a bias during the initial and the departure phase.

A second order analysis of the departure phase shows that there is no more significant difference in the directional choices between the two series (Watson-Williams test:  $F = 2.10$ ;  $p > 0.05$ ). There are no significant differences in steadiness during the departure phase (Mann-Whitney U-test:  $U = 22.0$ ;  $p > 0.05$ ), as well as the duration of the departure phase between the two groups (Mann-Whitney U-test:  $U = 17.0$ ;  $p > 0.05$ ). Speed during the departure phase, however, is significantly higher during the N30 series (Mann-Whitney U-test:  $U = 1.0$ ;  $p \leq 0.001$ ) and the vector lengths are significantly less scattered (Mann-Whitney U-test:  $U = 1.0$ ;  $p \leq 0.001$ ).

The distribution of the last points of decision (see Table 4.13), reveals that only one individual from the N30 series shows a distribution significantly different from random. On a second order level the distribution of the last points of decision of the N30 series are, however, significantly different from random, with a direction close to the home direction ( $-10^\circ$ ; 8999 m; Hotelling's one sample test:  $F = 29.69$ ;  $p \leq 0.01$ ), while the distribution of those of the S30 series, although also close to the home direction, is not ( $-16^\circ$ ; 10051 m; Hotelling's one sample test:  $F = 22.72$ ;  $p > 0.05$ ).

Behavior during the final homing phase seems to be very similar for all individuals, with 3 out of 3 (S30) and 8 out of 8 (N30) pigeons showing vector lengths significantly different from random (see Table 4.14). Biases are observed only in two cases during the N30 series where two pigeons had produced long



#### 4. Phases of the Flight

**Table 4.12.** – Individuals' behavior during the departure phase, after the first point of decision.

R. No.	N	$t_{dep}$	Bias?	$\Delta h_{dep}$	$r_{dep}$	Sign.?	$s_{dep}$	$v_{dep}$
<b>N30</b>								
07-354	5	90	n.s.	-27	0.71	n.s.	0.75	65
07-364	4	1155	n.s.	-9	0.94	*	0.81	67
07-366	4	195	n.s.	-24	0.97	*	0.87	65
07-382	5	75	**	-28	0.99	**	0.86	60
07-392	5	1635	***	-16	1.00	**	0.87	67
07-393	4	600	n.s.	-57	0.64	n.s.	0.77	57
07-399	4	203	n.s.	0	0.92	*	0.80	61
07-402	5	345	n.s.	-42	0.66	n.s.	0.64	59
07-410	5	345	n.s.	-18	0.93	**	0.74	62
<b>S30</b>								
08-752	5	90	n.s.	-135	0.30	n.s.	0.71	58
08-765	4	90	n.s.	-96	0.50	n.s.	0.45	54
08-771	4	458	n.s.	-17	0.13	n.s.	0.85	56
08-785	4	165	n.s.	-28	0.42	n.s.	0.82	52
08-797	5	405	n.s.	-19	0.53	n.s.	0.92	56

Variables used to describe the pigeon's behavior include the duration of the phase  $t_{dep}$  in seconds, the mean heading in relation to the home direction  $\Delta h_{dep}$ , the corresponding vector length  $r_{dep}$ , the median steadiness  $s_{dep}$  and the median speed  $v_{dep}$  in km/h. Significance levels are given for the deviation from the home direction defined by the confidence interval Bias? and for directional preferences by the Rayleigh test Sign.?.

**Table 4.13.** – Spatial distribution of the last points of decision of individual pigeons.

R. No.	N	PoD's	$PoD_{\Delta h}$	$PoD_{\Delta d}$	Sign.?
<b>N30</b>					
07-354	5	2	-2	5610	2.34
07-366	4	3	-20	8611	95.05*
07-382	4	3	-10	15660	25.01
07-386	4	2	-7	13664	7.94
07-392	4	1	14	686	3.58
07-393	4	2	-9	9010	6.70
07-399	4	3	-13	11515	5.40
07-410	5	3	-6	7533	18.87
<b>S30</b>					
08-758	4	2	-17	6711	2.43
08-785	4	3	-9	7432	2.08
08-797	5	2	-18	16076	15.17

Distributions are given as the direction of the center of the distribution from the release site in relation to the home direction  $PoD_{\Delta h}$  as well as the respective distance from the release site  $PoD_{\Delta d}$ . Included are also the sample size N as well as significance levels for distributions that differ from random as determined by Hotelling's one sample test Sign?. Also included are the total number of points of decision PoD's.

vectors (both 1.00), these, however, are not the same two individuals where biases were observed during the previous phases of the flight.

#### 4. Phases of the Flight

The behavior during the final homing phase does not differ significantly between both series. There are no differences in the directional choices (Watson-Williams test:  $F = 0.03$ ;  $p > 0.05$ ), vector length (Mann-Whitney U-test:  $U = 9.0$ ;  $p > 0.05$ ), steadiness (Mann-Whitney U-test:  $U = 4.0$ ;  $p > 0.05$ ), speed (Mann-Whitney U-test:  $U = 8.0$ ;  $p > 0.05$ ) or the time needed to return home after the last decision (Mann-Whitney U-test:  $U = 8.0$ ;  $p > 0.05$ ).

**Table 4.14.** – Individual behavior during the final homing phase, after the last point of decision.

R. No.	N	$t_{home}$	Bias?	$\Delta h_{home}$	$r_{home}$	Sign.?	$s_{home}$	$v_{home}$
<b>N30</b>								
07-354	5	1755	n.s.	-9	0.99	**	0.85	64
07-366	4	1380	n.s.	-8	0.97	*	0.89	65
07-382	4	893	n.s.	-13	0.99	**	0.84	58
07-386	4	1095	***	-5	1.00	**	0.94	66
07-392	4	1643	n.s.	-11	0.98	**	0.87	68
07-393	4	1860	n.s.	-11	0.99	**	0.89	55
07-399	4	1748	n.s.	-11	0.96	*	0.83	55
07-410	5	1470	***	8	1.00	**	0.86	63
<b>S30</b>								
08-758	4	1620	n.s.	-10	0.98	**	0.91	61
08-785	4	1530	n.s.	-10	0.99	**	0.89	60
08-797	5	885	n.s.	0	0.98	**	0.93	56

Variables used to describe the pigeon's behavior include the duration of the phase  $t_{home}$  in seconds, the mean heading in relation to the home direction  $\Delta h_{home}$ , the corresponding vector length  $r_{home}$ , the median steadiness  $s_{home}$  and the median speed  $v_{home}$  in km/h. Significance levels are given for the deviation from the home direction defined by the confidence interval Bias? and for directional preferences by the Rayleigh test Sign.?.

In order to analyze the differences between individual pigeons in more detail I used the same method for cross-comparison as described in the previous chapter. Due to the low sample size for the S30 series it was impossible to analyze these individuals and therefore the analysis is limited to individuals that had participated in the N30 series.

This comparison shows that the behavior of individual pigeons is fairly uniform; differences between individuals can mostly be attributed to one or two specific individuals (for details see Table 4.15). Yet the analysis also reveals some interesting aspects. Noteworthy is, for example, pigeon 07-382 whose

distribution of points of decision differs significantly from those of the other pigeons, whose initial heading seems to be much more concentrated in one specific direction and also has a significantly higher initial steadiness. The direction where this pigeon makes its first decision coincides with the choices of initial headings, but although the initial steadiness is extremely high, indicating that the pigeon more or less directly flew to this point, there is no indication that it made its decision faster than others.

**Table 4.15.** – Number of significant differences in behavior between the individuals of the N30 series for all three phases.

Variable	354	364	366	382	392	393	399	402	410
PoD's	-1	0	0	2	-4	0	1	1	1
First PoD	0	1	2	5*	1	1	0	2	2
Last PoD	1	-	2	1	0	3	0	0	1
<b>Initial Phase</b>									
$t_{ini}$	1	1	1	1	1	0	0	0	-5*
$\Delta h_{ini}$	0	0	1	2	3	1	1	0	0
$r_{ini}$	-1	-1	0	5*	-1	0	0	-1	-1
$s_{ini}$	-1	-1	-1	6*	-1	0	0	-1	-1
$v_{ini}$	3	2	2	3	-6*	-6*	2	2	-2
<b>Departure Phase</b>									
$t_{dep}$	0	1	0	-2	1	0	0	0	0
$\Delta h_{dep}$	0	0	0	1	1	0	0	0	0
$r_{dep}$	-2	2/-1	1	4/-1	5*	-6*	1/-2	-2	1
$s_{dep}$	-2	0	1	2	2	0	0	-3	0
$v_{dep}$	0	0	0	0	0	0	0	0	0
<b>Final Homing Phase</b>									
$t_{home}$	0	-	1/-1	0	-3	2	0	0	1
$\Delta h_{home}$	1	0	-	1	1	1	1	0	5*
$r_{home}$	2	-	-5*	1	2	-1	1	-3	3
$s_{home}$	0	-	0	0	0	0	0	0	0
$v_{home}$	0	-	2	0	2	2	-4	-4	2

For reference of the variables see previous tables. Significance for the differences in directions have been established using the Watson-Williams test and for all others using the Mann-Whitney U-test. Overall significance levels have been determined using the Sign test.

Pigeons 07-392 and 07-393 are both significantly slower than other pigeons, but also do not take longer to make a decision. More intriguingly while 07-393 shows more concentrated departure headings, those of 07-392 show considerably more scatter. The only pigeon that shows a general tendency to

#### 4. Phases of the Flight

make its decision faster than others is pigeon 07-410, yet its behavior otherwise does not differ significantly from others.

When looking at the final homing phase I find even less individual features in the pigeons' behavior. Only pigeon 07-366, who shows significantly more scatter in its heading during the final homing phase and pigeon 07-410, who heads out in directions that differ from most others, being the only pigeon showing a positive deviation from the home direction during the final homing phase, differ in their behavior from others.

Although pigeons display individual behavior, this extraordinary behavior seems to have no influence on later phases of the flight. Most of these individualities can be observed during the initial phase and as soon as the pigeons enter the final homing phase the behavior is mostly similar for all pigeons.

#### 4.6. Influence of Experience

In order to analyze the influence of experience on the pigeons' behavior I use the combined data from both series and perform correlations of the different variables with the number of flights from the specific release site. I disregard the tracks from the releases F13 and F16 of the N30 series, because the long break between those and the previous releases could have affected the pigeons' behavior. The results of this analysis can be found in Table 4.16.

**Table 4.16.** – Dependency between each variable of the three phases and the number of releases.

Variable	<i>t</i>	$\Delta h$	<i>r</i>	<i>s</i>	<i>v</i>
Initial Phase	0.392	-0.592	0.729*	0.121	-0.312
Departure Phase	0.883***	-0.733**	0.583	0.450	-0.042
Final Homing Phase	0.631	0.274	0.458	0.512	-0.101

Significance levels for the correlation coefficients are given by Spearman's rank correlation. The sample size for all correlations is N=9. For explanation of the variables see previous tables.

There is no evidence that increasing experience has any effect on the time until the point of decision and the number of decisions ( $p > 0.05$ ;  $R =$

–0.275), although the latter should be viewed with care due to the many tied ranks. Though there is an effect on the duration of the departure phase, thus indicating that the pigeons stuck longer to their first decision the more they were familiar with the release site. This indirectly supports the assumption that there is indeed a reduction in points of decision with increasing familiarity. The initial behavior, beside a tendency for increased vector lengths of the initial headings, is fairly unaffected by increased experience. This increase in vector length, however, indicates that the more the pigeons become familiar with a release site the more they tend to behave in a similar way.

Although not significant there is a certain trend for the headings during the initial phase to be closer to the home direction as the pigeons get more familiar with the release site, which could also explain the increased vector lengths. Steadiness and speed during the initial phase, however, do not improve with increasing experience. During the departure phase headings are closer to home, the more experienced the pigeons are. While vector length and steadiness show a slight, but not significant trend to increase, speed again remains completely unaffected by increasing experience. The behavior during the final homing phase is completely unaffected, with the strongest, non-significant correlation indicating increasing length of the final homing phase with increasing experience.

Increasing experience seems to have little effect on the initial phase beside the observed tendency that pigeons do depart closer to the home direction. It mainly affects the behavior after the first point of decision with pigeons choosing to head out into directions that tend to be closer to the home direction, while at the same time they also stick longer to these decisions. Experience seems to have its greatest influence on the pigeons while they are still relatively close to the release site and the final homing phase remains completely unaffected by increased experience.



## 4. Phases of the Flight

### 4.7. Influence of Abiotic Factors

In order to analyze the effects of abiotic factors, the respective data can be found in appendix D, on the pigeons' behavior I performed correlations between the behavior during all three phases of each release and the same abiotic factors as described earlier (see the corresponding section in the previous chapter). Like before I restrict the data to tracks recorded during the two series. The results of this analysis are shown in Table 4.17.

**Table 4.17.** – Influence of abiotic factors on the behavior during the 3 individual phases of the pigeons' flight.

Variable	Cloud Cover	Wind Speed	Wind Dir.	Temp.	Mag. Var.
<b>Initial Phase</b>					
N	11	11	7	11	11
$t_{ini}$	-0.543	-0.055	-0.393	0.257	-0.091
$\Delta h_{ini}$	-0.039	-0.377	0.107	0.430	0.382
$r_{ini}$	0.209	0.0095	0.161	0.080	-0.282
$s_{ini}$	0.664*	0.318	0.232	-0.561	-0.284
$v_{ini}$	0.059	-0.164	0.607	0.155	0.020
<b>Departure Phase</b>					
N	11	11	7	11	11
$t_{dep}$	-0.289	0.305	-0.107	-0.352	-0.682**
$\Delta h_{dep}$	0.130	-0.227	-0.107	0.298	0.600*
$r_{dep}$	-0.505	0.027	-0.036	0.025	-0.595*
$s_{dep}$	-0.311	-0.105	-0.286	-0.211	-0.745**
$v_{dep}$	0.205	-0.020	0.205	-0.445	-0.348
<b>Final Homing Phase</b>					
N	10	10	6	10	10
$t_{home}$	-0.321	-0.245	0.705*	0.442	-0.088
$\Delta h_{home}$	0.000	-0.221	-0.232	0.139	0.021
$r_{home}$	-0.609	0.145	-0.170	-0.124	-0.291
$s_{home}$	-0.558	0.100	-0.357	-0.276	-0.500
$v_{home}$	0.591	0.003	0.607	-0.473	-0.027

For the correlations between the individual variables and the wind direction, tracks from releases where no wind was measurable are ignored and absolute values are used for all correlations except for correlations between directional data and wind direction. Significance levels are given by Spearman's rank correlation. Also shown is the sample size N. For explanation of the variables see previous tables.

Cloud cover seems to have little effect, except on the steadiness during the initial phase, where increased cloud cover seems to lead to increased steadiness. It also seems to have certain, albeit non-significant and rather small influence

on the vector lengths during the departure phase and vector lengths, steadiness and speed during the final homing phase. Although not significant, it is also the factor with the strongest influence on the time until the first point of decision. While wind speed did not affect the pigeons' behavior in any way, the wind direction had its strongest effect on the length of the final homing phase with head winds leading to increased duration of the final homing phase.

The strongest effects on the behavior of the pigeons can, yet again, be observed in relation to the variation of the earth's magnetic field. Its effects, however, seem to be mainly confined to the departure phase. With increasing variation of the earth's magnetic field, I observe not only a reduced length of the departure phase, but also headings further away from the home direction, increased scatter in the groups choice of heading and a decrease in the steadiness of the pigeons' flight during the departure phase. The initial phase as well as the final homing phase seem to be unaffected, except for a slight, but non-significant, influence on the steadiness during homing.

### **4.8. General Behavior**

There is interesting correlative evidence that can be found when looking at the variables calculated before and after the first and also after the last point of decision. Unfortunately the number of decisions had too many similar values to allow a sensible analysis of the data. Yet, there are other interesting results to be found in Tables 4.18 to 4.20. For this specific analysis all releases have been included without any restrictions.

The time until the first point of decision has no significant influence on the behavior during the initial phase itself, as well as the departure or the final homing phase. The time needed to return home, however, seems to be higher if the pigeons take longer to make their decision (see Table 4.18).

#### 4. Phases of the Flight

**Table 4.18.** – Influence of the time until the point of decision  $t_{ini}$  on the behavior during the individual phases.

Phases	$t$	$\Delta h$	$r$	$s$	$v$
Initial Phase		0.019	0.058	-0.382	0.146
Departure Phase	0.396	-0.072	0.078	-0.010	-0.188
Final Homing Phase	0.704**	0.100	0.426	0.010	-0.487

Significance levels are given by Spearman's rank correlation. The sample sizes are N=15 for the initial and the departure phase and N=14 for the final homing phase. For explanation of the variables see previous tables.

Looking at how the variables within each phase depend on each other (see Table 4.19) reveals that the less the headings during the departure phase lead the pigeon away from the actual home direction, the longer does the pigeon fly in this direction and the more steady is its flight during this particular phase. This relationship is, as could be expected, reversed for the final homing phase, the more the pigeons deviate from the actual home direction the longer does it take them to return home. Also the steadiness during the final homing phase is higher, the more the individual pigeons headings are in accordance with each other.

**Table 4.19.** – Dependency between variables within each phase.

Variable	$t$	$\Delta h$	$r$	$s$	$v$
$t_{dep}$		-0.504**	0.168	0.641**	-0.184
$t_{home}$		0.558*	0.101	-0.382	-0.080
$\Delta h_{ini}$			-0.021	-0.338	-0.054
$\Delta h_{dep}$			-0.368	-0.575*	0.157
$\Delta h_{home}$			0.222	-0.440	0.234
$r_{ini}$				0.243	-0.109
$r_{dep}$				0.387	-0.020
$r_{home}$				0.743**	-0.145
$s_{ini}$					0.388
$s_{dep}$					-0.123
$s_{home}$					-0.109

Significance levels are given by Spearman's rank correlation. The sample sizes are N=15 for the initial and the departure phase and N=14 for the final homing phase. For explanation of the variables see previous tables.

Between the different phases (see Table 4.20), there is a clear dependency of the initial headings and the headings during the departure phase, meaning the further the initial headings are away from home, the further away are also the headings during the departure phase. There is an obvious correlation between the steadiness during the departure and the final homing phase which is probably due to the overlap between the two phases. Other than that the results of this analysis indicate that the phases themselves are fairly independent from each other.

**Table 4.20.** – Influence of behavior during one phase on other phases.

Phases	$\Delta h$	$r$	$s$	$v$
Initial-Departure	0.586**	0.003	-0.213	0.344
Initial-Homing	0.326	-0.325	-0.071	0.191
Departure-Homing	0.016	0.279	0.705**	0.447

Significance levels are given by Spearman's rank correlation. The sample sizes are N=15 for the initial and the departure phase and N=14 for the final homing phase. For explanation of the variables see previous tables.

## 4.9. Discussion

### 4.9.1. A First Decision

One of the questions concerning the points of decision is, whether they occur at specific places or at random positions around the release sites. If the decisions are made at a specific place that is characteristic for each release site it could indicate the use of landmarks at the release site. Of course the use of landmarks can not be ruled out if the decisions are made at random places, yet the question arises, if these decisions are made after a specific time interval and if so, whether the pigeons use the time before the decision to scan for navigational factors, so-called orientation flying (Hitchcock, 1952), or if the time spent is used simply for flight preparations or exploration. In the latter case, as suggested by a previous study (Schiffner & Wiltschko, 2009), increased experience would not

#### 4. *Phases of the Flight*

be expected to reduce the time needed to make a decision. The time needed to make a decision should also be independent of the type of decision. That is whether the pigeon decides to fly home or visits the nearest town before it actually decides to return home. The decision should also be independent of the availability and reliability of navigational factors.

In almost half of the releases the pigeons head out in preferred directions during the initial phase, the points of decision, however, are randomly distributed around the release sites, with only four exceptions, hence not advocating any obvious use of landmarks. Although not always significant the initial orientation from unfamiliar sites seems to coincide with the behavior to fly towards the nearest town or village, thus explaining the observed differences between the individual release sites (see previous chapter). This behavior is most evident during the releases from NE40 and N60. It therefore seems likely that the behavior to fly towards the nearest town is mostly limited to this initial phase.

With increasing familiarity an increase in agreement of the initial headings, with directions closer to the home direction can be observed. This suggests that pigeons know their home direction well before they finally make a decision. Earlier experiments, with pigeons released from boxes, indicate that pigeons may already know the home direction before they actually take off (Chelazzi & Pardi, 1972; Kowalski, 1994; Mazzotto *et al.*, 1999; Gagliardo *et al.*, 2001). Even before the pigeons are familiar with the release site there is already a tendency that pigeons which initially departed further from the home direction, also stay on a route further away from the home direction. This finding could indicate that the pigeons already head out in home direction during the initial phase if they want to depart towards home. There are no indications that increasing familiarity reduces the time until the point of decision and that the potential information gathered during that time has any effect on the decision itself and



the behavior afterwards. The directions in which the pigeons depart, meaning whether they head out to the nearest city or head home after the decision, are also independent of the time needed to make this decision. As indicated by the results of the comparison between the release sites in equivalent distances the time needed to make a decision also does not depend on the direction of displacement. The availability of navigational factors, as indicated by the comparison between the releases in the Vogelsberg anomaly, at NE40, and at the magnetically quiet release site SW40, has likewise no influence on the time until the point of decision. As neither familiarity, direction of displacement, availability of navigational factors, nor the task after the decision has any effect on the time needed to reach a decision, it is unlikely that the pigeons scan for navigational factors during that time. The results therefore suggest that the time spent is most likely used for flight preparations or exploration, rather than collecting information on the distribution of navigational factors around the release site. The present findings are therefore in accordance with early assumptions that the flight of the pigeons is initially governed by non-navigational processes (Heinroth & Heinroth, 1941). These findings also explain why the efficiency during the initial portion of the homing flight remains low even with increasing familiarity, as observed in the current (see previous chapter) and also previous studies (Biro *et al.*, 2002; Wiltschko *et al.*, 2007).

A general need for exploration may be indicated by a series of experiments which were originally designed to identify the use of familiar landmarks. In these experiments pigeons were either allowed or disallowed to view the surrounding landscape before release, sitting either in a transparent or an opaque release box (Braithwaite, 1993; Burt *et al.*, 1997; Biro *et al.*, 2002). The findings of these studies indicate an increase in homing speed of up to 16% (Burt *et al.*, 1997) for pigeons that were allowed to view the surrounding before release. A more detailed study with GPS recorder, however, revealed that the effect is limited

#### 4. *Phases of the Flight*

to the first 1000 m of the pigeons' flight (Biro *et al.*, 2002). This area roughly coincides with the distance until the first point of decision and therefore it might be argued that previewing could simply decrease the need to explore the surrounding area. There seems to be a dependence between the time needed to make a decision and the length of the final homing phase. This finding suggests that pigeons that are more likely to explore do so throughout the whole journey. The attractiveness of towns and villages close to the release site may then be explained as well. The pigeons may be generally more interested in exploring built-up terrain or prefer to make flight preparations above familiar and safe terrain instead of open fields, where they constantly need to be aware of predators.

##### **4.9.2. Behavior after the First Point of Decision.**

After the first point of decision most of the pigeons seem to make yet another decision. Although a possible influence of familiarity on the total number of points of decision was not directly detectable, the trend for increasing length of the departure phase and the trend for decreased deviations from the home direction on departure, may suggest such a decrease in the number of points of decision with increasing familiarity. In most cases, the headings of the pigeons after the point of decision indicate that the pigeons are at least initially driven by the intention to return home. Extreme biases can only be observed in the beginning of each series, as well as in two of the single releases. Due to such extreme biases it may not be surprising that there are on average two or more points of decision. However, pigeons still make on average two decisions even after they are clearly familiar with the release site and depart closer to the home direction.

A simple explanation for this could be that pigeons, unlike previous observations suggest, do occasionally divert from the task of homing under certain

circumstances (Wagner, 1970). Wagner reported that pigeons that are already on their way home, even fly over high mountain ridges without diverting from their current course, but do make detours, the closer such obstacles are to the release site. Wagner's observations, however, come from flocks of pigeons and pigeons released singly might simply be more prone to temporarily abandon the homing task if they spot conspecifics or encounter obstacles. Therefore it is possible that the additional points of decision are due to motivational shifts in the pigeon during homing. This assumption is supported by the fact that each point of decision is per definition initiated by a phase of decreasing cumulative velocity, indicating that the pigeons indeed divert from the task of homing. These phases of decreasing cumulative velocity are, however, short and usually do not last much longer than 3 minutes (not shown in results). This would also explain why more points of decision can be observed at release sites further away from the home loft, as the increased length of the journey simply increases the chance that the pigeon encounters situations where it may choose to divert from the task of homing.

However, as during the majority of the releases the pigeons seem to head towards home after the first point of decision and as these points almost never lie further away from the release site than 1000 m it can be concluded that the vanishing bearings which are usually recorded during traditional releases are indeed representative for the pigeons' ability to determine the home direction. What is also of particular interest in this matter is that steadiness and vector lengths are higher the closer the pigeons depart towards home and the further these headings lead the pigeons away from the actual home direction, the shorter does this specific phase last. This suggests that decisions leading to departures in directions different from the home direction are short lived phenomena and that the flight behavior during such phases differs from that observed during homing. Thus, it is also unlikely that these deviations are the

#### 4. *Phases of the Flight*

result of navigational errors, instead they appear to be intentional choices made by the pigeons for purposes other than finding their way home. Evidence for possible navigational errors may yet be found during the final homing phase. Steadiness during the final homing phase is highly correlated with the vector length. This may suggest that in cases where individual pigeons have problems to determine their home course, these problems are not restricted to that specific individual, but do in fact affect the whole group. Therefore these possible navigational errors are more likely the result of external influences and do indicate that the ability to perceive navigational factors is probably the same for all pigeons.

##### **4.9.3. Individual Behavior**

This does, however, not mean that there is no individuality at all. Yet, while certain individuals may fly faster, show more scatter in their repeated choices of initial headings and headings on departure or even make their decisions faster than others, such individualities in behavior always remain limited to specific phases of the flight and do not affect the individual's behavior during any other phase. Neither does a shorter time until the point of decision lead to less homeward directed departure headings, nor does a high speed during the initial phase ultimately result in high speed on departure. Most of these individual differences are also related to aspects of the pigeons' behavior that can be considered irrelevant to the pigeon's ability to successfully find its way home, meaning behavior during the initial phase or differences in speed. During the probably most important phase of the flight, the final homing phase, where it can be ensured that the pigeons foremost task is to fly home, there are hardly any difference in the behavior between individual pigeons. So, while these observations show that the individual's behavior may differ in certain aspects,

there are also clear indications that all of the pigeons basically possess the same abilities that allow them to successfully find their way home.

#### **4.9.4. Influence of Abiotic Factors**

As I said before it is more likely that the differences in behavior are due to influences of external factors, yet the previous analysis revealed no influence of abiotic factors on the pigeons' behavior other than the influence of the daily variation of the geomagnetic field. The tracks separated into individual phases now show more clearly that there is indeed an influence of other factors. There are, for example, indications that increased steadiness can be observed when cloud cover is high, which may be related to an increased motivation to leave the site. This is supported by a series of observations that are unfortunately not significant and therefore remain highly speculative. There is a slight tendency for decreased time until the first point of decision under dense cloud cover. The choices of headings during the following departure phase are slightly more scattered and steadiness as well as vector lengths during the final homing phase are also decreased. It also seems that the pigeons increase their speed in order to compensate for the time lost, which may also hint at an increased motivation to return home.

The increased scatter combined with the increased speed may seem odd, but the results may simply indicate that the pigeons, under dense cloud cover, may have trouble determining their home course using the sun compass and compensate for this problem by increasing their speed. This is supported by previous observations from pigeons released under overcast skies, where increased scatter on vanishing could be observed too (Wallraff, 1966). Although the sun was visible from the release site during all times, the pigeons may have encountered situations en route where it may have been more difficult to use the sun compass. While this clearly has not impaired the pigeons of the ability to



#### *4. Phases of the Flight*

home, as has been observed in young inexperienced pigeons (Keeton & Gobert, 1970), the current experiments could indicate that some problems may persist even for older and more experienced pigeons. Wind speed still does not seem to affect the pigeons' behavior in any way, but this may be yet again due to the fact that all releases were performed under mostly calm conditions where there was no or only little wind. Yet the wind direction did clearly affect the pigeons' behavior leading to increased homing times when the pigeons encountered head winds.

##### **4.9.5. Influence of the Earth's Magnetic Field**

The influence of the daily variation of the earth's magnetic field, while again having the strongest effect on the pigeons' behavior, seems to be mainly limited to the departure phase. Here it has adverse effects on the pigeons' orientation, influencing all calculated variables except the speed with which the pigeons travel. While there is also an effect on the steadiness during the final homing phase, this effect is considerably smaller and not significant. That there is no influence whatsoever on the initial phase, while the other phases are affected to some degree, is yet another strong indicator that the initial phase is not part of the navigational process. Unlike previous studies where the analysis of the involvement of the magnetic field, due to the fact that the releases were performed traditionally without GPS-tracking devices, had to remain limited to the initial part of the pigeons' flight, the results of the current study also show for the first time that anomalous magnetic conditions also affect the remainder of the pigeons' journey. As indicated by the headings during the departure phase, the pigeons are in most cases oriented towards home. Therefore the influence of the daily variation of the geomagnetic field on that phase is yet another strong indicator for the involvement of the factor in the actual homing process. It remains elusive so far why no significant effect can be observed

during the final homing phase. This, however, corresponds to the observation made in the previous chapter that there is also no significant effect on the overland efficiency. The variations of the earth's magnetic field always remained below 70 nT and therefore may also give some clue to the precision with which the pigeons can determine differences in the magnetic field. While it may not be possible to define the actual accuracy the results indicate that the difference which pigeons are able to detect are sufficient for navigation below 28 km.

Interestingly these considerably smaller deviations in the geomagnetic field, unlike stable magnetic anomalies, may have a much stronger influence on the pigeons. Such a strong influence was possibly observed on the first release from S30 where the second highest variability in the earth's magnetic field during the whole study made it seemingly impossible for the pigeons to return home on time. Although the increased sun activity decreased over the whole day, the pigeons were in almost all cases more than seven hours overdue. It is possible that the pigeons were either unable to identify the varying magnetic field as an unreliable source and therefore continued to use the magnetic field as a navigational factor or were due to other coincidental events unable to use different navigational factors to find their way home. That those factors are basically available may be indicated by the change in behavior on the fourth flight from the same release site, where most of the pigeons switched from a westerly to a northerly course. During this release the highest variability in the geomagnetic field was observed, yet the pigeons had no problem to return home on time.

What is also intriguing is that when comparing the departure phases of the flights from within the magnetic anomaly of the Vogelsberg and from outside the anomaly there are no significant differences. However, the headings during the departure phase, when released from SW40 are clearly homeward directed and those of the pigeons released from NE40 are random. That the direct

#### 4. *Phases of the Flight*

comparison does not reveal this may simply be related to the relatively small sample size and it should also be mentioned the test statistic for the comparison of the vector lengths was quite close to significance.

#### **4.10. Conclusion**

In this chapter I present conclusive evidence that the initial behavior of pigeons immediately after release is not driven by the motivation to fly home and is mostly unaffected by external factors, as well as experience. The strongest yet not significant effect on the time until the first point of decision can be observed under dense cloud cover, indicating an increased urge to home. There is also evidence that pigeons that head out into directions closer to home during this particular phase, will also depart closer to the home direction, indicating that the pigeons know the home direction well before they make the decision to leave the site and that the initial phase is not used to gather information about the distribution of navigational factors. Exploration and flight preparations therefore seem to dominate this initial phase. The following departure phase seems to be quite independent from this initial behavior and can be mostly characterized by steady and speedy flight that is in most cases directed towards home. Unlike the preceding phase the departure phase is clearly affected by the daily variations of the geomagnetic field indicating that the earth's magnetic field is an integral part of the navigational process. The points of decision, however, occur close to the release site indicating that the traditional vanishing bearings indeed record the behavior during the departure phase and are therefore representative for the pigeon's ability to determine the home direction. The behavior during the final homing phase is similar for all individuals and independent of previous experience. Therefore indicating that the navigational abilities are basically the same for all pigeons.

## 5. Time Series Analysis

### 5.1. Introduction

The individual phases of the pigeons' flight are a good basis for further evaluation. Yet it seems difficult, if not impossible, to determine common features of those individual phases simply by comparing average headings, steadiness and speed. It makes sense to compare the initial, the departure, and the final homing phase on such a level, because they can be linked to external references, the release site, in case of the first two phases, and the home loft, in the case of the final homing phase; however, such external references are difficult to define for all other phases. Therefore it is necessary to find new parameters that help to characterize the individual phases on a systematic level. Such parameters are the correlation dimension and the largest Lyapunov exponent. The correlation dimension is a measure of a system's complexity, e.g. the degrees of freedom of an underlying process and the largest Lyapunov exponent is a measure of a system's predictability. These variables are commonly used to describe so-called dynamic systems, such as pendulums, fluid convection, but also population dynamics. The behavior to fly along similar but not identical routes with portions where the tracks converge and later diverge again and to do so repeatedly and even when released from different starting points, are all indicators that the navigational process is a dynamic process of chaotic-deterministic nature. Yet, before I can attempt to analyze the underlying system, there are some initial requirements that need to be met:

## 5. Time Series Analysis

- The time series must represent a measurement of a meaningful variable.
- The time series must be bounded, which means that all values of the observed states must be limited by an upper and lower bound.
- The time series must be stationary. In a mathematical sense stationary means that the behavior of the underlying process does not change over time and space. Therefore the probability  $Px_{t_1+\tau}, \dots, x_{t_n+\tau} = Px_{t_1}, \dots, x_{t_n}$ , with  $\tau$  as the time lag, needs to remain fixed for all possible choices of  $t_1, \dots, t_n$  and  $\tau$ .
- Noise within the time series must be at an acceptable level.
- The measured time series must consist of a sufficient number of data points.

These requirements have implicit effects on the application of the methods on tracking data. The directly measured positional coordinates from the GPS receiver are not suited for this analysis. As mentioned before, the time series needs to be stationary and bounded. While it is difficult to define stationarity for a finite time series, it is quite obvious that the raw positional data from the GPS are by no means stationary. As the pigeon moves towards its goal, the coordinates ideally increase or decrease until the pigeon has reached its home and thus the positional data show clear trends. Furthermore, it can not be ensured that information contained in the positional data remains meaningful for all times. In cases where the pigeon flies along one of the principle axes, the coordinate that runs along this axis would constantly remain the same and thus contain no information that would allow analysis of the underlying process.

The individual phases, as defined in the previous chapter, are ideal candidates for this purpose. By using the headings relative to the home direction during each phases as a time series, it can be ensured that the variable remains meaningful for all times. The calculation of the headings relative to the home



direction introduces a stationary element, the home direction, and the separation into the individual phases increases the chances that each phase itself represents a stationary time series. Furthermore, I split, each time series, i.e. each phase of the pigeons' flight, into two halves which I then analyzed separately. If the results for the two parts do not differ from each other, then I assume that the original data set is stationary. This approach is an extension of the cross prediction method suggested by Kantz & Schreiber (1997).

Due to the precision of the modern GPS technology, influence of noise from the method of measurement can be considered negligible. A much bigger problem arises from another source of "noise", the behavior of the pigeon itself. As it can not be expected that the pigeon's behavior is solely governed by the urge to fly home, some parts of the track may represent non-navigational movement. Such non-navigational phases within the flight of the pigeon can also be considered as noise, yet the separation into the individual phases should also serve the purpose of separating non-navigational from navigational phases.

Experimental data are seldom at abundance and therefore it is really hard to meet the requirement of having a sufficient number of data points. While there are various suggestions how many data points are sufficient, Ruelle (1990) for example suggests:  $d < 2 \log_{10} N$ , with  $d$  being the number of dimensions and  $N$  the number of data points, the necessary number of data points completely depends on the nature of the underlying process. One possible way to deal with limited time series is using several shorter measurements of the same dynamical process to ensure the reliability of the calculated properties. The repeated releases from the same release sites can be considered as such. Now after having ensured that the individual phases do meet most of these initial requirements - some of them will be dealt with later - I can use the data to calculate characteristic values that describe the underlying process.

## 5.2. Time Series Analysis

The explanations given in this chapter are extremely concise and only serve the purpose of giving a short but still accurate overview of the methods used in this chapter. A detailed introduction into the subject of dynamic systems theory as well as detailed explanations of the methods and the principles behind these methods are provided in appendix A.

Calculation of the correlation dimension and the largest Lyapunov exponent usually requires extensive knowledge about all the variables involved in the process, but by applying time lag embedding (Whitney, 1936), it is possible to reconstruct the system from one single measured variable and in turn get reasonable estimates of the two parameters, even without a priori knowledge about the equations defining the system. With time lag embedding it is then possible to define a series of vectors  $x(t)$  that represent the reconstructed system:

$$x(t) \rightarrow x(t, t - \tau, t - 2\tau, \dots, t - m\tau)$$

with  $m$  as the embedding dimension and  $\tau$  as the time lag. For selection of the time lag  $\tau$  and embedding dimension  $m$  see appendix A.

### 5.2.1. The Correlation Dimension $d_2$

Estimation of the correlation dimension evolves around the simple idea that each object is comprised of a number of points that is directly related to the objects number of dimensions. This means that the number of points on a square, a two dimensional object is exponentially higher than on a line, an one dimensional object. Based on this idea, the correlation dimension can then be estimated by calculating the correlation integral  $C^m(r)$ . The correlation integral is simply a sophisticated way to count the number of such points and can be acquired through the following formula:

$$C^m(r) = \frac{1}{M(M-1)} \sum_{i,j=1}^M \Theta(r - \|x_i - x_j\|)$$

with  $i \neq j$ ,  $i$  and  $j$  as two points of the reconstructed system  $x(t)$ ,  $r$  the distance interval and  $m$  the embedding dimension.

$$M = N - (m - 1)\tau$$

with  $\tau$  the embedding lag,  $m$  the embedding dimension and  $N$  the number of data points in the time series.

$\Theta(x)$  denotes the so-called Heaviside step function defined as:

$$\Theta(x) = \begin{cases} 1 & x \geq 0 \\ 0 & x < 0 \end{cases}$$

$\|\dots\|$  denotes the so-called Euclidean norm, a measurement of length in Euclidean vector space.

From the correlation integral the correlation dimension  $d_2$  can then be obtained as the slope of  $\ln C^m$  versus  $\ln r$ :

$$d_2 = \lim_{r \rightarrow 0} \lim_{m \rightarrow \infty} \frac{\ln C^m(r)}{\ln r}$$

The slope of the curve is then a direct measure of the system's number of dimensions. Samples showing these slopes for individual calculations of the correlation dimension can be found in appendix B.

### 5.2.2. The Largest Lyapunov Exponent $\lambda$

Calculation of the largest Lyapunov exponent evolves around the idea of finding a scheme to predict future states of a system. Assuming that a process is completely predictable, a point  $x_i$ , of the reconstructed system which is as similar as possible to another point  $x_j$  can theoretically be used to predict all future states of  $x_j$  by simply looking at the future states of  $x_i$ . The difference between the future states  $\Delta s$  of  $x_i$  and  $x_j$  can then be calculated for each prediction step  $p$  by the following formula.

## 5. Time Series Analysis

$$\Delta s(p) = \|x_{i+p} - x_{j+p}\|$$

with  $i \neq j$  and  $i$  and  $j$  as two independent points of the reconstructed system  $x(t)$  and  $\|\dots\|$  denoting the so called Euclidean norm.

By calculating the average of  $\Delta s$  over all prediction steps  $p$ , using all possible states of the system as a starting point  $x_i$  for the prediction, it is then possible to estimate the largest Lyapunov exponent:

$$\lambda = \frac{1}{T} \langle \ln \Delta s \rangle$$

where  $\langle \rangle$  denotes the average,  $T$  is the system's sampling time and  $\Delta s$  the average prediction error. Samples of the increase in prediction error for individual calculations of the largest Lyapunov exponent can be found in appendix B.

### 5.3. Data Filtering

As stated earlier, there are some initial requirements that have to be met by every time series in order to guarantee reliable results. While the individual phases of the pigeons' flight already meet most of these requirements, it could not have been ascertained beforehand that the number of data points is sufficient and that the signal within each phase remains stationary. Therefore it is crucial to apply certain filters to remove non-stationary time series and time series with insufficient number of data points before the data can be evaluated. An overview of the individual filtering steps and the resulting reduction in data points and data sets, as well as averaged estimates for both variables is given in Table 5.1.

To get an estimate of the reliability of each result, calculations of the largest Lyapunov exponent and the correlation dimension are performed for each original series, as well as the first and second half of each time series

**Table 5.1.** – Individual data filtering steps and resulting data reduction.

<b>Data Set</b>	<b>T</b>	<b>N</b>	<b>n</b>	<b>N%</b>	<b>n%</b>	<b><math>d_2</math></b>	<b><math>\lambda</math></b>
Raw	167	848	473295	-	-	2.3	0.024
Prefiltered	140	263	316260	69%	33%	3.2	0.022
Correlation Dimension	91	107	194985	87%	59%	3.7	-
Largest Lyapunov Exponent	90	112	171615	87%	64%	-	0.019

Included in the table are the number of individual tracks  $T$  the number of individual time series  $N$ , the total number of data points  $n$ , the percental reduction in the number of time series  $N\%$  and number of data points  $n\%$ , relative to the values after the first filtering step (prefiltered), the average correlation dimension  $d_2$  and the average of the largest Lyapunov exponent  $\lambda$  for each filtering step. Results are presented for the raw data set, the data set after removal of all failed calculations (prefiltered) and the final data sets for the evaluation of the correlation dimension and the largest Lyapunov exponent after application of all filters.

separately. If the calculation of the largest Lyapunov exponent for one of these so-called sub-samples fails completely, this can be the result of two different reasons. On the one hand the number of data points may be too low for the sub-sample analysis to succeed or on the other hand the original time series may not be stationary. In the first case the estimates may be unreliable and in the second case the estimates are simply incorrect, hence including these results would be in violation with the initial requirements.

Through this initial filtering I achieve a general level of reliability, but in order to ensure a truly acceptable level of stationarity I also exclude all time series where the difference between the largest Lyapunov exponents of the two sub-samples is greater than 0.01. I also remove all time series with correlation dimensions below 2.0. Correlation dimensions below 2.0 could either suggest visually guided or random flight. In the absence of an underlying system the correlation dimension simply measures the steadiness of the flight path, with a straight line resulting in a correlation dimension of 1.0 and circling behavior in a correlation dimension close to 2.0. Unfortunately visually guided flight would result in a similar correlation dimension therefore the two cases are indistinguishably and need to be excluded from evaluation. Estimates below 1.0 are obviously the result of miscalculations and therefore are removed, too.

## 5. Time Series Analysis

After application of these basic filters I deal with the results for the largest Lyapunov exponent and the correlation dimension separately, as the requirements for calculation of a reliable correlation dimension estimate and the largest Lyapunov exponent are not necessarily the same, e.g. the calculation of the Lyapunov exponent requires less data points to succeed. The final filtering steps (see below) are introduced to increase the reliability of the individual estimates, by reducing the correlation between the number of data points and the estimate, as well as increasing correlation between the sub-samples; the criteria for filtering are selected accordingly.

For the final filtering step of the largest Lyapunov exponents I exclude all time series with less than 500 data points and those where the largest Lyapunov exponents of the sub-samples differ more than 0.005. These additional restrictions completely remove the correlation with the number of data points ( $r_{corr} = -0.057$ ;  $N = 112$ ;  $p > 0.05$ ), and ensure a high correlation between the sub-samples ( $r_{corr} = 0.857$ ;  $N = 112$ ;  $p \leq 0.001$ ).

Concerning the correlation dimension estimates I exclude all time series with less than 1000 data points, as the estimation of the correlation dimension is generally more dependent on the number of data points (see below) than the largest Lyapunov exponent, and also remove all time series where the correlation dimension of the sub-samples differ by more than 1.0. Although I was unable to completely remove the correlation with the number of data points ( $r_{corr} = 0.399$ ;  $N = 107$ ;  $p \leq 0.001$ ), further reduction seemed to be ill advised, as the number of individual time series was already lower than for the largest Lyapunov exponent. Yet, as a linear regression analysis indicates, the error induced by the correlation is with an increase of 0.0003 per additional data point almost negligible. The correlation between the sub-samples after filtering, on the other hand, can be considered acceptable ( $r_{corr} = 0.783$ ;  $N = 107$ ;  $p \leq 0.001$ ).



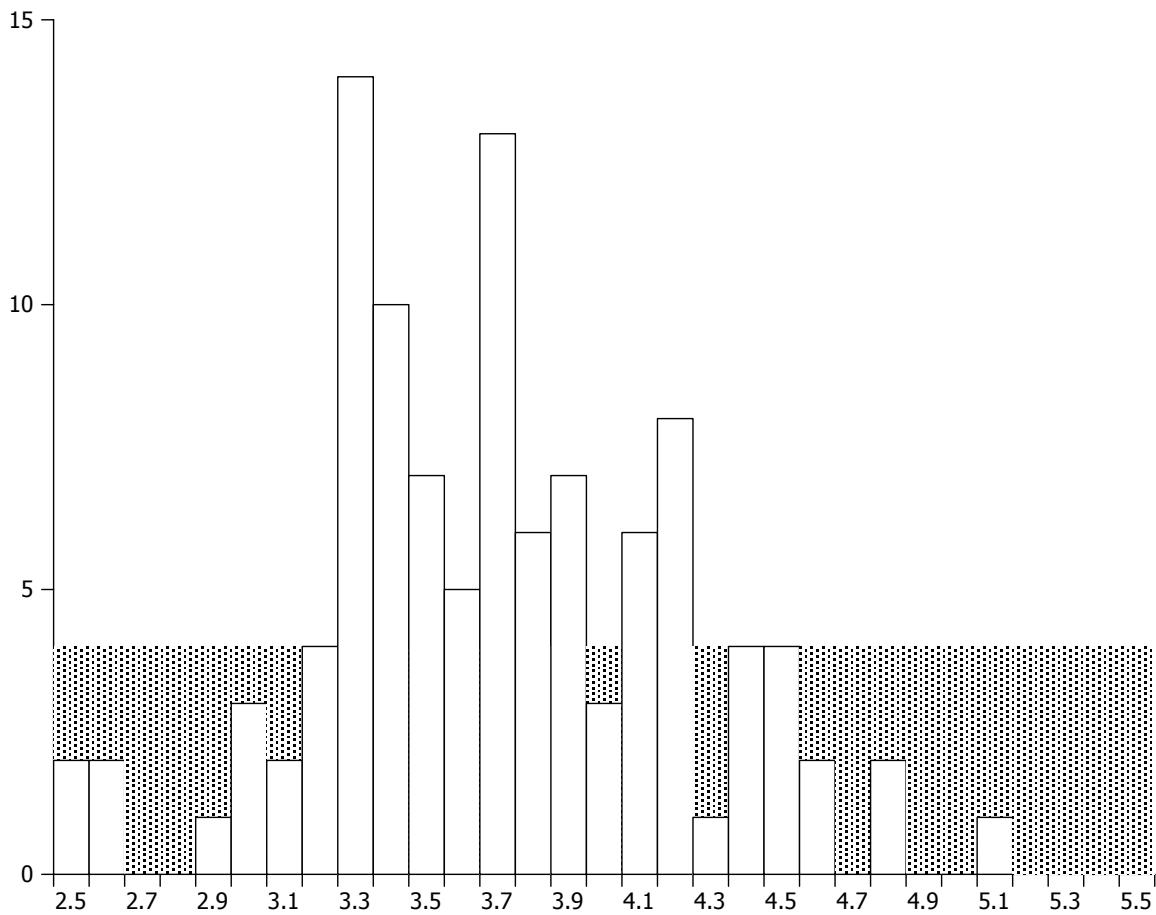
Before I continue with the analysis of the data I think it is necessary to put the resulting reduction in data into perspective. As shown 69% of the time series are not evaluable. However, the evaluable time series still come from 140 of the 167 tracks. This means that during almost any flight there is a phase that does fit the initial criteria, which is a good result considering that many tracks were incomplete to begin with. The reduction in data points is relatively low and the time series that are not evaluable include on average only 250 data points. This shows that these time series are mostly not evaluable because the number of data points is insufficient. The additional filtering steps reduce the number of individual time series even further. Yet, most of the tracks and roughly 40% of the total number of data points are considered for evaluation. At first glance the data reduction might seem rough, but considering the amount of data points that is still left after application of all filters, there is more than 1 hour of tracking data left for each of the 90 tracks, which can be considered more than enough time for the pigeons to return home, even from the most distant site used in this study.

### 5.4. Data Evaluation

The data, after filtering, still spreads over a considerable range of possible estimates ( $\lambda = 0.005 \leftrightarrow 0.045$ ;  $d_2 = 2.5 \leftrightarrow 5.1$ ) and therefore the question arises whether the differences are simply the result of calculation errors or due to the fact that the data set contains more than one valid estimate. In consequence I use histograms of the results to illustrate the range of correlation dimensions and Lyapunov exponents and identify valid and invalid estimates. From the total number of estimates I determine the number of occurrences that would be expected by chance. In the case of simple chance observations an equal number of occurrences of estimates over the complete range, defined by the lowest and the highest calculated estimate, should be observable. In any other

## 5. Time Series Analysis

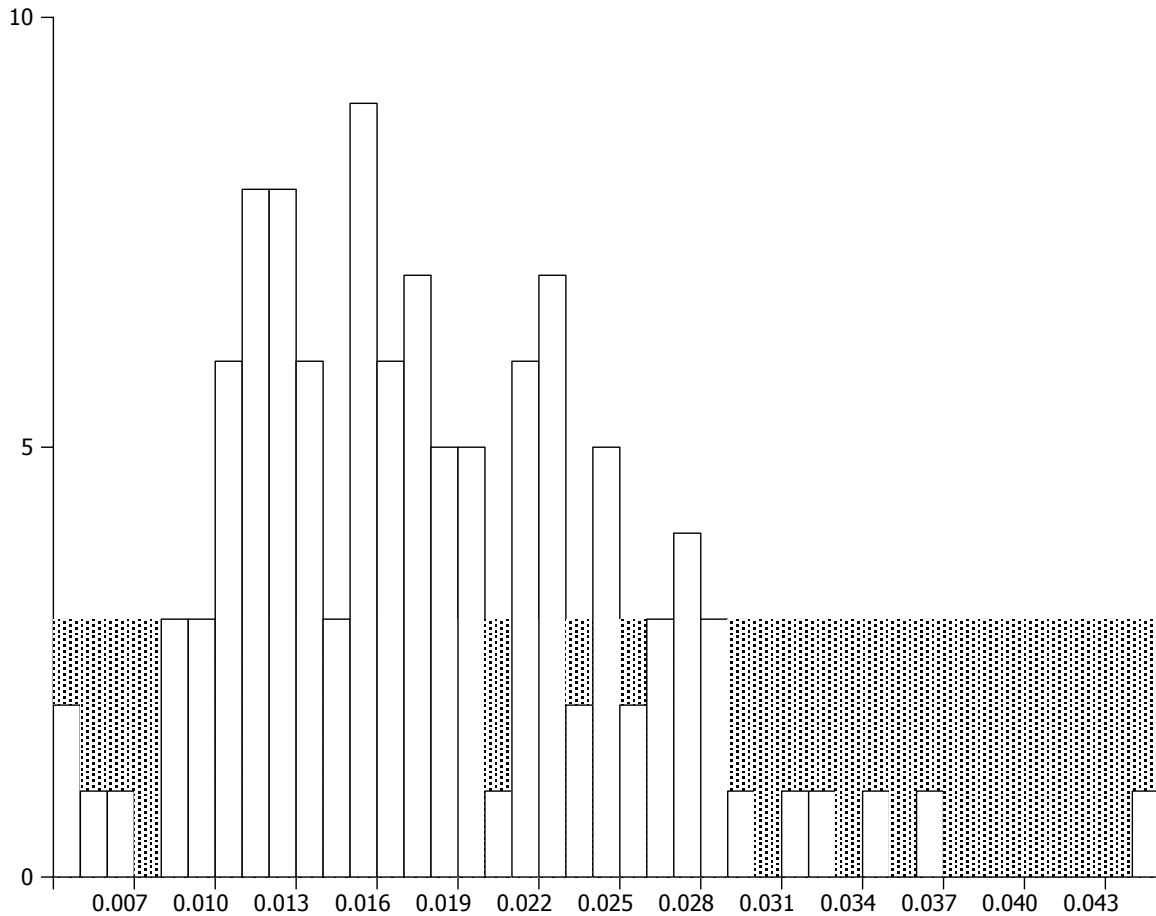
case occurrence of one or more estimates should exceed the number of chance observations. In addition to this purely subjective approach I also perform a statistical analysis of the two data sets, testing for random distribution, using the Chi-Squared test (Baschelet, 1981) and for normal distribution, using the Anderson-Darling test (Anderson & Darling, 1952).



**Figure 5.1.** – Histogram of the various correlation dimension estimates. The level of expected chance observation is indicated by the gray area.

As shown in Figure 5.1, the distribution of the individual correlation dimension estimates is neither random (Chi-Squared test:  $\chi^2 = 98.15$ ;  $df = 26$ ;  $p \leq 0.001$ ) nor are the individual estimates normally distributed (Anderson-Darling test:  $A = 0.7637$ ;  $p \leq 0.05$ ). When looking only at the area where occurrences are already above the level of chance observations then the re-

maining data are also not randomly distributed (Chi-Squared test:  $\chi^2 = 27.00$ ;  $df = 13$ ;  $p \leq 0.05$ ). As indicate by Figure 5.1, there are at least three different valid correlation dimension estimates, with peaks in the distribution at 3.3 , 3.7 and 4.2.



**Figure 5.2.** – Histogram of the largest Lyapunov exponents. The level of expected chance observation is indicated by the gray area.

The histogram of the largest Lyapunov exponents, as shown in Figure 5.2, is more difficult to interpret. Peaks in the distribution occur between 0.012 and 0.013, at 0.016, at 0.023 and between 0.025 and 0.028. The observed largest Lyapunov exponents range only from 0.005 to 0.045. This range is already very slim and strongly suggests a Gaussian distribution due to the presence of noise in the time series. The data are neither randomly (Chi-Squared test:

## 5. Time Series Analysis

$\chi^2 = 110.57$ ;  $df = 40$ ;  $p \leq 0.001$ ) nor normally distributed (Anderson-Darling test:  $A = 0.9604$ ;  $p \leq 0.05$ ). Yet, when looking at the area, where occurrences are already above chance level, the data within this limited area is no longer significantly different from random (Chi-Squared test:  $\chi^2 = 20.71$ ;  $df = 20$ ;  $p > 0.05$ ), indicating that the initial assumption of a noisy Gaussian distribution was indeed correct.

It seems that the differences in correlation dimension are not matched by differences in the largest Lyapunov exponent, meaning that while there are at least three different valid estimates for the correlation dimension, there is only one for the largest Lyapunov exponent. In case these three different correlation dimension estimates would come from the measurement of three completely different systems it would be expected to find three different largest Lyapunov exponents, as well. Therefore the findings may already indicate that there is only one underlying process with variable complexity and that the largest Lyapunov exponent is generally independent of the correlation dimension. In order to verify this assumption I reanalyze the data. I calculate medians of the largest Lyapunov exponents for each of the three correlation dimension estimates and perform a comparison between each estimate using the Man-Whitney U-test. The averages of the largest Lyapunov exponents for the correlation dimension estimates of 3.3, 3.7 and 4.2 lie between 0.018 and 0.020 and therefore it is not surprising that there are no significant differences between the Lyapunov exponents (see Table 5.2).

Due to these findings it can be assumed that the largest Lyapunov exponent is indeed independent of the correlation dimension. Therefore differences in correlation dimensions may be the result of the influence of external factors. The following sections are going to focus on finding indications of such relationships.

**Table 5.2.** – Differences in largest Lyapunov exponents between individual estimates of the correlation dimension.

$d_2$	N	$\lambda$	Q1 - Q3	3.3	3.7	4.2
3.3	14	0.019	0.015-0.026		86.0	52.5
3.7	13	0.020	0.016-0.023			43.5
4.2	9	0.018	0.014-0.022			

Included in the table are the sample sizes N as well as the medians of the largest Lyapunov exponent  $\lambda$  for each of the three correlation dimension estimates  $d_2$ , as well as the lower Q1 and upper Q3 quartile of the largest Lyapunov exponent. The corresponding U-Values for the cross-comparison are given by the Mann-Whitney U-test.

## 5.5. Influence of the Release Site

Tables 5.3 and 5.4 show the comparison between the largest Lyapunov exponents and the correlation dimensions of the flights from the different release sites.

**Table 5.3.** – Comparison of correlation dimensions

Site1	N1	$d_2$	Q1-Q3	Site2	N2	$d_2$	Q1-Q3	U-value
N30	6	3.6	3.6-3.7	S30	5	4.1	3.4-4.1	11.0
N60	9	3.4	3.2-4.4	S60	13	4.0	3.5-4.3	43.0
NE40	7	3.5	3.6-4.1	SW40	7	3.7	3.4-3.7	15.5

Table includes the abbreviations of the release sites that are being compared, the sample sizes N1 and N2, the correlation dimension for each sample  $d_2$  and the respective range from the lower to the upper quartile Q1-Q3, as well as the test statistic. All tests have been performed using the Mann-Whitney U-test. The comparison between the releases at N30 and S30 is a second order comparison and is based on the median values of the single releases. The other two are first order comparisons and are based on the data from individual pigeons.

There are no significant difference in correlation dimension between flights from N30 and S30 and although no such significance can be observed for flights from N60 and S60, as well as NE40 and SW40 too, it is intriguing that the correlation dimensions of flights from the south in general seem to be higher than those of flights from the north.

There are no significant differences in the largest Lyapunov exponents between flights from N30 and S30, between the flights from N60 and S60 and also between flights from NE40 and SW40.

## 5. Time Series Analysis

**Table 5.4.** – Differences in largest Lyapunov exponent for sites in equal distance

Site1	N1	$\lambda$	Q1-Q3	Site2	N2	$\lambda$	Q1-Q3	U-value
N30	6	0.017	0.016-0.018	S30	5	0.021	0.019-0.023	5.5
N60	7	0.013	0.011-0.015	S60	9	0.014	0.013-0.020	19.0
NE40	5	0.021	0.017-0.023	SW40	13	0.018	0.011-0.022	25.5

Table includes the abbreviations of the release sites that are being compared, the sample sizes N1 and N2, the correlation dimension for each sample  $\lambda$  and the respective range from the lower to the upper quartile Q1-Q3, as well as the test statistic. All tests have been performed using the Mann-Whitney U-test. The comparison between the releases at N30 and S30 is a second order comparison and is based on the median values of the single releases. The other two are first order comparisons and are based on the data from individual pigeons.

### 5.6. Differences between Individuals

Unfortunately the amount of time series from individual pigeons did not allow a meaningful analysis of the results in view of the individual's behavior. None the less I compiled the respective data for those individuals, where at least four time series from releases from S30 and N30 are available and compared those individuals using the Mann-Whitney U-test. The respective data is presented in Tables 5.5 and 5.6.

**Table 5.5.** – Differences in correlation dimension between individuals released from N30 and S30.

ID. No.	N	$d_2$	Q1-Q3	07-382	07-393	07-410
07-366	4	3.3	3.3-3.5	7.0	3.5	5.0
07-382	4	3.3	3.1-3.5		3.0	4.5
07-393	4	3.9	3.6-4.3			8.5
07-410	5	3.7	3.7-3.9			
08-785	4	4.0	4.0-4.3	-	-	-

The table includes the sample sizes N and the median of the correlation dimension  $d_2$ , as well as the lower and upper quartile Q1-Q3 for each release and the U-values with corresponding significance levels for each comparison.

As shown there is no significant difference in behavior between the individuals when comparing either the correlation dimensions or the largest Lyapunov exponents. Unfortunately there was only one individual from the S30 series, where enough data was available. The range of values of both variables, as indicated by the lower and upper quartiles, is similar to the range that can



**Table 5.6.** – Differences in largest Lyapunov exponent for individuals released from N30 and S30.

ID. No.	N	$\lambda$	Q1-Q3	07-382	07-389	07-410
07-354	4	0.017	0.012-0.018	5.0	7.0	8.0
07-382	4	0.023	0.015-0.028		5.0	8.5
07-389	4	0.018	0.013-0.021			11.5
07-410	6	0.018	0.017-0.020			
08-785	5	0.023	0.012-0.025	-	-	-

The table includes the sample sizes N and the median of the largest Lyapunov exponent  $\lambda$ , as well as the lower and upper quartile Q1-Q3 for each release and the U-values with corresponding significance levels for each comparison.

be observed for the individual releases, indicating that there are probably no individual differences.

## 5.7. Influence of Experience

The differences in correlation dimension and the largest Lyapunov exponent between the repeated releases from the N30 are shown in Tables 5.7 and 5.8, those for the S30 series are shown in Tables 5.9 and 5.10.

**Table 5.7.** – Differences in correlation dimension for releases from N30.

F. No.	N	$d_2$	Q1-Q3	F4	F8	F12	F13	F16
F1	5	3.7	3.7-3.7	10.0	23.5	19.0	18.0	17.5
F4	5	3.6	3.5-3.7		24.5	17.5	17.0	17.0
F8	10	3.6	3.3-4.0			32.0	35.0	37.5
F12	8	3.6	3.2-4.0			27.0	34.5	
F13	8	3.7	3.5-3.8					27.5
F16	9	3.4	3.3-3.8					

Table includes the sample sizes N and the median of the correlation dimension  $d_2$ , as well as the lower and upper quartile Q1-Q3 for each release and the U-values with corresponding significance levels for each comparison.

During the complete N30 series there are no significant differences in correlation dimension. Yet, there is a significant difference in the largest Lyapunov exponent on the fourth release. On this release the pigeons experienced relatively strong head winds, which could have affected the pigeons' behavior (for influence of head winds see the following section).

## 5. Time Series Analysis

**Table 5.8.** – Differences in largest Lyapunov exponent for releases from N30.

<b>F. No.</b>	<b>N</b>	<b><math>\lambda</math></b>	<b>Q1-Q3</b>	<b>F4</b>	<b>F8</b>	<b>F12</b>	<b>F13</b>	<b>F16</b>
F1	7	0.017	0.016-0.024	10.0	22.0	23.5	31.0	28.5
F4	6	0.026	0.021-0.028		7.0**	8.0*	10.5*	12.5*
F8	9	0.016	0.012-0.020			37.0	28.0	38.5
F12	9	0.018	0.010-0.019				34.0	40.0
F13	9	0.017	0.016-0.022					37.0
F16	10	0.016	0.014-0.021					

Table includes the sample sizes N and the median of the largest Lyapunov exponent  $\lambda$ , as well as the lower and upper quartile Q1-Q3 for for each release and the U-values with corresponding significance levels for each comparison.

**Table 5.9.** – Differences in correlation dimension for releases from S30.

<b>F. No.</b>	<b>N</b>	<b><math>d_2</math></b>	<b>Q1-Q3</b>	<b>F2</b>	<b>F4</b>	<b>F8</b>	<b>F12</b>
F1	2	4.1	3.7-4.4	-	-	-	-
F2	6	4.1	3.9-4.4		4.5**	17.0	-
F4	9	3.4	3.2-3.7			6.0**	-
F8	7	4.1	3.9-4.2				-
F12	2	3.4	2.9-3.8				

Table includes the sample sizes N and the median of the correlation dimension  $d_2$ , as well as the lower and upper quartile Q1-Q3 for for each release and the U-values with corresponding significance levels for each comparison.

**Table 5.10.** – Differences in largest Lyapunov exponent for releases from S30.

<b>F. No.</b>	<b>N</b>	<b><math>\lambda</math></b>	<b>Q1-Q3</b>	<b>F2</b>	<b>F4</b>	<b>F8</b>	<b>F12</b>
F1	2	0.019	0.015-0.024	-	-	-	-
F2	6	0.023	0.020-0.024		14.5	16.5	15.0
F4	7	0.018	0.015-0.023			22.5	16.0
F8	7	0.021	0.016-0.023				16.5
F12	6	0.023	0.015-0.029				

Table includes the sample sizes N and the median of the largest Lyapunov exponent  $\lambda$ , as well as the lower and upper quartile Q1-Q3 for for each release and the U-values with corresponding significance levels for each comparison.

During the S30 series I find a significant difference in the correlation dimension on the fourth release compared to the other two statistically evaluable releases. On the fourth release from S30 a marked shift in the course taken by the pigeons was observed (see chapter 3), which could be linked to this change in complexity of the underlying process. The largest Lyapunov exponent, however, does not differ significantly between any of these releases.

To asses the influence of previous experience on the correlation dimension and largest Lyapunov exponent in more detail I again restrict the data set

to the first 12 flights from the two release sites N30 and S30 and performed correlations of the median of both variables with the number of flights from the release site. As already indicated by the previous analysis increasing familiarity has no significant effect on the correlation dimension ( $r_{sp} = -0.454$ ;  $N = 12$ ;  $p > 0.05$ ) and the largest Lyapunov exponent ( $r_{sp} = 0.079$ ;  $N = 12$ ;  $p > 0.05$ ).

## 5.8. Influence of Abiotic Factors

Once again I limit the data set for the analysis of the influence of abiotic factors, the respective data can be found in appendix D, to those tracks recorded during the releases at S30 and N30. For details on the analysis and why this approach has been chosen, please see the corresponding section in chapter 3. The results of the analysis are shown in Table 5.11.

**Table 5.11.** – Influence of abiotic factors on the correlation dimension and the largest Lyapunov exponent.

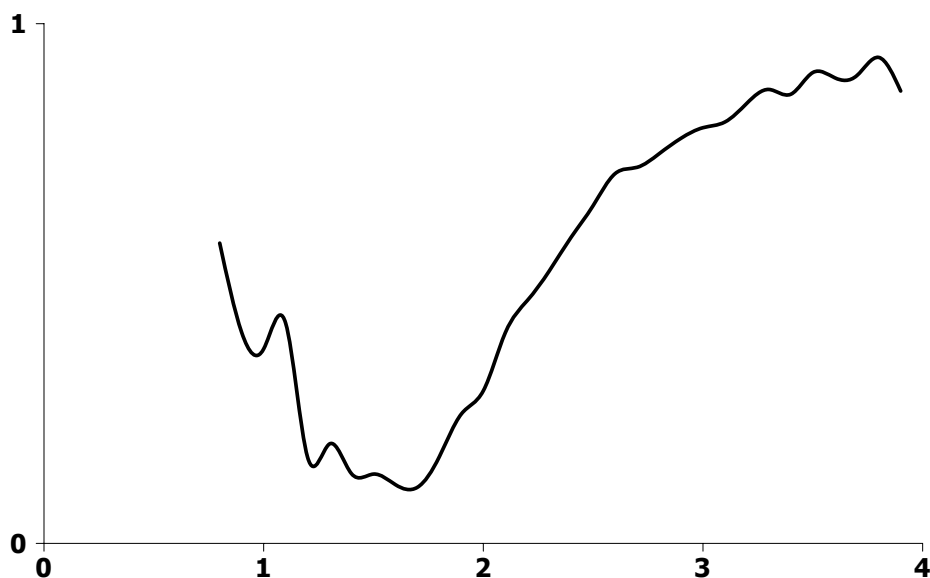
Variable	Cloud Cover	Wind Speed	Wind Dir.	Temp	Mag. Var.
N	11	11	7	11	11
$d_2$	0.014	0.191	-0.473	-0.155	-0.205
$\lambda$	-0.291	-0.007	-0.902**	0.064	0.261

For the correlations between the individual variables and the wind direction, tracks from releases where no wind was measurable are ignored and absolute values are used for all correlations. Significance levels are given by Spearman's rank correlation. Also shown is the sample size N. For explanation of the variables see previous tables.

The results clearly show that the correlation dimension is completely independent from any measured factor. There is, however, a clear dependency between the wind direction and the Lyapunov exponent, with tail winds resulting in lower Lyapunov exponents and head winds in larger Lyapunov exponents. Such an influence has been observed before and corresponds to the results from the analysis of the repeated releases from N30 in the preceding section.

## 5.9. Precision of the Flight

In order to determine if there is a relationship between the correlation dimension and the precision of the pigeon's flight, I calculate estimates of the correlation dimension as sliding means over 180 time steps in fixed intervals of 30 seconds for all tracks, irrespective of the release site and experience, and compare these estimates with the steadiness of the pigeons' flight over the corresponding time period. For this analysis I use the complete tracks instead of the individual phases. Due to the reduced number of data points used for the reconstruction of the underlying process the calculation of the correlation dimension no longer yields exact results. Therefore the calculated values should not be considered representative for the systems true correlation dimension, however, they may serve as very rough estimates (Ramsey & Yuan, 1990; Stefanovska *et al.*, 1997). As such the approach should still allow to determine changes in the correlation dimension of the underlying process.



**Figure 5.3.** – Relationship between correlation dimension (x-axis) and steadiness (y-axis) of the pigeons' flight averaged over all flights from all release sites.

As shown in Figure 5.3, the absolute minima in steadiness corresponds to a correlation dimension of 1.7. From this minimum onward the steadiness increases steeply with increasing correlation dimension. The results show that when the correlation dimension increases, the steadiness likewise increases, indicating that increasing complexity results in increased steadiness and therefore precision of the flight.

## 5.10. Complexity of the Flight

In order to analyze if there is a dependence between the correlation dimension and the pigeon's current position I use the same method as in the previous analysis, but now calculate the average of the correlation dimension in 500 m steps relative to the home loft. I analyze the results separately for each release site and also calculate the absolute minimum and maximum of the correlation dimension for each distance step. The results for the two series N30 and S30, also including the releases from the two distant sites N60 and S60, are shown in Figure 5.4 and the results for the single releases NE40 and SW40 are shown in Figure 5.5. An overview of the results is given in Table 5.12.

**Table 5.12.** – correlation between correlation dimension and distance from the loft for each site

Release Site	N	$d_2max.$	$d_2avg.$	$d_2min.$
N30	57	-0.865***	-0.919***	-0.596***
S30	60	-0.853***	-0.894***	-0.851***
N60	57	-0.278*	-0.202	0.125
S60	60	-0.522***	-0.637***	-0.595***
NE40	89	-0.499***	-0.786***	-0.657***
SW40	84	-0.235*	-0.590***	-0.709***

Table shows the correlation coefficients, as determined by Spearman's rank correlation, for the distance and the correlation dimension at each site, as well as the respective sample size N. Correlations are based on the maximum correlation dimension  $d_2max.$  the average correlation dimension  $d_2avg.$  and the minimum in correlation dimension  $d_2min.$  of each 500 m distance step from home.

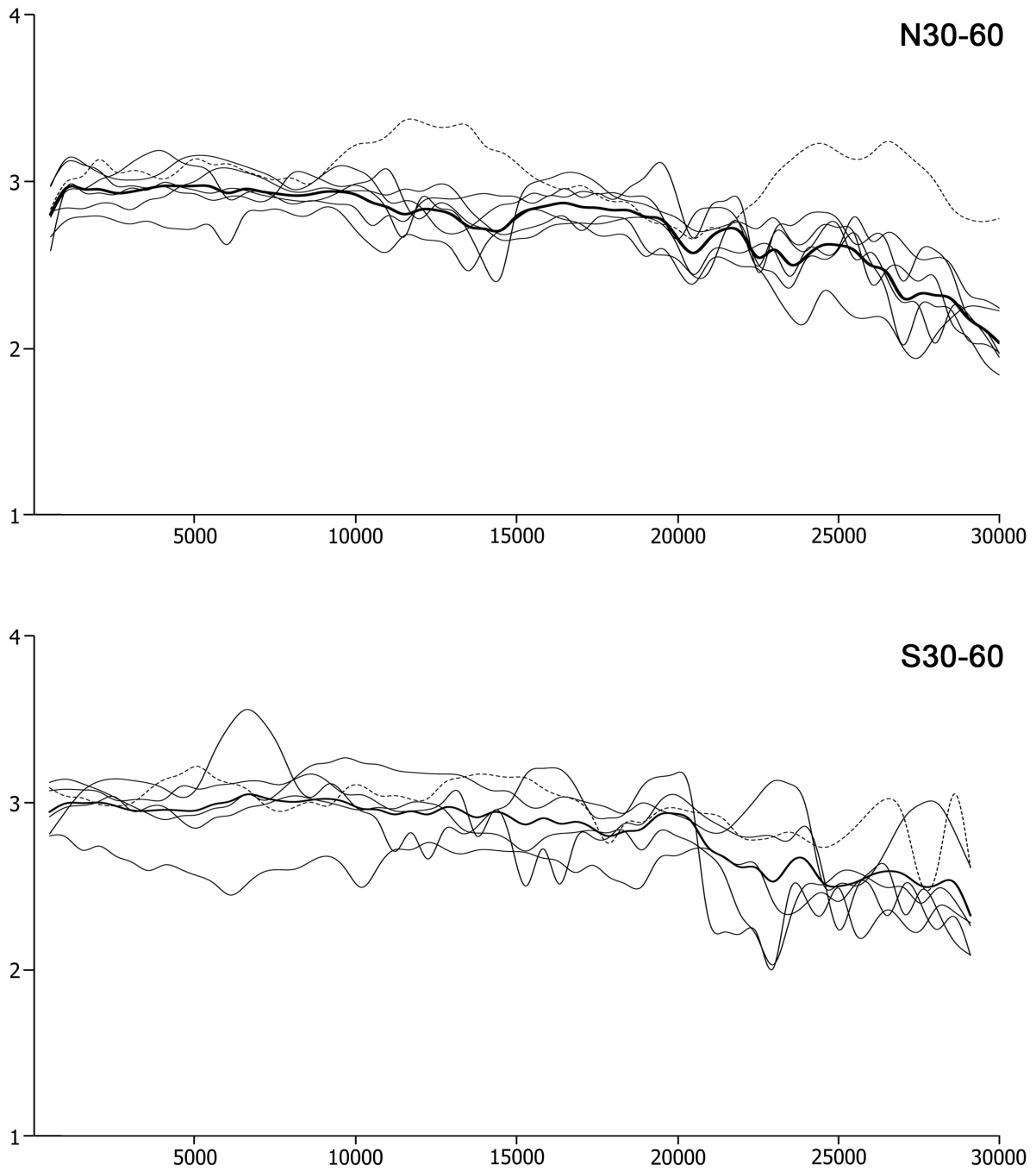
In all cases there is an overall trend for increasing correlation dimension, as the pigeons approach their home. This tendency is strongest for the releases from N30 and S30. In the region where the flights from N60 and N30 overlap

## 5. *Time Series Analysis*

such a tendency can not be observed and although such a tendency can be observed for the flights from S60 it is considerably weaker. The tendency is also stronger for the release from within the magnetic anomaly (NE40) than it is from outside the anomaly (SW40). Yet in both cases the tendency is again weaker than those observed for the releases from N30 and S30.

A correlation between the maximum correlation dimension of each distance step and the distance towards the loft can be observed in all cases. Again this tendency is strongest for the releases from N30 and S30 and considerably weaker for all others. The correlation between the minimum correlation dimension of each distance step and the distance towards the home loft can be observed in 5 out of the 6 cases. It is not significant for the release from N60, probably explaining why such a relationship could not be observed for the average of the correlation dimension. While the correlation between the maximum correlation dimension seems to be stronger or equally strong as the correlation with the minimum correlation dimension for the releases in the north and the south, this relationship seems to be reversed for the releases in the east and the west.





**Figure 5.4.** – Relationship between the average correlation dimension (y-axis) and the distance to the home loft (x-axis) for all individual releases from N30 and S30 (thin lines), the average over all releases (thick lines) and the overlapping region from the release at N60 and S60 (dotted lines).

5. Time Series Analysis



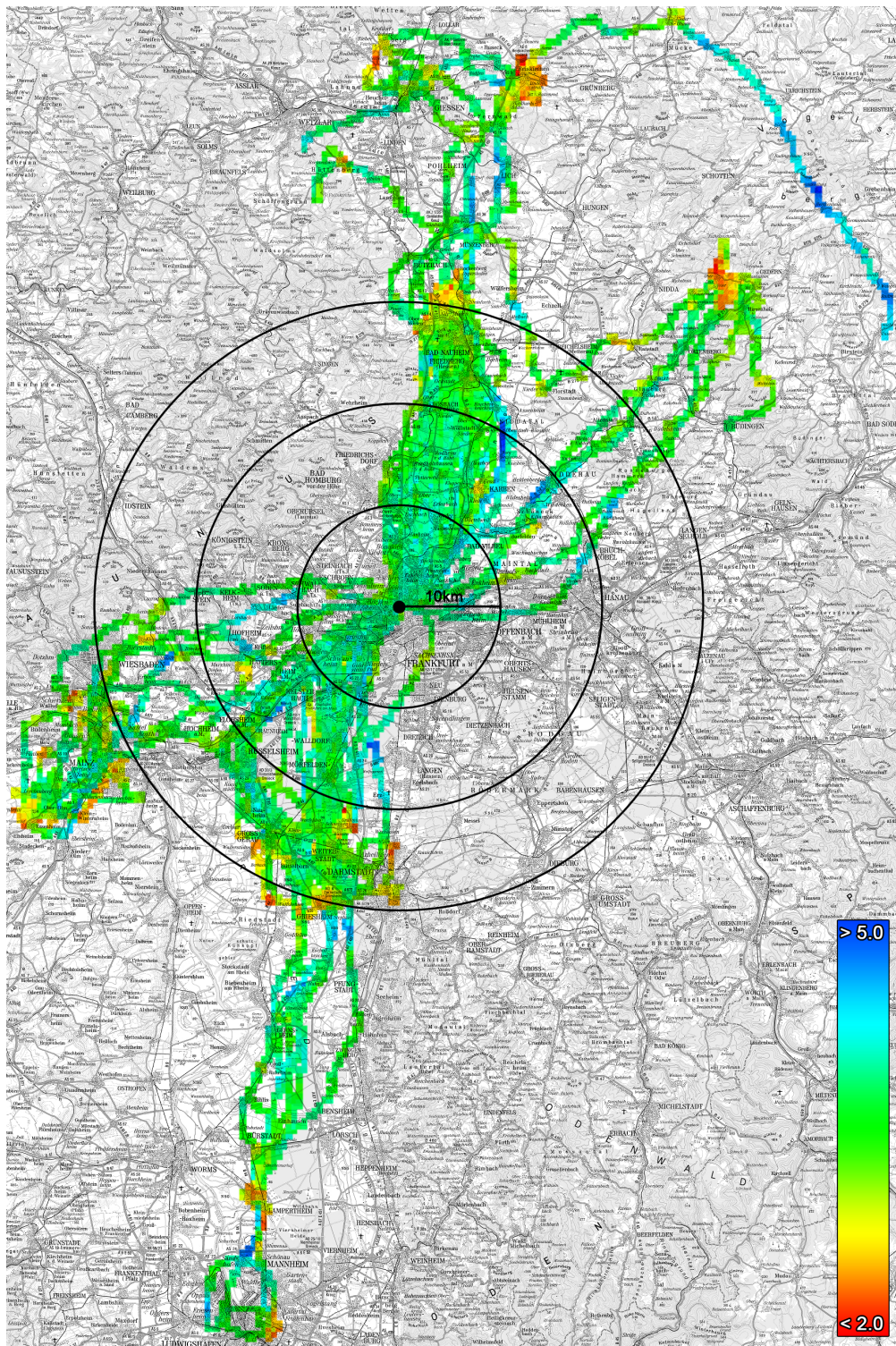
**Figure 5.5.** – Relationship between the average correlation dimension (y-axis) and the distance to the home loft (x-axis) for the releases from NE40 and SW40.

### 5.11. Mapping the Navigational Process

In a final step I calculate the average correlation dimension, as described before, for each 1x1 km segment covered by the tracks and plot the results of this analysis on an ordnance survey map of the area around Frankfurt. The result of this analysis is shown in Figure 5.6.

Mainly in the beginning of each flight, as the pigeons are still close to the release site, portions of the tracks with low complexity can be observed. When the pigeons fly over open fields and depart from the release site, there is a tendency for increase in complexity of these tracks. The same is true for flights over villages and towns, no obvious reduction in complexity can be observed. Despite the tendency for increasing complexity, as the pigeons approach their home loft, which has already been described in the previous section, portions of flights with lower complexity can also be observed further away from the home loft. Flights from the north seem to be less complex, with those tracks that depart further to the east tending to be more complex. From the south the increase in complexity as the pigeons approach home is less obvious and there are in general more transitions between complex and less complex portions. While the flights from the south are in the beginning less complex local maxima in complexity are reached in approximately 20 and 10 km distance from the home loft. After each of these distance steps there is a sudden decrease in complexity, followed by another increase until the next maximum is reached. Flights of very low complexity can be observed within the magnetic anomaly, yet pigeon 07-393 crossing the anomaly, when released from N60 shows highly complex flying behavior, although it is on a completely wrong course the track is also extremely straight.

## 5. Time Series Analysis



**Figure 5.6.** – Average of the correlation dimension as calculated for each 1x1 km segment covered during the homing flights of the pigeons. The correlation dimension is indicated by the different colors, ranging from red to blue, with red indicating lower values and blue indicating higher values.

## 5.12. Discussion

### 5.12.1. Non-Navigational Phases

Lower correlation dimensions can mostly be observed in the beginning of the flight, while the pigeons are still near the release site. In the previous chapter this initial phase of the flight has already been identified as a non-navigational phase. The observation that the initial phase is characterized by low correlation dimensions also strongly coincides with an observation from another study. In this study it has been found that the initial phase of the pigeons' flight is also characterized by increased spatial entropy (Guilford *et al.*, 2004), which could suggest random flying. Considering these observations it seems to be legitimate to assume that phases of the flight with low correlation dimensions are indeed non-navigational phases, mostly attributed to exploration or flight preparations. Therefore the calculation of the correlation dimension can serve the purpose of discriminating between navigational and non-navigational phases during the homing flight of pigeons. It should be mentioned, however, that the method can not discriminate between non-navigational behavior and other possible forms of navigation that are of lower complexity, such as piloting.

### 5.12.2. Navigational Strategies and Processes

The results could indicate that up to three different navigational strategies are applied during the pigeons' homing flight, as is indicated by the three valid estimates for the correlation dimension. This, however, would mean that the largest Lyapunov exponent would be the same for all three navigational strategies, which is quite unlikely. Therefore, it is reasonable to assume that the three different estimates for the correlation dimension represent modulations of the same navigational process. The question then is how and when those modulations occur.

## 5. *Time Series Analysis*

The largest Lyapunov exponent and the correlation dimension are both mostly independent of previous experience and external factors, like weather or the daily variation of the geomagnetic field, thus excluding these as the cause for the observed differences in correlation dimension. There is indeed a strong influence from the wind direction on the largest Lyapunov exponent. This is most likely the result of the pigeon's ambition to counteract unfavorable wind conditions, meaning that the pigeon probably avoids flying into directions where headwinds prevail. Such behavior could act as a form of natural noise, inducing a random variable into the actual homing process. This could then result in the observed decrease of predictability and also explain the noisy distribution of the largest Lyapunov exponents. The influence of wind, however, remains relatively low and does not affect the correlation dimension.

Differences in the correlation dimension, although not significant, can be observed when comparing the releases from the north with those from the south, with a slight tendency for flights from the south being more complex than those from the north. Also, during each individual release there is a clear increase in complexity as the pigeons approach their home loft. The increase in the maximum of the correlation dimension with decreasing distance indicates that the observed increase is not alone dependent on the reduction of non-navigational phases as the pigeons approach home. These findings strongly suggest that the differences in complexity of the underlying process are probably related to the pigeon's whereabouts and therefore most likely related to differences in the availability and reliability of navigational factors. The increase in complexity again hints at an intrinsic connection between the individual correlation dimension estimates. This suggests that the process itself is of a modular nature, meaning that individual components, i.e. navigational factors, can be included or excluded. The individual factors, as is indicated by the fractal nature of the navigational process, seem to be weighted independently. This weighting



probably depends on the reliability of the individual navigational factors. This in accordance with the recent demand that evaluation of the reliability and precision of navigational factors, needs to be an important step in any navigational process (Pfuhl *et al.*, 2010). A multi factorial gradient map, with redundant, overlapping navigational factors, as proposed by Keeton (1973), could serve this purpose quite easily; deviations between different navigational factors containing the same potential information could serve as means to determine their reliability. That such a weighting of factors occurs is also indicated by previous findings. In experiments, where pigeons were treated with a short magnetic pulse, designed to influence putative magneto receptors in the upper beak of pigeons (Hanzlik *et al.*, 2000; Williams & Wild, 2001; Winklhofer *et al.*, 2001; Fleissner *et al.*, 2003, 2007; Tian *et al.*, 2007), differences in the size of the pulse-effect could be observed depending on the release site (Beason *et al.*, 1997). Thus the effect of the pulse could already be a direct indicator of how magnetic factors are weighted at different sites.

### 5.12.3. Precision of the Navigational Process

An important, but probably less obvious, finding of the current study is that the calculations succeed at all and that the results are fairly independent of the number of data points. This clearly shows that the underlying process is repeated quite often during the pigeons' homing flight. In previous simulation experiments it was assumed that the pigeon would re-determine its course every 5 km (Wiltschko & Nehmzow, 2005). The time lag calculated for the purpose of embedding the time series is on average 12 seconds. While the time lag may not be a very precise indicator it is generally assumed that it does indicate how often a process is repeated. Therefore one could assume that the pigeons re-determine their home course roughly every 12 seconds. If the pigeons do indeed have to re-determine their course that often, it could also explain why

## 5. Time Series Analysis

pigeons seem to prefer to follow linear features (see chapter 3). Following such linear features could reduce the need to re-determine the home course, while at the same time allowing to maintain the course.

The precision of the navigational process itself seems to be largely independent of its actual complexity. Assuming that a correlation dimension above 3.0 indicates that a pigeon is currently navigating towards its goal, the precision of the course determination process, as indicated by a steadiness of 0.80, is on average  $\pm 36^\circ$ . This precision increases up to  $\pm 21^\circ$  the more complex the process becomes, i.e. the closer the pigeon gets towards its goal. A precision of  $\pm 21^\circ$  seems to be very imprecise, but simulation experiments indicate that the precision of the compass is already roughly  $\pm 15^\circ$  (Wiltschko & Nehmzow, 2005); therefore only  $\pm 21-5^\circ$  of the error in precision would be related to difficulties determining the position. Assuming that the pigeon travels with a speed of 16 m/s and would determine its position every 12 seconds this would equal errors of  $\pm 73.68-16.80$  m, indicating that the precision would be sufficient enough for the pigeon to find its way home. The improvement in precision, however, seems to be almost negligible, therefore it is likely that the purpose of the increase in complexity, due to the involvement of additional navigational factors, is mainly to compensate for the increasing difficulty of determine quantitative differences in the individual factors as the pigeon gets closer to its home loft. This would ensure that the pigeon's ability to determine its course towards home remains on an equal level throughout the whole journey.

### 5.12.4. Complexity of the Navigational Process

In the most minimalistic case the navigational process of the pigeons seems to be a 3.3 dimensional system. This means that the behavior of the pigeon can be fully described by four differential equations. This also suggests that at least four independent navigational factors are involved in this process (Skinner,

1994), thus again strongly supporting the theory of a multi factorial map. However, the results also indicate that during some portions of the flight the underlying navigational process is even more complex. The highest correlation dimension observed for a single individual is 5.1, indicating that the pigeon used at least six individual navigational factors to determine its course. But even in the less complex case of a 3.3 dimensional process it is impossible to say if not more than four individual factors are already involved. The correlation dimension is a mere abstract measure and its value does not only depend on the number of factors involved, but also how these factors are weighted and how much information they provide. As a result it can not be said with absolute certainty how many factors are involved in the actual navigational process. It can, however, be concluded that a compass and only two natural gradients are insufficient to explain the complexity of the navigational process. In order to achieve these levels of complexity additional factors need to be involved.

Considering that the process gets increasingly complex as the pigeons approach their loft it could be assumed that this increase is due to the involvement of familiar landmarks in the vicinity of the loft. Although it has been shown that the pigeons from Frankfurt can find their way home without the aid of visual cues (Schmidt-König & Schlichte, 1972), the pigeons in the current experiments were not deprived of visual cues. The experiments with frosted lenses do as such not exclude the possibility that visual cues are used if they are available. What is quite intriguing, however, is that the additional factors result only in a fractal increase of the correlation dimension and therefore are probably weighted differently, indicating that these additional factors are used as means to support a set of basic factors instead of fully replacing them. This means that if the additional factors included into the process are really visual cues, then the information provided by the two theoretical maps, the gradient

## 5. *Time Series Analysis*

map and the mosaic map (Wallraff, 1974) are most likely used simultaneously, as just recently proposed by Wiltschko & Wiltschko (2009).

Initially disturbing might be the observation that neither the predictability nor the complexity of the process seems to be affected by the daily variation of the geomagnetic field, although it has been shown in the previous chapters that both efficiency and steadiness are decreased on days with high variation (see chapters 3 and 4). This finding, however, is completely expected and altogether supports the theory that the magnetic field remains an integral part of the navigational process. The variations in the earth's magnetic field seem to be small enough to allow the pigeons to continue using the factor throughout the complete journey. In the case an effect on the correlation dimension would have been observed it would have meant that the pigeons, weighted this cues differently, completely abandoned it or used other cues to compensate for the loss of this information. In the two preceding chapters it has also been observed that the effect is no longer significant during the final homing phase, as well as during the overland flight. The increasing in complexity now offers a viable explanation for this phenomenon, indicating that the decrease in effect is not related to different weighting of the cue itself, but due to introduction of additional navigational factors as the pigeons approach their loft.

### **5.13. Conclusion**

The homing flight of the pigeon is governed by a highly predictable modular process. This process is mostly independent of external factors and experience indicating that the navigational strategy applied by the pigeons is reliable and does not change under varying conditions or with increasing experience. The process itself is based on at least four, but maybe even more, independent navigational factors, including the compass. Additional factors, which are introduced into this process as the pigeons approach their home, are weighted

differently, indicating that they only serve as means to support a set of basic navigational factors instead of completely replacing them. The nature of these additional factors remains unknown. They could be familiar landmarks, but if they are, the results also indicate that the information provided by the two hypothetical maps, the gradient map and the mosaic map, is used simultaneously.





## 6. General Discussion and Conclusion

GPS receivers, for scientific purposes, have been around since the beginning of the millennium (von Hünenbein *et al.*, 2000; Steiner *et al.*, 2000). However, the increased amount of data has not yet widened our understanding of the navigational processes involved in the pigeons' homing flight. So far, studies involving GPS have mostly supplied supporting evidence for already existing theories. As such it may be interesting to know that the effect of previewing is limited to the first 1000 m (Biro *et al.*, 2002) and that the increase in homing speed that can be observed in traditional previewing experiments (Braithwaite, 1993; Burt *et al.*, 1997), is due to higher efficiency during this portion of the flight. It may be re-ensuring that the decreased effect of the clock-shift treatment, as originally proposed by Wiltschko & Wiltschko (2001), is indeed a result of the simultaneous use of the magnetic compass and the sun compass (Gagliardo *et al.*, 2009). And it may be comforting to know that the behavior recorded on vanishing does represent oriented behavior, as the distance at which vanishing bearings are taken is clearly further away from the release site than the first point of decision (Schiffner & Wiltschko, 2009). But do such findings really advance our understanding of the navigational process? The methods I now introduce into the field of behavioral research may not yet answer all our questions, but helps us to begin to understand the complexity of the navigational process.

### **6.1. The Navigational System**

Until today, many researchers still assume that navigation requires different navigational strategies for different situations. When the pigeons are still young and do not yet have acquired a map of the area around their loft they are believed to use information gathered during the outward journey to find their way home, using the magnetic field as an external reference (Wiltschko & Wiltschko, 1978, 1985). This is considered to be a back-up mechanism based on route information that is to be replaced by information provided by the navigational map, as soon as this map is available. Basically, there are two types of information a pigeon could use to build up such a map: one type is point-like information, information stored in reference to a specific place, like familiar landmarks, the other type is information based on environmental gradients, like the magnetic field (Wiltschko & Wiltschko, 2003a). Point-like information could also be used in two ways, either as direct means of navigation, where the path towards home is defined by a series of successive landmarks, a strategy called piloting (Griffin, 1952b), or as part of a mosaic map (Wallraff, 1974) where the landmarks indicate the compass course towards the home loft.

The type of information used, i.e. route information, point-like information or natural gradients, and how this information is stored, i.e. piloting or mosaic map, has direct consequences on the complexity of the underlying process. If pigeons use landmarks for piloting then the underlying process is indeed rather simple, as the information provided is simply the direction towards the next landmark. Therefore it can be assumed that such behavior would be indicated by lower correlation dimensions close to 1.0. Navigation within a mosaic map, in comparison, requires the involvement of at least one additional factor, the compass. Therefore we can already assume that navigation based on a mosaic map would result in a more complex process with a correlation dimension of at least 2.0. If pigeons use environmental gradients as navigational means the

complexity of the process depends on the number of gradients used, where weighting of several gradients that provide similar information could lead to fractal correlation dimensions. A change in the complexity of the navigational process could then indicate a change in the navigational strategy applied by the pigeons.

### **6.1.1. Navigational Strategies**

Some theories evolve around the idea that pigeons use natural gradients to navigate from unfamiliar sites and use familiar landmarks to navigate from familiar sites (for example, the olfactory hypothesis, see Papi & Wallraff, 1982). However, such a switch in strategy, when the pigeons become familiar with a release site, is not indicated by my results. Although the behavior on the fourth flight of the two main series differs from the first release from either site, this change in behavior is limited to the fourth flight alone and the later flights do not differ from the first flight anymore (see chapter 5). Therefore the current results indicate that the strategy employed by the pigeons remains the same, whether they fly from familiar or unfamiliar sites.

Another theory assumes that there is a switch from gradient-based navigation to navigation using the mosaic map in the vicinity of the loft (Wiltschko & Wiltschko, 1999). If pigeons process the information provided by the mosaic map differently, this would also mean a switch in strategy, but such a change in strategy during the journey is likewise not supported by my results. There is indeed a clear increase in complexity as the pigeons approach their home loft, suggesting that indeed additional factors are used to determine the home course when the pigeons are close to their home loft. Yet there are two findings that make it unlikely that this increase is the result of a switch in navigational strategy. The analysis of the cumulative increase in efficiency indicates that during a rather extended portion of the pigeons' journey there is likely no

## 6. General Discussion and Conclusion

change in the strategy employed by the pigeons. This encloses an area of up to 20 km around the home loft (see chapter 3). Furthermore, the Lyapunov exponent seems to be independent of the actual complexity of the underlying process, thus suggesting that these additional factors are simply means to support the same process. It is indeed quite conceivable that additional factors are used in this way and the reasons are the same as those that are put forward for the use of the mosaic map. It is unlikely that the birds' ability to detect differences in environmental gradients is unlimited. Therefore the position determination process is prone to become increasingly difficult as the distance between the pigeons current position and its goal decreases. The use of additional factors, like the involvement of visual cues as navigational means, could compensate these problems. My results therefore indicate that if this increase in complexity is indeed due to an involvement of visual cues, then the potential information of both types of maps is used simultaneously and is most likely part of the same navigational process. The simultaneous use of both maps, has just recently been proposed by Wiltschko & Wiltschko (2009). However, as the relative importance of visual cues for the pigeons from Frankfurt, has already been proven to be lower, than for pigeons from other lofts, these findings may only apply for the pigeons from Frankfurt (for comparison see Schmidt-König & Schlichte, 1972; Schmidt-König & Walcott, 1978).

The new methods introduced here now allow to formulate certain hypotheses and test if indeed different navigational strategies are employed at different lofts. For example, the hypothesis that pigeons from Oxford navigate using piloting after extensive habituation (Biro *et al.*, 2004; Meade *et al.*, 2005; Biro *et al.*, 2007; Mann *et al.*, 2010). In the case of piloting, the correlation dimension estimates should be considerably lower than what is observed for the pigeons in Frankfurt and it should also be lower than what can be observed for the pigeons before they have been habituated with the route. Also, previ-

ous flights from the same individual released at the same site should be better predictors than those of other individuals or than the first half of the same individual's flight.

It may also be possible to test whether pigeons rely on olfactory cues, independent of whether they are used as part of a mosaic map or as part of a gradient map (for review see Papi & Wallraff, 1982; Wallraff *et al.*, 2003). If pigeons rely on olfactory cues it could be assumed that a higher daily variability and a higher influence of varying wind conditions could be observed than in the current study. Wind had no significant effect on the correlation dimension, indicating that olfactory cues, play only a minor role in the navigational process of the pigeons from Frankfurt (see chapter 5). This is also in agreement with earlier findings that olfactory deprivation had little effect on the orientation of pigeons from Frankfurt (Wiltschko *et al.*, 1987).

As previous findings already suggest, route information is no longer essential for the navigational process after the pigeons have acquired a navigational map (Wiltschko & Wiltschko, 1978, 1985). Yet it can not be excluded that pigeons make use of the information if it is available and are simply able to compensate for the loss of this type of information. The new methods provided here now allow to test, whether or not adult pigeons still use route information in addition to their navigational map. In case route information is still used by adult pigeons, there should be a difference in the correlation dimensions between pigeons that had access to that type of information and those that had not. If there is a difference, it might also be possible to determine if route information is a crucial part of the navigational process. If the correlation dimension of the experimental group is higher than that of the untreated controls other factors had to take its place, in the case a reduction is observed route information is probably non-crucial and completely redundant.

## 6. General Discussion and Conclusion

### 6.1.2. Navigational Factors

Aside from the assumptions that several different strategies are involved in the homing flight of the pigeons, it is also often assumed that the navigational factors involved in the navigational process are few in numbers. Most theories, independent of which factors they advocate, claim that pigeons use only one or two navigational factors simultaneously to determine their home course (e.g Wallraff, 1974; Biro *et al.*, 2004; Gagliardo *et al.*, 2005; Dennis *et al.*, 2007). Only few have assumed so far that more factors of different nature might be involved (e.g Wiltschko & Nehmzow, 2005; Wiltschko *et al.*, 2009a, 2010). The high correlation dimensions found in my study now show for the first time that at least four, up to six, but maybe even more, factors are involved in the pigeon's navigational process. In view of such findings it can be assumed that the pigeons rely on several redundant navigational factors and therefore the relative importance of each individual navigational factor stands to question.

### 6.1.3. The Role of Landmarks

Landmarks or, in general, visual cues are usually thought to be important factors involved in the navigational process. Theories about how the pigeons could use visual cues are manifold. They could be used for short range navigation, as part of the mosaic map (Wallraff, 1974), but also at familiar sites at greater distances, either as direct navigational cues in the sense of piloting (e.g Biro *et al.*, 2004; Meade *et al.*, 2005; Biro *et al.*, 2007; Mann *et al.*, 2010), for site recognition, allowing the pigeons to directly determine the home direction (Füller *et al.*, 1983), or as linear features that stabilize the flight of the pigeons (Lipp *et al.*, 2004).

In experiments with pigeons that claim to support the use of familiar landmarks in the vicinity of the loft, pigeons were either allowed or disallowed to



view the surrounding area of the release site (Braithwaite, 1993; Burt *et al.*, 1997; Biro *et al.*, 2002). Previewing then did affect the pigeons homing times, where pigeons that had the opportunity to preview the surrounding landscape homed faster than those that did not have this opportunity. This effect, however, seems to be limited to an area 8 km around the pigeons home loft, as no differences in behavior were observed at release sites beyond this distance (Braithwaite, 1993). My results do not exclude the possibility that familiar landmarks may play a role in the vicinity of the home loft, yet indicate that even so close to the home loft they are probably not the only cues used by the pigeons to determine their position. This claim is supported by the finding that the effect of previewing is severely restricted and only affects the pigeons' behavior during the first 1000 m of their journey, where the pigeons that had not been allowed to preview the surrounding landscape flew less efficient (Biro *et al.*, 2002). This inefficient flying was interpreted as information gathering, so called orientation flying (Hitchcock, 1952). Considering that the results of my study indicate that the initial behavior is not used for gathering information, it is questionable whether previewing does affect the navigational process at all or whether it simply reduces the need for exploration (see chapter 4). This is also supported by experiments involving releases from cages, where pigeons leaving the cage already head out into the directions in which they later depart (Chelazzi & Pardi, 1972; Kowalski, 1994; Mazzotto *et al.*, 1999; Gagliardo *et al.*, 2001). The effect of previewing, as indicated by experiments in up to 3 km distance from the home loft, ultimately results in a increase in homing speed of about 16% (Burt *et al.*, 1997). Although it is not clear whether the additional cues used in the vicinity of the loft are indeed visual cues, the observed fractal increase in complexity may well be in agreement with the finding that access to familiar landmarks can increase homing speed by 16% (see chapter 5). Therefore my findings, as well as previous findings, suggest that the

## 6. General Discussion and Conclusion

contribution of familiar landmarks to the navigational process is limited and that they probably serve as means to support a set of basic navigational factors comprised of natural gradients in the vicinity of the home loft.

The analysis of the points of the decision did not indicate an obvious use of landmarks at the release site (see chapter 4). As observed there is also no increase in efficiency with increasing familiarity during the first 2.5 km from the release site (see chapter 3). In general, findings that are supposed to indicate the use of familiar landmarks at the release site come from clock-shift experiments (e.g. Gagliardo *et al.*, 2005). These studies show that the effect of a clock-shift treatment is lower than expected at familiar sites. However, attributing this reduction to the use of familiar landmarks is unsupported, as the pigeons do still significantly deviate from the direction of controls (Wiltschko *et al.*, 1994a). Furthermore, there are also conflicting findings, indicating that pigeons highly familiar with a release site show a more pronounced shift (Füller *et al.*, 1983). Another study showed that the reduced deviation observed in previous studies is probably due to a cue conflict between the magnetic compass and the sun compass these pigeons had experienced on previous homing flights (Wiltschko *et al.*, 2005).

The simultaneous use of the magnetic compass and the sun compass, which would explain this cue conflict, has been shown by applying bar magnets on the back of clock-shifted pigeons, where pigeons treated this way showed almost 100% of the expected deflection (Wiltschko & Wiltschko, 2001). At first seemingly conflicting results had been reported, where no significant differences between the two treatment groups could be detected in the vanishing bearings (loalè *et al.*, 2006). Yet a more recent study employing GPS receivers, where likewise no significant difference between the two treatment groups was found in the virtual vanishing bearings, showed that the routes of the pigeons with bar magnets on their back displayed a greater deflection throughout the entire

journey (Gagliardo *et al.*, 2009). In view of such findings it seems unlikely that clock-shift experiments can serve as an indicator for the use of familiar landmarks at the release site. If anything at all, these experiments may serve as evidence that even high familiarity with a site can not nullify the effect of the clock-shift treatment. Therefore we can assume that familiar landmarks are not an essential part of the navigational process and that pigeons surely do not use piloting to follow these landmarks to find their way home.

Another observation that speaks against the importance of landmarks at the release site is the effect of the daily variation of the geomagnetic field on the pigeons orientation at the release site. This effect is long known (Keeton *et al.*, 1974; Larkin & Keeton, 1976; Kowalski *et al.*, 1988) and has also been observed in the current study (see chapters 3 and 4). Last but not least, studies involving pigeons released with frosted lenses depriving the pigeons of the ability to perceive visual cues, are probably the strongest indicator that landmarks are not an essential part of the navigational process (Schmidt-König & Schlichte, 1972; Schmidt-König & Walcott, 1978; Benvenuti & Fiaschi, 1983). However, these studies also indicate that the importance of landmarks may increase as the pigeons get closer to the loft and may also depend on the region around the loft, as pigeons from different lofts, unlike the pigeons from Frankfurt (Schmidt-König & Schlichte, 1972), only approached the loft, but did not find the loft itself (Schmidt-König & Walcott, 1978).

A clear use of familiar landmarks as sole means of navigation, so-called route stereotypy, has only been observed after extensive habituation with a specific route (Biro *et al.*, 2004; Meade *et al.*, 2005; Biro *et al.*, 2007; Mann *et al.*, 2010). Yet, the current study (see chapter 3), as well as a previous study involving pigeons from the same loft (Wiltschko *et al.*, 2007), did not reveal any indications that pigeons from Frankfurt behave in the same way. Pigeons from Frankfurt flew along different routes even after multiple releases from the

## 6. General Discussion and Conclusion

same site, suggesting that the behavior reported for the pigeons from Oxford may be a special trait of those pigeons.

This, however, does not mean that there are no indications whatsoever, that pigeons from Frankfurt use visual cues. Pigeons released from a more distant site have been observed to circle over a previous release site, with which they were highly familiar (see chapter 3). This could be interpreted as indication that visual cues may be used for site recognition, yet it cannot be excluded that other, non-visual cues enabled the pigeons to recognize the site. The use of landmarks in the sense of linear features that stabilize the flight could be indicated by the observation that pigeons from Frankfurt seem to prefer to fly along series of towns (see chapter 3). Such use of visual features has also been observed in a previous study, where pigeons were found to follow other linear features like roads and highways if these roughly coincided with the home direction (Lipp *et al.*, 2004). This behavior does not seem to be limited to pigeons, as similar findings had been reported for migratory birds (von Schweppenburg, 1933)

### 6.1.4. Navigational Gradients

The flight paths of the pigeons, as observed in the current study, lead to the impression of distinctive flight corridors. Pigeons re-enter the same corridors when released in similar directions at much more distant sites (see chapter 3) or when released along the corridor (Wiltschko *et al* in prep.). The distributions of the release site biases, i.e. the deviation from the home direction, in the region around Frankfurt already seem to indicate these corridors (Grüter *et al.*, 1982). The corridors therefore support Keeton's (1973) hypothesis that biases are a regional and not a local phenomenon, reflecting the distribution of navigational factors within that area. With the methods provided here, it is now possible to objectively separate the flight of the pigeons into distinctive phases. The

influence of variations in potential navigational factors on these phases can then serve as means to identify the involvement of these factors in the navigational process, as has been shown in the current study for the influence of the earth's magnetic field.

### **6.1.5. The Earth's Magnetic Field**

At first glance, the influence of the daily variation of the earth's magnetic field seems to be limited to the departure phase, where it has adverse effects on the pigeons' orientation, influencing the headings in which the pigeons depart, the respective vector lengths and the steadiness, but not the speed with which the pigeons travel (see chapter 4). While there are indications that the steadiness during the final homing phase may be affected too, this effect is considerably smaller and not significant. This, however, obviously corresponds to the observation that there is also no significant effect on the overland efficiency (see chapter 3). Yet the fact that a small effect on these two independent measures, the steadiness during the final homing phase and the efficiency during the overland flight, can be observed may already serve as an indicator that the earth's magnetic field remains involved in the navigational process. My results therefore point out for the first time that varying magnetic conditions may also affect the remainder of the pigeons' journey. The reduced effect of the daily variation on the later parts of the pigeons' flight, however, suggests that the magnetic field is not the only factor the pigeons use to determine the course towards home. This is supported by the previously mentioned observation that an increase in complexity can be observed as the pigeons approach their home loft (see chapter 5). Due to this increase in complexity, which is most likely due to the involvement of additional factors, it is no surprise that there is no significant effect of the daily variations of the geomagnetic field on the later parts

## 6. General Discussion and Conclusion

of the pigeons journey. It can be assumed that the involvement of additional factors would mask such an effect.

The involvement of the magnetic field in the navigational process is also supported by the observation that there are differences in behavior of pigeons released within the magnetic anomaly of the Vogelsberg compared to releases in magnetically quiet regions (see chapters 3 and 4, as well as Wiltschko *et al.*, 2009a, 2010). However, the previous studies have also shown that the magnetic field can most likely be replaced if the information provided is no longer useful or if the pigeons can not access the information at all. The finding that the daily variation of the earth's magnetic field also influenced the pigeons behavior during the remainder of their journey suggests that the magnetic field remains an integral part of the navigational process. Yet it should be mentioned that these time dependent fluctuations of the magnetic field, did not exceed 70 nT and are much smaller compared to those the pigeons experienced when released within the magnetic anomaly. Therefore the magnetic field may have still been useful after all. Although circumstantial, the current study also suggests that the magnetic field as a factor can be replaced if necessary, as shown by the highly complex flight of one pigeon crossing the Vogelsberg anomaly (see chapter 3). The findings that magnetic cues can be replaced by others are, however, in strong contrast to the idea that pigeons could home using the magnetic field alone (Dennis *et al.*, 2007).

### 6.1.6. Identification of Navigational Factors

In view of the observation that pigeons seem to be able to compensate the loss of specific cues it seems more likely that they have access to several navigational factors that supply similar information and can replace each other. As a result, testing for the involvement of specific navigational factors is not a simple matter. It is generally assumed that any cue can be tested for its

involvement in the navigational process by depriving pigeons of this specific cue. It should, however, be kept in mind that in a system that probably relies on multiple redundant factors the effects of deprivation may be different than what would be expected. Deprivation therefore does not necessarily lead to a detectable impairment of the ability to home, as other factors can take its place. This may also explain why it is so difficult to find influences from external factors on the pigeons behavior. Therefore we either have to ensure that the anomalous conditions during the experiment do not render the pigeon unable to use that specific cue or use the correlation dimension to assess whether or not extreme anomalous conditions or deprivation has affected the complexity of the underlying navigational process. Deprivation does also not necessarily lead to a reduction in the complexity of the underlying process. The effect observed ultimately depends on how well that factor can be replaced and in cases where access to a cue is denied multiple other cues may take its place resulting in an increase in complexity. Only in those cases where cues can not be replaced or are of lesser importance a reduction in complexity of the underlying process can be expected. As long as we keep this in mind deprivation of single cues can still remain a viable option to identify their involvement in the navigational process.

For example, it could be tested through deprivation of visual cues, whether those are the reason why an increase in complexity of the navigational process can be observed as the pigeons approach their home loft. It could also be tested whether deprivation of magnetic or olfactory cues results in a change in the correlation dimension of the navigational process. However, deprivation of olfactory cues does always equal a deprivation of several and not only a single cue and therefore should be viewed with caution (Wallraff *et al.*, 2003). In cases where olfactory cues contribute to the navigational process deprivation may indeed lead to an impairment in the pigeons' ability to home. Yet this



## 6. *General Discussion and Conclusion*

does not exclude that other cues are still involved. The deprivation of several, even redundant, cues may also interfere with the pigeons' ability to weight cues accordingly and therefore result in the observed disorientation. As long as it is not possible to eliminate a single specific olfactory cue, the effects of olfactory deprivation remain difficult to interpret.

### **6.1.7. Simulating Navigation**

Of course our efforts to understand the navigational process are not limited to actual experiments. The findings of the current study point out some interesting aspects of the underlying navigational process, which can be used in simulation experiments. So far, only few attempts have been made to simulate the navigational process of pigeons. In the earliest attempts the focus was mainly on establishing olfactory cues as potential navigational factors (Wallraff, 1989b,a, 2000). Although little can be inferred about the general mechanisms from these simulation experiments, they showed very nicely that several less reliable sources of information are as good as a few more reliable sources. In the most recent attempt to simulate pigeon navigation, which focused much more on the general mechanisms of the navigational process, it was shown that increased variability within the gradients can, for example, explain the phenomenon of release site biases and that a lower precision in the compass step has less dramatic effects on the pigeons performance than a lower precision during the position determination step (Wiltschko & Nehmzow, 2005). In this study it was assumed that the pigeon re-determines its course every 5 km, can determine the compass direction with a precision of  $\pm 15^\circ$  and the position with an accuracy of  $\pm 3$  km using two artificial gradients. The results of the current study suggest that the navigational process is repeated much more often, roughly every 12 seconds (but see chapter 5). It has also been shown that at least four up to six, but maybe even more individual factors are used to de-

termine the home course, that these factors are weighted differently and that additional factors seem to be introduced into the process as pigeons approach their home loft.

Last but not least the findings of my study may also give some idea about the precision of the navigational process. As has been shown, the precision depends on the complexity of the process, where increases in complexity also lead to an increase in precision. The precision of the course determination process seems to lie in the range of  $\pm 21^\circ$  to  $36^\circ$ . Therefore the combined error of the compass and the map step should be in a similar range in any future attempt to simulate pigeon navigation. Following the assumption that the precision of the compass is roughly  $\pm 15^\circ$  this would indicate that only  $\pm 5^\circ$  to  $21^\circ$  of the error in precision would be related to difficulties determining the position. I previously pointed out that assuming that a pigeon travels with a speed of 16 m/s and would determine its position every 12 seconds this would equal errors in the range of  $\pm 16.80$  to 73.68 m. Although these calculation do not necessarily need be representative for the pigeons' true ability to determine their current position, we either have to assume that the precision of the compass step is higher than  $\pm 15^\circ$  or that the accuracy with which pigeons can determine their position is more accurate than  $\pm 3$  km.

We can also conclude that, if this precision were to be achieved using only the information provided by the earth's magnetic field, the pigeons were required to discern differences in intensity below 0.042 nT. Besides the fact that a second factor would still be required, it has also been shown that neuronal activity alone can induces magnetic anomalies of roughly 0.22 nT (Wikswa *et al.*, 1980). Considering that the daily variations of the earth's magnetic field often exceed 50 nT (Skiles, 1985), the calculated precision is unrealistic and can by no means be achieved by only one or two navigational factors. Therefore it would be very interesting to test if such a precision can be achieved using

## 6. General Discussion and Conclusion

realistic gradients by simply increasing the number of gradients and introducing weighting of the individual factors.

### 6.1.8. A Redundant System

My findings support the assumption that the pigeon's ability to navigate is based on a highly complex modular process utilizing several navigational factors providing similar information. It is due to the redundancy of these individual factors and the modular nature of the process, allowing the pigeons to weight the available information, that pigeons can achieve high levels of precision and find their way home even under anomalous conditions.

## 6.2. A General Model for Navigation in Birds?

### 6.2.1. Homing in Other Birds

Usually, homing experiments are conducted with pigeons, yet there is a huge body of evidence that other birds, migratory and non-migratory species, are also able to successfully home after displacement. Homing experiments have till today been conducted with a wide variety of birds, including starlings (*Sturnus vulgaris*: Rüppell, 1935, 1936, 1937), swallows, like barn swallows (*Hirundo rustica*: Rüppell, 1936, 1937; Nastase, 1982), bank swallows (*Riparia riparia*: Sargent, 1962; Baldaccini *et al.*, 1999), house martins (*Delichon urbica*: Rüppell, 1936) and purple martins (*Progne subis*: Southern, 1959), Eurasian wrynecks (*Jynx torquilla*: Rüppell, 1937), red-backed shrikes (*Lanius collurio*: Rüppell, 1937), wood thrushes (*Hylocichla mustelina*: Able *et al.*, 1984) and seabirds, like Leach's petrels (*Oceanodroma leucorhoa*: Griffin, 1940), herring gulls (*Larus argentatus*: Griffin, 1943), arctic terns (*Sterna paradisaea*: Hatch, 1971), common terns (*Sterna hirundo*: Griffin, 1943), noddy terns (*Anous stolidus*: Watson & Lashley, 1915), sooty

terns (*Sterna fuliginosa*: Watson & Lashley, 1915) and northern gannets (*Morus bassanus*: Griffin & Hock, 1949).

Despite the successful returns of many of these birds, sometimes over vast distances, it is still frequently assumed that the mechanisms applied by migratory birds during homing differ from those of pigeons and other non-migratory birds or that there is a general difference between the task of homing and migration (e.g. Keiser *et al.*, 2005). This is basically due to prolonged return times and bad initial orientation that is often (e.g. Griffin & Hock, 1949), but not always, reported in such homing experiments (e.g. Sargent, 1962; Nastase, 1982; Able *et al.*, 1984). So the question is whether there are other reasonable explanations as to why these birds take longer to return to their homes. Already Rüppell (1935; 1936; 1937) mentioned that his birds successfully homed despite the extreme stress and hardship they had to endure. He mostly attributed unsuccessful or late returns to this observation, to the possibility that the birds had fallen prey or simply to the difficulty to accurately record homing times and homing success.

The observation that even displacements over short distances can already result in prolonged homing times indicates that such experiments are a huge intrusion into the life of wild birds (Griffin, 1943; Griffin & Hock, 1949). An interesting observation concerning this matter comes from a study of wood thrushes (Able *et al.*, 1984). Here the birds were displaced up to 17.3 km, yet took several days to complete the journey home. Because the birds were tracked using radio transmitters it became evident that the birds flew on average only 2.1 km per day, yet each of these short trips was directed towards home.

In their study of northern gannets Griffin & Hock (1949) made some interesting observations, namely that releases over land resulted in much longer homing times compared to releases over sea and that birds that had reached the coast during the early phases of the experiment homed faster. They attributed

## 6. *General Discussion and Conclusion*

these findings to the use of familiar landmarks. Yet these observations could also indicate problems related to the unusual environment. As indicated by experiments with three different species of forest birds, unusual environment can have quite dramatic effects on homing performance (Bélisle *et al.*, 2001). In this study, it was found that birds that had to cross non-forest areas did either not return home at all or took significantly longer than those that did not need to cross non-forest areas, even when displaced over short distances.

Most of the distances chosen in homing experiments are well beyond the normal home range of the species (Rüppell, 1936, 1937; Griffin, 1940, 1943). Such distances were chosen to exclude the possibility that the birds could use familiar landmarks to find their way home, yet these distances may also place the birds in situations where the initial task may not be to find the way home, but to look for food or even for a place to spend the night. Some birds indeed cover even larger distances during migration, but during migration the birds are physiologically adapted for this task and even then they still need to sleep and find food. It should be kept in mind that pigeons cover much larger distances during pigeon races - up to 1000 km - in a single day than most migratory birds, but in order to achieve this level of performance even pigeons require extensive training.

Therefore it may be not surprising that after displacements over such distances the initial response of the birds might not be to find home, but probably locate food. Southern (1959) interprets the initial behavior of his bird as not related to the task of homing. Experiments with rock doves, the feral ancestors of the homing pigeon, likewise indicate that a trend to orient towards home can only be observed in autumn, when the rock doves feed almost exclusively near the colony site (Baldaccini *et al.*, 2001). This finding suggests that even wild pigeons primarily choose to look for food after displacement.

Therefore the initial orientation of domestic pigeons may be as good as it is because the pigeons know they will find food when they return home.

The weather conditions in homing experiments with wild birds are often not favorable, as the experimenters did not want to keep the birds in captivity longer than necessary. It is often observed that the homing times and initial orientation improve under better weather conditions (Griffin & Hock, 1949). Influence of weather on the behavior of pigeons has also been identified in the present study, but can be considered weak; However, all experiments in the current study, as well as any other study on pigeon homing are usually conducted under more favorable weather conditions than any study of homing in wild birds - hence the weather conditions may also contribute to the poorer initial orientation and increased homing times observed in wild birds.

### 6.2.2. Physiological and Behavioral Similarities

Now that I have pointed out that the differences between wild birds and homing pigeons are most likely due to problems that are not related to the navigational process itself, a view that is shared by several other researchers (e.g. Wiltschko, 1992; Wallraff *et al.*, 2003), I want to focus on physiological and behavioral similarities between pigeons and migratory, as well as other birds. A very common observation in homing experiments is that birds familiar with a release site are able to home faster (Sargent, 1962; Baldaccini *et al.*, 1999), a tendency which is also observed in pigeons (Kowalski & Wiltschko, 1987). This tendency is often attributed to the use of familiar landmarks or visual cues in general. From pigeon experiments, however, we know that the birds are still able to home without the aid of visual cues (Schmidt-König & Schlichte, 1972; Schmidt-König & Walcott, 1978; Benvenuti & Fiaschi, 1983). Also multiple experiments with seabirds indicate that the homing process does not rely on familiar landmarks (Watson & Lashley, 1915; Griffin, 1940, 1943; Griffin &

## 6. General Discussion and Conclusion

Hock, 1949; Hatch, 1971). In many cases, it is possible to observe good initial orientation in displaced wild birds, and even Griffin (1943) found that most of his gannets oriented towards their home, before they wandered off in different directions. However, this is not always the case, and also pigeons are not always directed towards home in their initial orientation - two such cases of so-called release site biases, can be found in the current study (see chapter 3).

A very interesting experiment published just recently shows that there is indeed no difference in homing performance between migratory and non-migratory birds (Keiser *et al.*, 2005). This is indicated by equal homing performance of two subpopulations of dark-eyed juncos (*Junco hyemalis*). The authors, however, in view of their previous finding that the neurons in the hippocampus of the migratory sub population are more densely packed and that their performance during spatial tasks in arenas is better than that of the non-migratory sub population (Cristol *et al.*, 2003), conclude that both, homing and migration, are different tasks. The authors argumentation, however, is not convincing. The increased neuronal density and the significantly better performance in the spatial task may simply be a result of the need to remember a increased number of food sources along the migratory route. Therefore the findings may be interpreted in the way that the neuronal density of the hippocampus as well as the ability to perform spatial tasks may be important to remember an increased number of locations. These may include important stop-over sites, as well as two different familiar areas, the area around the breeding ground and the wintering area. However, remembering these places may not be important for navigation itself.

Like migratory birds, homing pigeons also possess a magnetic compass (Keeton, 1971; Walcott & Green, 1974). It has been shown that the magnetic compass of migratory birds is located in the right eye (Wiltschko *et al.*, 2002). Due to the lack of histological evidence in pigeons, it cannot be shown that



the receptors in pigeons and migratory birds are identical. Yet it is known that the magnetic compass of migratory birds, like the Australian silvereye or the European robin, is light dependent and ceases to work under light of long wavelengths (Wiltschko *et al.*, 1993; Wiltschko & Wiltschko, 1995). The same wavelength-dependency has also been observed in homing pigeons: Young, unexperienced pigeons are known to use their magnetic compass to determine their course towards home (Wiltschko & Wiltschko, 1978, 1985), they have been shown to be unable to integrate the path back to their loft if they were transported in total darkness (Wiltschko & Wiltschko, 1981, 1985) or under light of long wavelength (Wiltschko & Wiltschko, 1998). Indirect evidence for similar mechanisms in other birds comes from experiments with young geese (Saint Paul, 1982). After either passive or active displacement, i.e. after they were transported using a wagon or after they had followed the human they were imprinted on, young geese were able to find their way home on a direct course, even if the path included several detours. Their ability to do so could only be impaired by transporting them without access to light.

Similarities can not only be observed in the compass mechanism, but also in the map step. Putative receptors that could function as magneto-receptors, which are probably used to determine the birds current position (Wiltschko *et al.*, 2009a, 2010), have been described in homing pigeons (Hanzlik *et al.*, 2000; Williams & Wild, 2001; Winklhofer *et al.*, 2001; Fleissner *et al.*, 2003, 2007; Tian *et al.*, 2007) as well as other birds. These include zebra finches (*Taeniopygia guttata*), yellowhammers (*Emberizia c. citrinella*), brown-headed cowbirds (*Melothus ater*) (Williams & Wild, 2001), European robins (*Erithacus rubecula*), garden warblers (*Sylvia borin*) and even domestic chicken (*Gallus domesticus*) (Stahl *et al.*, 2006).

Behavioral responses to treatments that affect the map step do also not differ between homing pigeons and other birds. A quite popular experiment is

## 6. General Discussion and Conclusion

the application of a short pulse, designed to alter the magnetization of the small magnetic particles found in the upper beak. Migratory birds, like Australian silvereyes (*Zosterops l. lateralis*) (Wiltschko *et al.*, 1994b, 1998, 2009b) and bobolinks (*Dolichonyx oryzivorus*) (Beason *et al.*, 1995), treated with such a pulse show a deviation from the controls similar to those of pigeons (Beason *et al.*, 1997). The pigeons, however, responded to this treatment with much smaller deflections from the direction of untreated controls than the migratory birds. Yet these differences could be simply related to the fact that the migratory birds were tested in laboratory situations and probably did not have access to cues that might have been available to the pigeons. Also olfactory deprivation has similar effects in pigeons and other birds. Like pigeons, swifts (*Apus apus*) and starlings show a decrease in homing speed after olfactory deprivation (Fiaschi *et al.*, 1974; Wallraff *et al.*, 1995).

The process of building a navigational map takes place in the early phases of a pigeon's life (Wiltschko & Wiltschko, 1985) and also determines the pigeon's fidelity to the loft. Due to this it is necessary to acquire young pigeons from another loft before they have undertaken their first flights, because otherwise they would always try to return to their original loft. In an experiment with young collared flycatchers (*Ficedula albicollis*: Löhrl, 1959) displaced to a new location, where they were raised in cages, and released at a third site, it could be shown that after migration the birds only returned to the release site if they were given ample time to get familiar with the new site. Similar experiments with pied flycatchers (*Ficedula hypoleuca*: Berndt & Winkel, 1979) support these earlier findings and show that the process of building a familiar map is probably the same in all migratory birds and pigeons.

### 6.2.3. The Routes Chosen

Last but not least there is an intrinsic similarity between migratory routes and tracks of homing pigeons. The precision of the route determination process lies in equal ranges, i.e. 6-33° for Swedish ospreys (*Pandion haliaetus*: Hake *et al.*, 2001), and as shown in the current study, 21-36° for homing pigeons (see chapter 5). There is, like in pigeons, a huge difference between the behavior of young and adult birds, with young birds showing considerably more scatter, probably due to the difference in the applied navigational strategy and the increased need for exploration to build a navigational map (Hake *et al.*, 2001, 2003, Schiffner *et al.* in prep.). Like tracks of pigeons, migratory routes resemble dynamic processes, where there is high divergence among individual tracks, even from the same individuals in successive years, but also convergence during certain portions of the tracks. When comparing tracks of different species, e.g. Swedish ospreys and honey buzzards (*Pernis apivorus*), which have roughly the same target area, one finds that both species fly roughly along the same corridors. As has been shown in the current study, the distribution of biases does already indicate the course of these corridors (see chapter 3). Biases are a phenomenon which is not restricted to pigeons alone. Keeton (1973), for example, found that bank swallows from a colony near his pigeon loft produced similar biases as his pigeons, suggesting that the factors causing these biases are the same for these two species. Migratory routes therefore may also be affected by the distribution of the navigational factors. The existence of these corridors and the convergence at specific points plays an increasingly important role in bird conservation, as this convergence is used to identify important stopover sites. Yet convergence does not only occur at important stopover sites, as is indicated by the analysis of repeated journeys of Swedish ospreys (Alerstam *et al.*, 2006). The authors term these points of convergence, intermediary goal areas; a mathematician, however, would call them attractors. The divergence

## *6. General Discussion and Conclusion*

and convergence in these areas is a clear indicator that the navigational process of the migratory birds is, like that of the pigeons, governed by an underlying chaotic-deterministic process.

### **6.2.4. The Bottom Line**

Considering the existence of so many similarities between pigeons and other birds, the pigeon indeed seems to be an ideal model for the research of the underlying navigational process. As is indicated by the observed increase in complexity, as the pigeons approach home, long range navigation is most likely a less complex process, where the underlying process itself remains the same. Therefore it can be assumed that the study of close range navigation in pigeons can also help to explain long range navigation in migratory birds.

## 7. Summary

With the help of miniaturized GPS recorders I recorded 167 tracks of 48 individual pigeons during their flight from 6 different sites around Frankfurt. The experiments consisted of two main series of repeated releases from two sites 30 km north and south from the pigeons' home loft. From the site in the south the pigeons homed 12 times and from the site in the north 16 times. After the final release from these sites, the pigeons were released at 60 km distance from home. These additional sites were selected so that the pigeons would presumably fly over the previous release site with which they were highly familiar. After conclusion of the main series two additional releases were performed, one within the magnetic anomaly of the Vogelsberg and one in a magnetically quiet region. To make these releases comparable, both release sites were selected so that the distance from the home loft was 40 km.

All data obtained during these experiments were subjected to a threefold analysis, mostly based on methods that I had developed by myself or adapted for this specific study. In the first step, data were analyzed traditionally, evaluating variables similar to those that can be found in current literature. I therefore calculated values that correspond to those obtained by visual observation, like virtual vanishing bearings and intervals after one minute and after 2.5 km. Additionally I calculated the efficiency of the flights and efficiencies for specific portions of each flight, to derive variables that describe the behavior after vanishing. In the second step, which served also as a preparation for the mathematical analysis, the flight of the pigeons was separated into distinctive

## 7. Summary

phases of the flight by the so-called points of decision. The flight of the pigeon can usually be separated into an initial phase of flying about, a departure and/or final homing phase. In more complex cases, however, several points of decision and a multitude of intermediary phases can be defined. Yet, the initial phase, the departure phase and the final homing phase can be defined for all tracks and therefore have been selected as appropriate candidates for a thorough analysis. In the last step I employed the so-called method of time lag embedding to reconstruct the underlying navigational process of the pigeons' homing flight. This method is based on the principles of chaos theory and is regularly employed for the analysis of dynamic systems. Its application allows the reconstruction of the underlying processes from experimentally recorded data without any a priori knowledge of the underlying system itself. For these reconstructed systems I calculated characteristic properties which are unique for each system. These are the so-called correlation dimension, describing the complexity of the system, and the so-called largest Lyapunov exponent, describing its predictability. Based on the knowledge gathered from these reconstructions, I used a variation of the previous methods to identify navigational phases, by calculating the correlation dimension as a sliding mean over the complete track. From these data I then derived further characteristics of the underlying process, such as its precision and differences in complexity depending on the pigeon's current position.

All variables obtained from the three analytical steps were analyzed in view of possible influences of the position of the release site, in view of differences in individual behavior and in view of influences of previous experience at the release site and abiotic factors, such as cloud cover, wind and temperature, as well as the influence of the daily variation of the geomagnetic field. I additionally looked for general dependencies between the different variables calculated in

each of these analytical steps to infer some general features of the pigeons' flight, i.e. whether initial behavior does affect later portions of the flight.

The study shows that the time the pigeons spend at the release site, before they finally decide to leave, is independent of the release site, i.e. the direction from the home loft, is independent of familiarity with the release site and the availability and reliability of navigational factors such as the earth's magnetic field. The time spent is also not characteristic for specific individuals and is independent of the behavior after the decision. These findings strongly argue against the possibility that the pigeons use this time to scan for navigational factors. Earlier studies already indicated that the pigeons know their home direction well before they take off. My findings support this assumption. On the one hand, the pigeons' behavior during the initial phase shows an increased tendency towards home the more they are familiar with the respective release site. On the other hand, the results indicate that pigeons tend to fly towards home during the initial phase, if they later depart in home direction. The time until the first point of decision is therefore most likely used for flight preparation, which is also supported by the finding that the behavior close to the release site is also characterized by lower correlation dimension than later portions of the flight. During this phase the flight of the pigeons often converge over the nearest town or village. This may indicate that the pigeons preferentially do such flight preparations over familiar and secure terrain, where the risk of predation is minimal.

The behavior after the first point of decision does differ from that of the initial phase. The behavior during the departure phase is usually homeward directed. While the behavior at the release site, as mentioned before, is less complex, the behavior during the later portions of the flight is more complex and is also characterized by low Lyapunov exponents, around 0.02, and is therefore highly predictable. This indicates that the behavior of the pigeons during



## 7. Summary

homing is governed by a chaotic deterministic process. The departure phase is the first phase of the pigeon's flight that is clearly affected by the magnetic conditions on release. Both, anomalous magnetic conditions at the release site, as well as the daily variation of the geomagnetic field have an adverse affect on the behavior during the departure phase. This is indicated by the decreased steadiness and increased scatter of the headings during this phase. Likewise the behavior up to 2.5 km is also affected, as indicated by the increased time the pigeons need to cover that distance and the decreased efficiency during this portion of the flight, as well as the increased scatter of the virtual vanishing bearings 2.5 km from the release site. These findings strongly suggest that the magnetic field is an integral part of the pigeons' navigational process and can be affected by magnetic variations even below 70 nT. During the later phases of the flight this influence is no longer significant, but can yet be found to have adverse affects on the pigeons' ability to navigate as indicated by a decrease in overland efficiency and steadiness during the final homing phase. The reduction in the effect of variable magnetic conditions can be explained by the increase in complexity that can be observed as the pigeons get closer to their home loft. Due to this increase a reduction in the influence of one single variable is to be expected. However, the reduced influence seems not to be related to a decrease in importance of the earth's magnetic field as an navigational factor, but due to the increase in the number of navigational factors involved in the homing process.

The routes taken by the birds are highly variable, even when comparing routes from the same individual. They also seem to be largely independent of the pigeons previous experience at the release site. Some of the routes create the distinctive impression of flight corridors. Even when released from the more distant sites, the pigeons still reenter the same corridors and sometimes even do so when released from other sites. During certain portions of the flight, these

corridors coincide with series of towns and villages that may act as stabilizing features that happen to coincide with the distribution of navigational factors in that region. The possibility that the pigeons use these villages as some sort of landmarks, however, can be excluded for two reasons: (1) the pigeons do follow these villages from their very first flight and (2) such behavior would be indicated by a reduction in complexity of the underlying process. Such a reduction can not be observed and the underlying navigational process remains highly complex, even during these portions of the flight.

The correlation dimension in the range of 3.2. to 4.1 indicates that there are at least four, maybe even more, independent navigational factors, including the compass, involved in the navigational process. The observed levels of complexity are of a fractal nature and therefore indicate that the individual factors are weighted separately. The process, as said before, gets increasingly more complex as the pigeons approach their home loft. The increase in precision, achieved by the introduction of additional factors, seems to be negligible, suggesting that the new factors are included into the process mainly to compensate for the increasing difficulty to determine quantitative differences from the home value for single factors. The results therefore show that the pigeons' ability to find their way home can be attributed to a complex chaotic deterministic process of modular nature. The pigeons probably have access to several navigational factors and may be able to weigh the available information against each other. The nature of these factors, however, remains largely unknown. It has been shown that one of these factors is most likely the earth's magnetic field, yet the magnetic field is just one of the multiple factors available to the pigeons. It is possible that during the final parts of the pigeons' journey visual cues, such as landmarks, may play an increasingly important role. Yet if they do, they still only serve as means to support gradient based navigation. There-

## 7. *Summary*

fore the information provided by the two hypothetical maps, i.e. the gradient based map and the mosaic map, is probably used simultaneously.

## 8. Zusammenfassung

Mit Hilfe von miniaturisierten GPS-Rekordern habe ich 167 Flugwege von 48 Tauben bei ihren Flügen von 6 verschiedenen Auflassorten aufgezeichnet. Die Experimente bestanden dabei aus zwei Hauptserien, während derer die Tauben wiederholt von Orten in 30 km Entfernung vom Heimatschlag aufgelassen wurden. Insgesamt flogen die Tauben dabei 12 mal von einem Auflassort im Süden und 16 mal von einem Auflassort im Norden. Nach der letzten Auflassung vom jeweiligen Ort wurden die Tauben zusätzlich in 60 km Entfernung vom Heimatschlag aufgelassen. Diese zusätzlichen Auflassorte wurden dabei so gewählt, dass die Tauben aller Wahrscheinlichkeit nach über den vorherigen Auflassort, mit dem sie ja nun vertraut waren, fliegen würden. Nach Beendigung dieser beiden Hauptserien wurden noch zwei zusätzliche Versuche, einmal innerhalb der magnetischen Anomalie des Vogelsbergs und einmal in einer magnetisch normalen Region durchgeführt. Um sicherzustellen, dass auch diese Auflassungen vergleichbar sind, wurden die Auflassorte so gewählt, dass in beiden Fällen die Distanz zum Schlag ungefähr 40 km betrug.

Alle so gewonnenen Daten wurden im Folgenden einer dreischichtigen Analyse unterzogen. Die angewendeten Methoden sind dabei fast ausschliesslich von mir selbst entwickelt oder von mir speziell für diese Studie adaptiert worden. Im ersten Schritt wurden die Daten entsprechend der in der aktuellen Literatur verwendeten Methoden, sozusagen "auf traditionelle Weise", analysiert. Dabei wurden Werte ermittelt, die denen entsprechen die bei Beobachtung mit dem Fernglas gemacht werden, wie virtuelle Verschwinderichtungen nach einer Mi-

## 8. Zusammenfassung

nute und in 2.5 km Entfernung vom Auflassort, sowie Verschwindezeiten in 2.5 km Entfernung vom Auflassort. Zusätzlich wurden Effizienzen für die einzelnen Flüge und einzelne Flugabschnitte bestimmt, um das Verhalten über das bei traditionellen Experimenten unzugängliche Verhalten nach dem Verschwinden zu erhalten. Im zweiten Schritt, der auch als eine Art Vorbereitung für den letzten Analyseschritt diente, wurden die Flugwege der Tauben durch Bestimmung sogenannter Entscheidungspunkte ("Points of Decision"), nach objektiven Kriterien, in charakteristische Phasen des Fluges aufgeteilt. Der Flug einer Taube lässt sich dabei üblicherweise in eine Anfangsphase ("Initial Phase"), während der die Vögel scheinbar ungezielt in der Nähe des Auflassortes umherfliegen, und eine Abflug ("Departure Phase") und/oder eine Heimkehrphase ("Final Homing Phase") aufteilen. In komplizierteren Fällen lassen sich jedoch auch mehrere "Zwischenphasen" definieren. Die Anfangsphase, die Abflugphase und die finale Heimkehrphase lassen sich jedoch für alle Flüge definieren und sind somit ideale Kandidaten für eine genauere Untersuchung. Im letzten Schritt wurden dann, basierend auf der Methode des sogenannten "Time Lag Embedding", die einzelnen Phasen des Fluges dazu verwendet, um den der Navigation zugrundeliegenden Prozess zu rekonstruieren. Die verwendete Methode basiert dabei auf den Prinzipien der Chaos-Theorie und wird oft dazu eingesetzt, dynamische Systeme zu charakterisieren. Sie erlaubt es, die zugrundeliegenden Prozesse eines Systems aus experimentellen Daten zu rekonstruieren, ohne dass genaueres Wissen über das Zusammenspiel der involvierten Faktoren vorhanden sein muss. Für den so rekonstruierten Prozess habe ich dann für das System charakteristische Eigenschaften bestimmt. Diese Eigenschaften beschreiben zum einem die Komplexität des Systems, die sogenannte "Korrelations Dimension" und zum anderen die Vorhersagbarkeit des Systems, der sogenannte "größte Lyapunov Exponent". Basierend auf den so gewonnenen Erkenntnissen über die Eigenschaften des Systems, habe ich dann eine Variation der vorangehenden Methode entwickelt, um

navigatorische Phasen im Flug der Tauben zu identifizieren. Hierzu wurde die Korrelations Dimension als gleitendes Mittel über den gesamten Flugweg der Taube berechnet. Aus diesen zusätzlichen Ergebnissen habe ich dann weitere Eigenschaften des Systems, wie die Genauigkeit der Kursbestimmung und die räumliche Abhängigkeit der Komplexität des Systems, abgeleitet.

Alle so bestimmten Variablen habe ich dann darauf hin untersucht ob ein Einfluss von der Lage des Auflassortes besteht, ob Unterschiede im Verhalten von einzelnen Individuen bestehen, ob das Verhalten von Ortserfahrung oder Umweltfaktoren, wie Wolkenbedeckung, Windrichtung und -geschwindigkeit und Temperatur, so wie Tagesvariation des Erdmagnetfelds, beeinflusst wird. Zusätzlich habe ich die Daten auf generelle Zusammenhänge untersucht, z.b. ob das Verhalten am Auflassort das spätere Verhalten beeinflusst.

Die Ergebnisse der Studie weisen nun darauf hin, dass das Verhalten am Auflassort, also bevor die Tauben sich entscheiden diesen endgültig zu verlassen, unabhängig vom Ort selbst, der Richtung vom Schlag, der Vorerfahrung am Ort und der Verfügbarkeit und Zuverlässigkeit von potentiellen Navigationsfaktoren, wie dem Erdmagnetfeld, ist. Die Zeit, die Tauben brauchen, ist nicht spezifisch für das jeweilige Individuum und die benötigte Zeit hat auch keinen Einfluss auf das spätere Verhalten. Aufgrund dieser Befunde scheint es höchst unwahrscheinlich, dass die Tauben die Zeit bis zum ersten Entscheidungspunkt nutzen, um Orientierungsinformationen zu sammeln. Auch aus früheren Studien geht bereits hervor, dass Brieftauben schon bevor sie losfliegen die Heimrichtung kennen. Meine Befunde bestätigen diese. Zum einen lässt sich bei den Tauben die Tendenz beobachten, dass sie mit zunehmender Erfahrung bereits während der Anfangsphase zunehmend in Richtung Heimat fliegen. Zum anderen lässt sich aus den Ergebnissen ableiten, dass Tauben bereits während der Anfangsphase in Heimrichtung tendieren, wenn sie später auch in Heimrichtung abfliegen. Es scheint somit wahrscheinlicher, dass die Tauben die Zeit damit ver-

## 8. Zusammenfassung

bringen, sich für den folgenden Heimflug vorzubereiten. Diese Vermutung wird auch dadurch gestützt, dass sich das Verhalten zu Beginn des Fluges durch eine geringere Korrelations Dimension, als in den späteren Teilen, auszeichnet. In der Anfangsphase scheinen die Tauben häufig zu dem nächstgelegenen Dorf zu fliegen und dort einige Zeit zu verbringen. Dies könnte darauf hindeuten, dass die Tauben es bevorzugen, solche Flugvorbereitungen über sicherem und vertrautem Gebiet durchzuführen, wo z.B. die Gefahr, Beute von Greifvögeln zu werden, geringer ist.

Das Verhalten nach dem ersten Entscheidungspunkt ist grundlegend anders als das in der Anfangsphase. Das spätere Verhalten ist in der Regel heimgerichtet. Während sich das Verhalten am Auflassort, wie bereits erwähnt, durch geringere Komplexität auszeichnet, sind die späteren Teile des Fluges wesentlich komplexer und zeichnen sich auch durch niedrige Lyapunov Exponenten, um 0.02, aus, also dadurch dass sie hochgradig vorhersagbar sind. Dies deutet darauf hin, dass das Verhalten der Brieftaube während des Heimfluges von einem chaotisch-deterministischen Prozess bestimmt wird. Die Abflugphase ist die erste Phase des Heimfluges, bei der sich ein Einfluss der äusseren magnetischen Bedingung bemerkbar macht. Hierbei beeinflussen sowohl lokale magnetische Anomalien am Auflassort, als auch die Tagesvariation des Erdmagnetfelds das Verhalten der Brieftauben auf negative Weise. Dies äussert sich zum einen in geringerer Stetigkeit und grösserer Streuung der Flugrichtungen während der Abflugphase und zum anderen im Verhalten innerhalb der ersten 2.5 km vom Auflasspunkt. Hier kann gleichfalls beobachtet werden, dass die virtuellen Verschwinderrichtungen der Tauben stärker streuen und die Brieftauben zudem länger brauchen, um diese Distanz zurückzulegen, bzw. wesentlich ineffizienter während dieses Teilstücks fliegen, wenn anomale Bedingungen vorherrschen. Die vorliegenden Befunde verdeutlichen somit, dass das Magnetfeld der Erde ein integraler Bestandteil des Navigationsprozesses ist. Dabei können bereits



kleine Änderungen in den magnetischen Bedingungen, wie sie zum Beispiel durch die Tagesvariation verursacht werden - sogar unter 70 nT - das Verhalten der Tauben beeinflussen. Der Einfluss auf das spätere Verhalten ist zwar nicht signifikant nachweisbar, jedoch macht sich ein gewisser Einfluss in der Effizienz während des Überlandfluges und der Stetigkeit während der Heimkehrphase bemerkbar. Dass der Einfluss magnetisch anomaler Bedingungen geringere Auswirkungen auf die späteren Teile des Heimfluges hat, kann jedoch durch den Anstieg der Komplexität des navigatorischen Prozesses, der beobachtet wird, wenn sich die Tauben dem Heimatschlag nähern, erklärt werden. Aufgrund dieses Anstiegs entspricht es durchaus den Erwartungen, dass sich ein Einfluss einer einzelnen Variable weniger deutlich bemerkbar macht. Dies deutet somit darauf hin, dass der verringerte Einfluss magnetisch anomaler Bedingungen nicht etwa daher rührt, dass dem Erdmagnetfeld weniger Bedeutung beigemessen wird, sondern, dass zusätzliche Navigationsfaktoren in den Prozess mit einbezogen werden.

Die Wege die Tauben für ihren Heimflug wählen, sind dabei sehr unterschiedlich. Dies gilt selbst für wiederholte Flüge der selben Taube vom gleichen Ort. Die Wahl des Weges scheint also unabhängig von der vorausgehenden Erfahrung zu sein. Trotz ihrer Individualität hinterlassen die Wege beim Betrachter den Eindruck, dass die Tauben entlang bestimmter Korridore fliegen. Selbst von weiter entfernten Orten wählen die Tauben Routen, die sie wieder auf diese Korridore hinführen. Auch von Orten in unterschiedlichen Richtungen kann man ab und zu beobachten, dass einige der Tauben entlang der selben Korridore nach Hause fliegen. Dabei scheinen Teilstücke dieser Korridore über Ansammlungen von Ortschaften zu führen. Das Verhalten, entlang solcher Serien von Ortschaften zu fliegen, scheint dabei hauptsächlich dazu zu dienen den eingeschlagenen Kurs zu stabilisieren. Die Übereinstimmung zwischen den Korridoren und den Ansammlungen von Ortschaften scheint somit eher zufälli-

## 8. Zusammenfassung

ger Natur zu sein. Da die Tauben bereits während ihres ersten Fluges von den jeweiligen Orten entlang ähnlicher Routen nach Hause finden lässt sich ausschliessen, dass diese Dörfer im Sinne von Landmarken verwendet werden. Darüber hinaus sollte sich ein solches Verhalten, also das Folgen von Landmarken, sogenanntes *Piloting*, durch geringere Komplexität auszeichnen. Eine Reduktion der Komplexität des zugrundeliegenden navigatorischen Prozesses lässt sich jedoch nicht beobachten. Auch während des Fluges über Dörfer bleibt der Prozess auf einem hohen Komplexitätsniveau.

Die Korrelations Dimension liegt im Bereich von 3.2 bis 4.1. Dies deutet darauf hin, dass mindestens vier, aber möglicherweise auch mehr unabhängige Faktoren einschliesslich des Kompasses, an dem navigatorischen Prozess beteiligt sind. Die dabei zu beobachtenden Grade an Komplexität sind fraktaler Natur und weisen somit darauf hin, dass die herangezogenen Faktoren individuell gewichtet werden. Der Prozess wird, wie bereits erwähnt, komplexer, je näher die Taube dem Heimatschlag ist. Der Gewinn an Präzision, der dadurch erzielt wird das zusätzliche Faktoren miteinbezogen werden, bleibt jedoch vernachlässigbar. Dies deutet darauf hin, dass die zusätzlichen Faktoren hauptsächlich dazu dienen die immer grösser werdenden Probleme bei der Bestimmung quantitativer Unterschiede einzelner Faktoren zu denen am Heimatschlag zu bestimmen, zu kompensieren. Die ausserordentliche Fähigkeit der Tauben, ihren Weg nach Hause zu finden, ist somit dadurch begründet, dass der navigatorische Prozess modularer Natur ist. Die Taube kann dabei höchst wahrscheinlich auf eine Vielzahl von Faktoren zurückgreifen und so die vorhandenen Informationen gegeneinander abwägen. Welcher Art diese Faktoren sind, bleibt auch weiterhin größtenteils unklar. Einer der Faktoren, wie bereits erwähnt, ist vermutlich das Erdmagnetfeld, jedoch handelt es sich hierbei auch nur um einen der vielen Faktoren, die der Taube zur Verfügung stehen. Es ist durchaus möglich, dass vor allem während des letzten Teilstücks des Fluges visuelle Faktoren zuneh-

mend eine größere Rolle spielen. Wenn dies tatsächlich der Fall sein sollte, dann spielen aber auch diese nur eine untergeordnete Rolle und dienen dazu, die Gradienten-basierte Navigation zu unterstützen. Es ist somit wahrscheinlich, dass die Informationen die von den beiden den Tauben zugeschriebenen Navigationskarten, der Gradientenkarte und der Mosaikkarte, gleichzeitig verwendet werden.



## Appendix



# Appendix A.

## Dynamic Systems Theory

### A.1. Introduction

In the following chapter I will give an introduction into the basic principles behind dynamic systems theory and explain how they can be used to obtain characteristic values that describe the behavior of a system in a mathematical sense.

### A.2. Definition of Dynamic Systems

A dynamic system is a system, where each state  $x(t)$  is defined by a more or less simple mathematical equation which describes the system for all times  $t$ . A very basic example of a dynamic system is the ideal pendulum where the course of the pendulum  $\theta(t)$  is given for all times by the following definition:

$$\theta(t) = \theta_0 \cos\left(\frac{2\pi t}{T}\right)$$
, with  $\theta_0$  as the amplitude and  $T$  as the period of the swing.

By measuring the pendulum's movement over a limited time period one receives a so-called time series. Due to the fact that the ideal pendulum is a deterministic system it is possible to use this time series to precisely predict all future states of the pendulum, even without any previous knowledge of the

equation defining the system. In dynamic systems theory one takes advantage of this simple fact, as the same basic principle applies to even more complex systems. Each system can be described by its predictability, where a system can be either stochastic, i.e. unpredictable, deterministic, i.e. predictable or chaotic. Chaotic systems are predictable for only a short time, but do not allow accurate long term prediction. The predictability of a system, however, is not the only means by which a system can be described. In phase space dynamical systems can also be uniquely described by the geometry of their trajectories, the so-called attractor, where phase or also state space is the space that fully describes the system's behavior for all times. An attractor, however, is defined as a set towards which a dynamical system evolves over time and therefore the ideal pendulum is a bad example. It does not evolve over time and each point in phase space is infinitesimally close to another point. The clock pendulum is a better example, its trajectory describes a so-called limit cycle and in case of the damped pendulum the attractor is a fixed point. The attractor of a dynamical system can have various geometrical shapes and has in deterministic cases a integer dimension. Stochastic systems have an infinitesimal number of dimensions and chaotic systems describe complicated sets with a fractal structure known as strange attractors.

### **A.3. Phase Space Reconstruction.**

According to Whitney's embedding theorem (1936), every dynamic system can be fully described in a phase space with a maximum of  $2n+1$  dimensions, where  $n$  is the number of degrees of freedom and each state in phase space is uniquely defined by its position and impulse along each degree of freedom. This means that each single state of a system can be described as a vector of  $2n+1$  variables. The ideal pendulum for example has only one degree of freedom and can already be fully described in a two-dimensional phase space. Taken's (1980) extension



of this embedding theorem states that a topologically equivalent representation of a system's phase space can also be acquired by embedding a single time lagged variable in a  $m$ -dimensional space, where  $m = 2n + 1$  is the so-called embedding dimension. With time lag embedding it is then possible to define a series of vectors  $x(t)$  from a one dimensional time series that is equivalent to a system's original phase space:

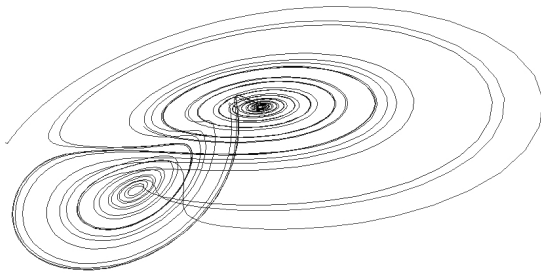
$$x(t) \rightarrow x(t, t - \tau, t - 2\tau, \dots, t - m\tau), \text{ with } m \text{ the embedding dimension and } \tau \text{ the time lag.}$$

Phase space reconstruction evolves around the idea that a measured variable  $x(t)$  does not only contain information about itself, but also information on the remaining variables and thus the underlying system. The most famous example of a dynamic system that can display chaotic behavior, the so called Lorenz system (Lorenz, 1963), can be fully described by three differential equations. Each state of the Lorenz system is uniquely defined by the three coordinates  $x(t), y(t)$  and  $z(t)$ :

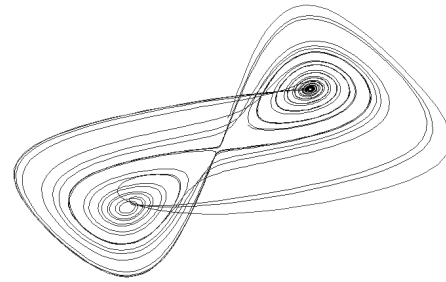
$$\frac{dx}{dt} = \sigma(y - x), \quad \frac{dy}{dt} = x(\rho - z) - y, \quad \frac{dz}{dt} = xy - \beta z, \text{ where values for } \sigma, \beta \text{ and } \rho \text{ can be chosen freely, but should be } > 0. \text{ Usual values are } \sigma = 10, \beta = \frac{8}{3} \text{ and } \rho \text{ is varied. The system exhibits chaotic behavior for } \rho = 28.$$

Theoretically each of the three coordinates could serve as a basis to reconstruct the original system, yet not all three are equally good candidates. While  $x(t)$  and  $y(t)$  play a primary role in all three equations and therefore the determination of all three variables,  $z(t)$  does not occur in the first equation and thus "only" plays a secondary role. Therefore, one could assume that while  $z(t)$  is less suited for phase space reconstruction,  $x(t)$  and  $y(t)$  are good candidates, and this is indeed the case, as can be seen from the phase space reconstructions from the individual coordinates in Figure A.1.

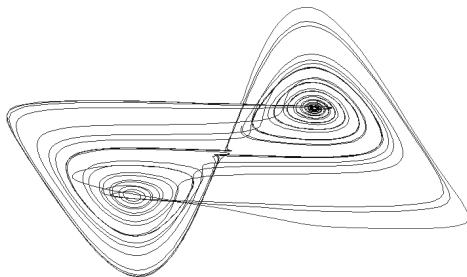
x y z



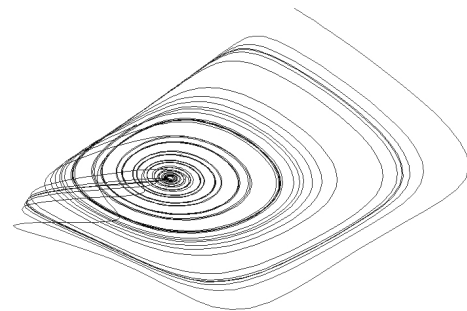
x



y



z



**Figure A.1.** – The original Lorenz attractor (xyz) and phase space reconstructions from each of its three coordinates embedded in a three-dimensional view space, the time lag was  $\tau = 12$ , the variables for the Lorenz system are as follows:  $\sigma = 10$ ,  $\beta = \frac{8}{3}$  and  $\rho = 28$ .

In experimental situations things are even more complicated, as the variables that can be measured are limited. If indeed a relevant variable can be measured, the information contained in this single measurement should be equivalent to any other and therefore suffice for the purpose of reconstruction. While the reconstructed phase space may not have the same scale and orientation as the original phase space, both, the original phase space, also referred to as state space, and its reconstruction, have the same basic properties, such as Lyapunov exponents, entropy and correlation dimension

## A.4. Choosing the Embedding Parameters

In order to determine such properties for a system from experimental data it is first necessary to reconstruct the system's phase space from the one-dimensional time series. Therefore one has to choose proper embedding parameters, the embedding dimension  $m$  and the embedding lag  $\tau$ .

### A.4.1. Choosing the Embedding Dimension

If the embedding dimension is chosen too low, the phase space trajectory will not be unfolded properly. This means that the trajectory may visit points in a lower dimensional space to which it would never even get close if it were embedded in the proper dimension. In a simple example, one could choose a time series with two dimensions and embed it in a phase space with zero dimension, then all points of the system would occupy the same place, the trajectory would not be properly unfolded. As the embedding dimension is increased, the trajectory will unfold itself until it is embedded in two dimensions and further increase of the embedding dimension yields no further change. A commonly underestimated problem when choosing an embedding dimension is that the trajectory does not only need to be properly unfolded, but also that the data points need to be properly oriented towards each other. This factor is seldom considered in the most commonly used methods and therefore I decided to use the less common, but far superior method of "false strands" (Small, 2005).

In order to apply this method, I compare a fixed number of nearest neighbors, i.e. the nearest points in phase space, and their immediate successors in a  $n$ -dimensional embedding space, with the nearest neighbors and their successors in the embedding space, with the next higher dimension  $n + 1$ . Once I have ensured that the nearest neighbors remain the nearest neighbors, even if I increase the embedding dimension further, the data set can be considered

properly unfolded. If their successors also remain the same, I have also ensured that orientation of the trajectories in phase space remains constant. Once the same set of neighbors with the same orientation remain nearest neighbors in a higher dimensional embedding space, an acceptable embedding dimension has been found (A detailed explanation of the method, its advantages over other methods, as well as its implementation can be found in appendix B).

#### A.4.2. Choosing an Embedding Lag

The basic idea behind selecting an embedding lag is to avoid spurious effects from autocorrelation, with autocorrelation meaning that two points close in time,  $x(t)$  and  $x(t + 1)$ , are bound to be similar in some way and so is their progression over time  $t \rightarrow \infty$ .

Choosing a time lag that is too small may result in a superficial enhancement of the calculated phase space properties. Although this effect is commonly considered to be negligible (Theiler, 1986), it drastically increases when the length of the time series is finite. Selection of a proper time lag can also reduce the impact of noise on the calculation and therefore is mandatory for any experimental time series. While there is a wide spectrum of possible methods that can serve as criteria for selecting an embedding lag, the most favored method is the average mutual information (Fraser & Swinney, 1986); it is also used in this study.

Given a time series  $x(t)$ , the average mutual information  $I(x, y)$  is the amount of information shared with another time series  $y(t)$  and vice versa. In the specific case of selecting a time lag,  $y(t)$  is nothing else but a time lagged version of the original time series  $x(t)$ :

$$y(t) = x(t + \tau), \text{ with } \tau \text{ being the time lag.}$$

The basic principle of the method evolves around finding a lag  $\tau$  where the highest amount of new information can be found, i.e. the information shared between the two time series reaches a minimum. While there may be several minima it has been shown that the first of these can already serve as an appropriate choice for a time lag (for details on why this specific method has been chosen and how it has been implemented see appendix B).







## **A.5. Correlation Dimension $d_2$**

Estimation of the correlation dimension is one of various methods to estimate the degrees of freedom of a dynamic system. Before I explain how to calculate the correlation dimension, I will first explain different concepts of dimensionality and how they are linked to each other.

### **A.5.1. Concepts of Dimensionality**

From a mathematical point of view, a point is an object with zero dimension, a line an object with one dimension, a surface an object with two dimensions and a body an object with three dimensions and so on. This concept of dimensionality is called the topological dimension (see Figure A.2). Understanding objects with more than three dimensions gets increasingly difficult. While it may be not so difficult to grasp a four-dimensional object as a volume moving through time, imagining an object with five dimensions is virtually impossible.

This is basically due to the fact, that we perceive the world as a three-dimensional system and perceive what we see as space. This concept is the concept of the so-called view space. It is, however, simple for us to imagine a two-dimensional space. Whether we look at a drawing of a point or a sphere on a chalkboard, we perceive both objects as two-dimensional, although we already

Object	Topological Dimension	Fractal Dimension
	0	0.00
	1	1.00
	1	1.54
	2	2.00
	2	2.12
	3	3.00

**Figure A.2.** – Topological and fractal dimensions of different objects (from top to bottom , a single point, a line, a jiggly line, a square, a rectangle folded into a three-dimensional space and a box). The given fractal dimensions are only guesses of what the true fractal dimension could be and are by no means meant as accurate measures.

know that their topological dimensions differ. This is, of course, because these two objects are embedded in a two-dimensional space, the chalkboard.

Both concepts I just mentioned are extremely limited in their application, with view space being limited to only three dimensions and topological dimension being limited to only full degrees of freedom. When looking at an atom in space we could simply define it by its position in space, but if this atom is moving and others can take its place we require more variables to define it, thus we could add the time at which it is at those specific coordinates. Furthermore

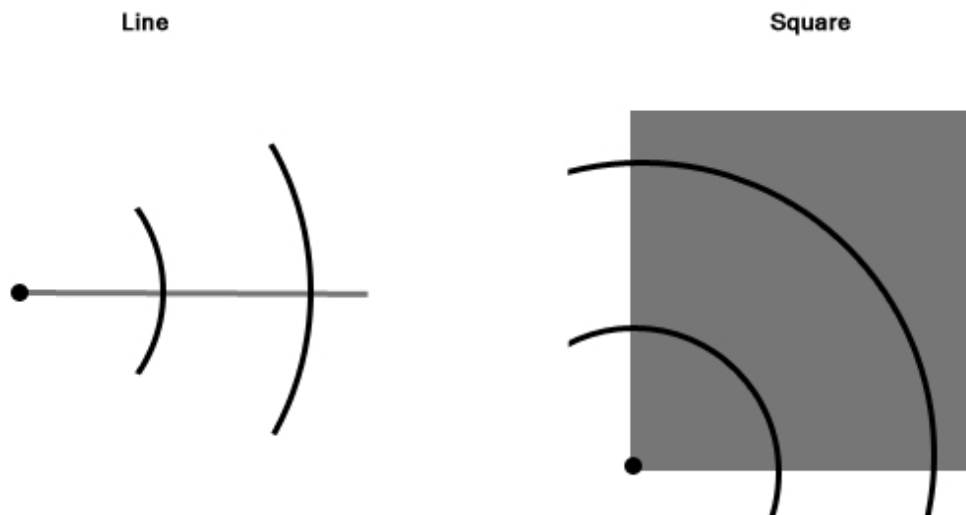
if the atoms are moving and the same places are repeatedly occupied by other atoms, we have to add more details like its mass and charge, to discriminate periodic movements. In turn we have already started to perceive a single atom as an six-dimensional system where each coordinate and property required to identify the system are separate degrees of freedom. Therefore, each n-dimensional object can simply be perceived as an object with n different input variables where neither of these variables necessarily needs to be a coordinate in space.

The last and final concept I am going to introduce is the concept of fractal dimensions. In order to understand this concept let us look at two different lines, a straight line and a jiggly line. From a topological point of view both have a topological dimension of one, but while the straight line has only one degree of freedom, it can only move along one dimension, the jiggly line does sometimes move along another degree of freedom. The fractal dimension is a measure to what extend such additional degrees of freedom are used.

### **A.5.2. Basic Ideas and Principles**

The correlation dimension as defined by Grassberger & Procaccia (1983a,b) is an estimation of the dimension of an underlying system. Although there is a multitude of methods that allow estimation of the number of dimensions, the correlation dimension is the easiest to implement and more or less the only method applicable to experimental data. The method is derived from the simple idea of counting distances between the points that comprise an object (see Figure A.3).

For example, if one counted all points on a square within a specific range, one would find exponentially more points on the square as on a line. In theory an object with  $d$  dimensions consists of  $N^d$  points, the exponential increase in the number of points is therefore directly linked to the object's number of dimensions.

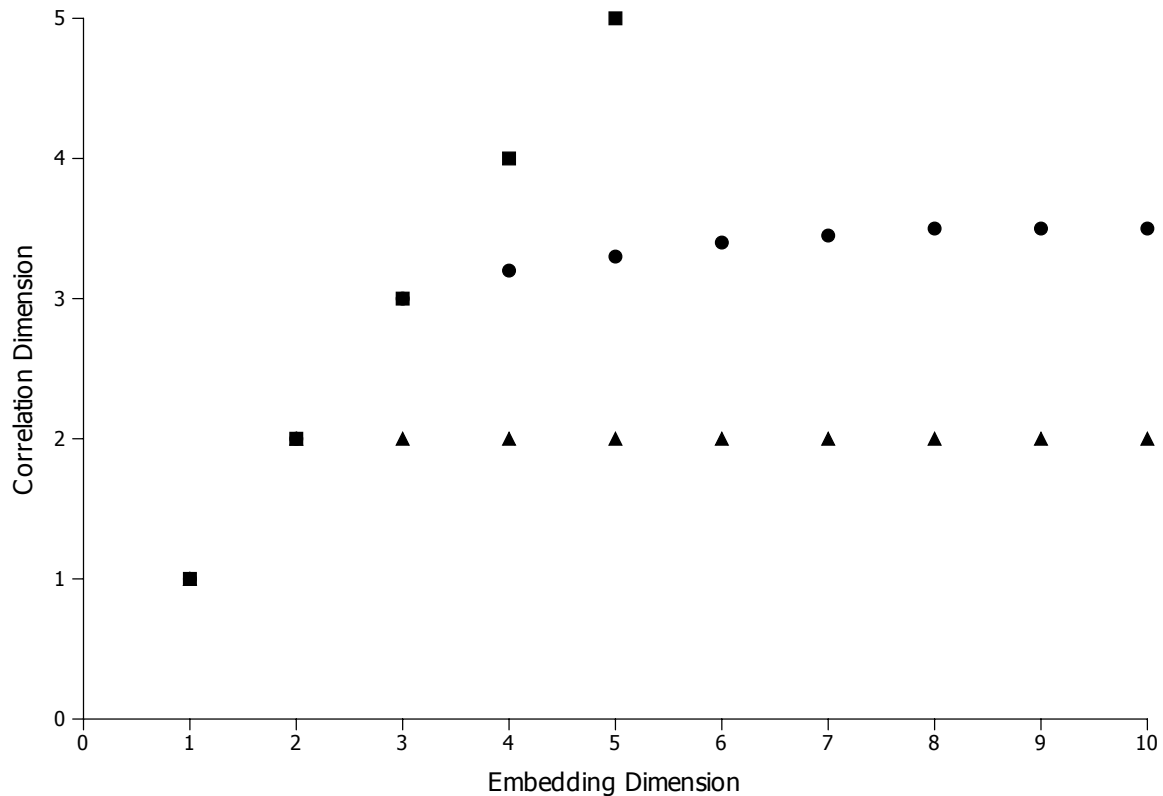


**Figure A.3.** – When counting points on a line and a square in specified distance intervals, there are exponentially more points to be found on the square than on the line.

In order to calculate the number of distances in the correct way, they need to be counted in the proper dimension. There would be no difference between the two objects if both objects were treated as one-dimensional. In the case of the line and the square, one automatically searches for distances within the proper topological dimension. It is a bit more complicated with systems where the topological dimension needs yet to be determined. In order to approach this problem the system needs to be embedded over and over again, with ever increasing embedding dimension, until there is no further change in the number of distances. As a starting point for the embedding, I choose  $m - 1$  as estimated from the false strands method (see section “Choosing an Embedding Dimension”). This approach works because it does have virtually no effect when a  $n$ -dimensional system is embedded in a  $n + x$ -dimensional space - it will still retain its original dimensionality. This idea is equivalent to transferring the previously mentioned two-dimensional square into a three-dimensional view



space, whether I look at it in two or three dimensions has no effect on its actual appearance, at least as long as the dimension I embed the object in is higher than the dimension of the object itself.



**Figure A.4.** – The stochastic system’s (squares) correlation dimension increases steadily with increasing embedding dimension. The chaotic system (circles) shows a plateau region with a non-integer correlation dimension of 3.5. The deterministic systems (triangles) shows a clearer plateau region and has an integer correlation dimensions of 2.0.

Estimation of the fractal dimension does not only serve the purpose of defining a system’s degrees of freedom, it also is an indicator of chaotic behavior (see Figure A.4). In a truly stochastic system the correlation dimension continuously increases with increasing embedding dimension, meaning it is not possible to find an embedding dimension where a change in correlation dimension can no longer be observed. In deterministic or chaotic systems one will find a “plateau region” where an increase of the embedding dimension has virtually no effect on the dimension of the system. In purely deterministic systems

the correlation dimension will asymptotically approach an integer value, while chaotic systems will approach a non-integer value. A non-integer correlation dimension, therefore, is the first evidence for the chaotic nature of a dynamic system.

### A.5.3. Calculation of the Correlation Dimension $d_2$

The estimation process itself, in accordance with what has just been explained, starts with calculating the correlation integral  $C^m(r)$  according to the following formula:

$$C^m(r) = \frac{1}{M(M-1)} \sum_{i,j=1}^M \Theta(r - \|x_i - x_j\|)$$

with  $i \neq j$ ,  $r$  the distance interval and  $m$  the embedding dimension.

$$M = N - (m - 1)\tau$$

with  $\tau$  the embedding lag,  $m$  the embedding dimension and  $N$  the number of data points in the time series.

$\Theta(x)$  denotes the so-called Heaviside step function defined as:

$$\Theta(x) = \begin{cases} 1 & x \geq 0 \\ 0 & x < 0 \end{cases}$$

$\|\dots\|$  denoting the so called Euclidean norm, a measurement of length in Euclidean vector space.

From the correlation integral the correlation dimension  $d_2$  can be obtained as the slope of  $\ln C^m$  versus  $\ln r$ :

$$d_2 = \lim_{r \rightarrow 0} \lim_{m \rightarrow \infty} \frac{\ln C^m(r)}{\ln r}$$

The slope of the curve is then a direct measurement of the dimensionality of the system's underlying process where defining the slope is yet another problematic issue that has to be solved by the experimenter. In appendix B I am giving a solution to this problem.

## A.6. Lyapunov Exponents $\lambda$

One of the principle properties of chaos is the sensitive dependence on initial conditions, which means in chaotic systems two initially infinitesimally close trajectories will always diverge exponentially over time. As explained before, chaotic systems like deterministic systems, are attracted to a specific set of points in space. Unlike deterministic systems, chaotic systems never actually reach these points and therefore the attractors of a chaotic systems are called strange attractors. Due to this attraction the trajectories do not diverge forever and quasi-periodically return to similar states, yet these states are never exactly identical and therefore the trajectories will diverge again. The average rate of this exponential divergence is called the largest Lyapunov exponent  $\lambda$ . The existence of a positive Lyapunov exponent and therefore exponential divergence is yet another indicator for chaos. In deterministic systems no such divergence can be observed, the largest Lyapunov exponent is zero. In contrast, a stochastic system will have an infinitesimal high largest Lyapunov exponent.

As the trajectories can not diverge forever, every system with a positive largest Lyapunov exponent also must have at least one negative Lyapunov exponent. More generally, every system has a number of Lyapunov exponents equal to its number of dimensions. Although there are several existing approaches to calculate the full or a partial spectrum of Lyapunov exponents (only positive spectrum, see Wolf *et al.* (1985), full spectrum see Sano & Sawada (1985)), these approaches are unsuitable for experimental data and I will therefore concentrate on calculating only the largest Lyapunov exponent (for details see the corresponding chapter in appendix B).

Due to its properties, the largest Lyapunov exponent can also be understood as a measurement of predictability. An inverse approach therefore is to devise a method to forecast a system's behavior and calculate the largest Ly-

Lyapunov exponent from the decrease in predictability over time. The simplest scheme for forecasting is treating the system as if it would be periodic and fully deterministic. Under these conditions one could predict future behavior of the time series at any given point  $x(t)$  by finding another point  $x(t')$  that is as similar as possible to the selected point  $x(t)$ . The difference between the evolution of  $x(t)$  and  $x(t')$  over time is then a measure of the time series predictability. In a fully deterministic system it will be possible to predict all future states and errors in prediction are either the result of initial errors or due to the presence of noise within the time series. In a stochastic system the prediction scheme will fail and the selection of a random point from the time series would be an equivalently good predictor. In a chaotic system, the prediction error will increase over time until prediction is as good as a random guess. This prediction approach is the most common and most applicable to experimental data (Rosenstein *et al.*, 1993; Kaplan & Glass, 1995; Kantz & Schreiber, 1997). In order to do a statistically solid prediction, it requires a little bit more than what I just described, yet the basic steps remain the same. First the time series needs to be properly embedded in phase space, then for each vector  $x(t, t - \tau, t - 2\tau, \dots, t - m\tau)$  a number of closest neighbors in phase space  $x(t', t' - \tau, t' - 2\tau, \dots, t' - m\tau)$  are selected and the average separation  $\Delta s$  between the original vector's trajectory and that of its closest neighbors is calculated. These steps are repeated until every vector of the time series has served as a starting point for the original trajectory. From the mean of the average separation the largest Lyapunov exponent can then be calculated using the following formula:

$$\lambda = \frac{1}{T} \langle \ln \Delta s \rangle, \text{ where } \langle \rangle \text{ denotes the average, } T \text{ the systems sampling time and } \Delta s \text{ the average separation}$$

A detailed explanation on the implementation of the method can be found in appendix B.

## **A.7. Application on Data**

In order to utilize these methods I implemented them all in one concise program. This program includes algorithms for the actual estimation processes for the correlation dimension and largest Lyapunov exponent, as well as algorithms to define the proper embedding parameters. A detailed explanation on how each method was implemented in this program can be found in appendix B, along with an overview of other methods and the improvements I have implemented to get more reliable results.



# Appendix B.

## Algorithms Explained

### B.1. Introduction

The focus of this appendix is to provide the reader with the required knowledge to allow him to calculate the largest Lyapunov exponent and the correlation dimension, as well as determine correct embedding parameters on his own. In this appendix I will introduce several applicable methods to determine these factors, point out the advantages of the currently employed approach and provide solutions for common problems, like defining objective criteria for the selection of the correlation dimension and the largest Lyapunov exponent.

### B.2. Choosing a Embedding Dimension

Probably the most common method to choose an embedding dimension is constant over-embedding of the time series. Starting at a very low embedding dimension  $m$ , properties for a time series are recalculated over and over again, with ever increasing embedding dimension  $m \rightarrow \infty$ , until appropriate results are achieved (Small, 2005; Kaplan & Glass, 1995). While being easy to implement the method is not only time consuming, but also useless when those properties are not known, which is generally the case when dealing with experimental time

series. Still the method is worth mentioning, as the basic principles of the more sophisticated methods are similar.

Also commonly accepted is the method of false nearest neighbors (Small, 2005; Kantz & Schreiber, 1997). Here a set of nearest neighbors in one embedding dimension  $m_x$  is compared with the nearest neighbors in the next higher dimension  $m_{x+1}$ . Once it is ensured that the nearest neighbors in one dimension  $m_x$  are still nearest neighbors in the next higher dimension  $m_{x+1}$ , they are considered to be true nearest neighbors and an appropriate embedding dimension has been found. While this method is less time consuming it has the flaw of generating false positives, as the method ignores proper phase space orientation, meaning that the method ignores whether the trajectories in phase space run in the same direction or not.

A sufficient solution for the problem, however, can be found in the so called method of false strands (Small, 2005). Instead of just comparing the nearest neighbors, the method also takes their immediate successors into account. Once the same nearest successors in one embedding dimension, are still the nearest successors in the next embedding dimension an acceptable embedding dimension has been found.

Implementation of the method of false strands is rather simple. I choose the 10 nearest neighbors for each point in the time series  $x(t)$  and perform a simple one step prediction. By comparing the average euclidean distance between all original successors and the successors of the 10 nearest neighbors with the average euclidean distance of 10 randomly chosen points, I get an estimate of how well the neighbors are oriented in phase space. As soon as increasing the embedding dimension does no longer result in a decrease in prediction error I have found a appropriate embedding dimension. This is due to the fact that the one step prediction error is directly linked to the number of false nearest neighbors at the specific embedding dimension.



### B.3. Choosing a Embedding Lag

Inappropriate choices of embedding lags  $\tau$  have considerably less dramatic consequences. In fact there is a wide range of suitable embedding lags that would lead to correct results. It would also be possible to define a so-called embedding window, with different embedding lags for each embedding dimension (Small & Tse, 2004; Small, 2005). Yet it is completely sufficient to choose a single embedding lag, as the improvements are minor and most certainly lie below what is detectable in experimental time series. Still, selection of a proper time lag is not a simple process and there are several methods that are supposed to help the experimenter to make an appropriate choice.

Probably the most common method is the auto-correlation function. The auto-correlation function (Small, 2005; Kantz & Schreiber, 1997) can be calculated for all time lags  $\tau$  by the following formula:

$$p_\tau = \frac{\text{cov}(y, y_{t+\tau})}{\text{var}(y, t)}$$

The embedding lag is considered to be appropriate, when  $p_\tau$  drops below a certain value. The literature provides multiple suggestions for that value, with the most common ones being 0 and  $\frac{1}{e}$  (the so-called decorrelation time). As the auto-correlation function is a linear measure; it may not be the best choice when dealing with nonlinear time series. While the auto-correlation function can serve the purpose of selecting a proper embedding lag, especially when dealing with low dimensional maps, like the logistic map or the Henon map, the choices will be much less suitable, when dealing with differential equations, like the Lorenz system.

Through calculation of the average mutual information (Fraser & Swinney, 1986; Small, 2005), a non linear method that measures the information shared between the original time series and a time lagged equivalent, much better

results can be achieved. While it is not generally superior to the auto-correlation function it is clearly the method of choice and is also used in the current study.

In order to calculate the average mutual information the data must first be partitioned. Therefore the measured values of the time series are commonly divided by the range  $x_{min}$  to  $x_{max}$ . The marginal probabilities  $P(x)$  and  $P(y)$ , as well as the joint probability  $P(x, y)$  can then be estimated from histograms of the partitioned data  $N_x$  and  $N_y$  (where  $N_x = N_y$ ) using the following formula:

$$\bullet I(x, y) = \sum_{i=1}^{N_x} \sum_{i=1}^{N_y} P(x, y) \log_2 \left( \frac{P(x, y)}{P(x) * P(y)} \right)$$

While this rather naive approach is quite easy to implement, it also has its drawbacks. The approach is based on the error-prone assumption that the data are normally distributed, a problem that gets increasingly severe, when dealing with finite time series. In consequence the calculation depends strongly on the method of partitioning. Partitioning itself is a controversially discussed topic, and while there is a multitude of possible solutions for this specific problem, all of them fail to generate reliable results in general (for review see Papan & Kugiumtzis, 2008). In order to avoid this problem, a priori knowledge of the underlying system would be required.

In order to circumvent problems with unevenly distributed data I choose a new non-parametric approach, where I assign a fixed number of elements to each partition. I divide the data into  $\log_2 N$  partitions and then assigned each value to the corresponding partition. The difference in the current attempt is that I assigned values by rank and not the parametric value itself. Due to this non-parametric approach I am able to ascertain an even distribution of the data among all partitions, ultimately resulting in much better convergence and better defined minima and maxima, as shown in Figures B.1 and B.2.

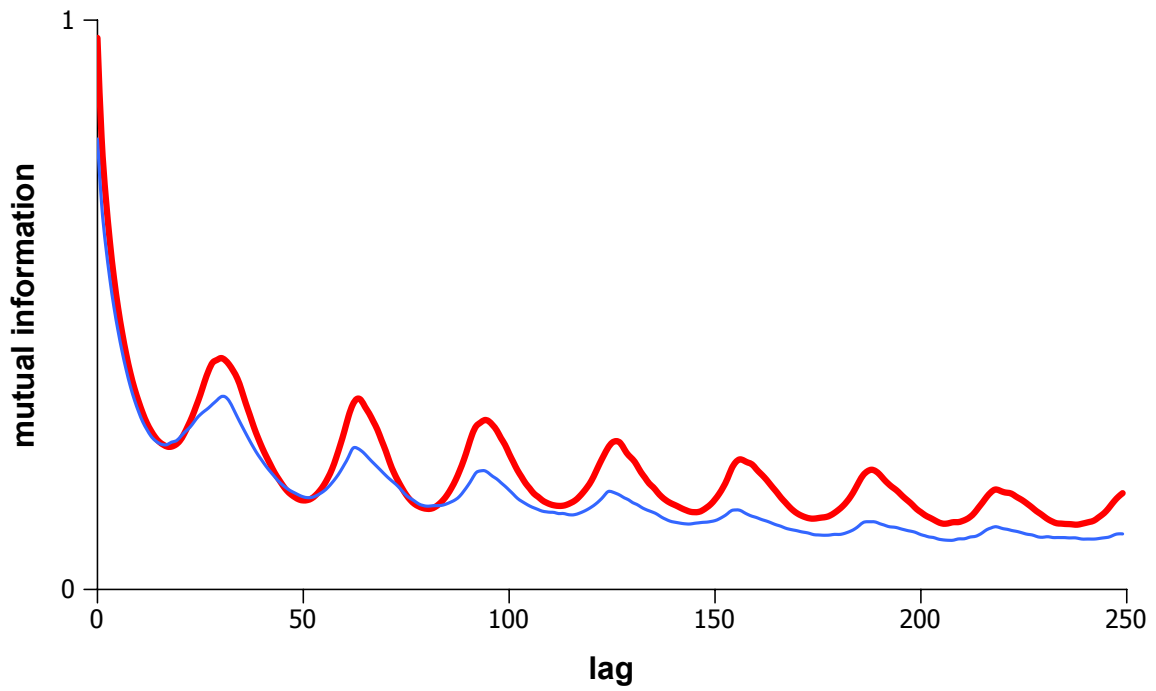


Figure B.1. – Mutual information of the Lorenz system with increasing lag, displayed are both the new non-parametric (thick, red line) and the old parametric approach (thin, blue line).

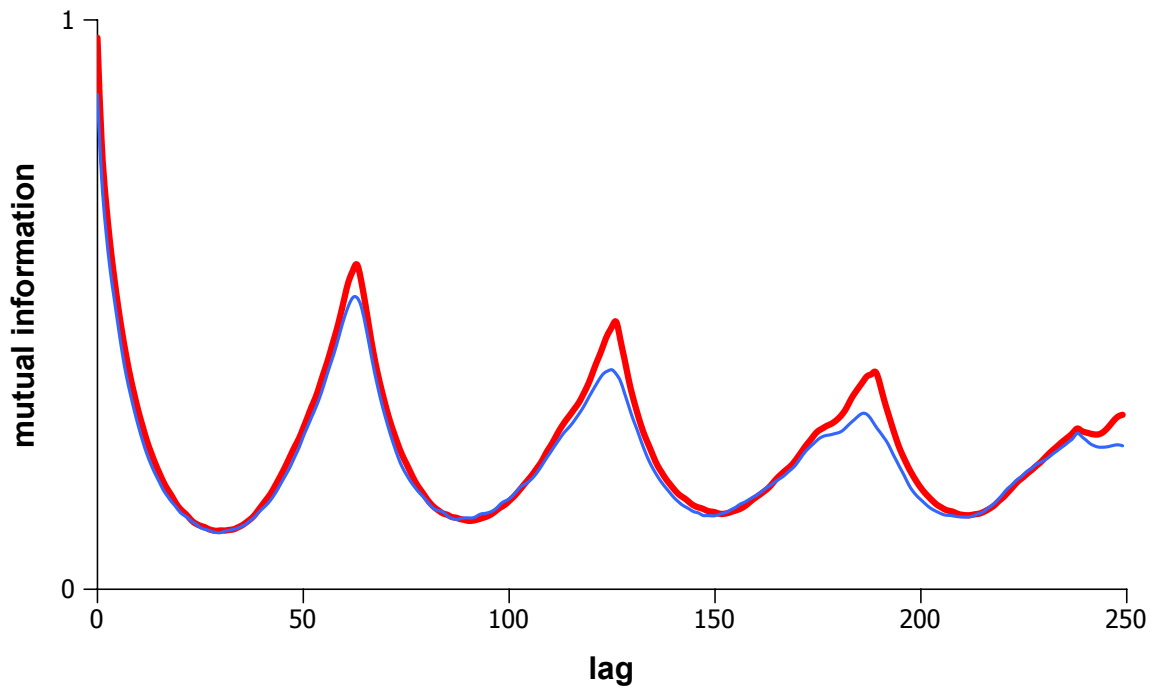


Figure B.2. – Mutual information of the Rössler system with increasing lag, displayed are both the new non-parametric (thick, red line) and the old parametric approach (thin, blue line).

## B.4. Correlation Dimension Estimation

As the basic algorithm for the calculation of the correlation dimension has already been described in appendix A “Dynamic Systems theory” I am going to focus mainly on the problem of finding a proper scaling region and getting reliable results based on objective criteria, as in contrast to the commonly employed completely subjective approaches.

Per definition, one has to select a scaling region  $r_s$  so that  $r \rightarrow 0$ . Yet if the choice of  $r$  is too small, statistics will be poor, due to increased influence of noise and the limited number of data points used for the calculation. On the other hand, as  $r$  approaches the size of the attractor, estimates of the correlation dimension will be too low, due to finite size effects. So far there are no really objective and generally applicable criteria for the selection of a proper scaling region. One exception is the “rule of five”, as proposed by Theiler & Lookman (1993), but there are many occasions where the method fails or it is simply impossible to apply the method at all.

Based on the idea that I have to look for a plateau-like region, I simply have to ensure that the selected scaling region remains the same for three successive embeddings ( $m - 1$  to  $m + 1$ ), thus that  $r_{m-1} = r_m = r_{m+1}$ . I therefore select the minimum in standard deviation over all three embeddings to define a proper scaling region. As the deviation of the correlation integral tends to be very small when  $r$  approaches the size of the attractor, in the so called “depopulation region”, it is necessary to add some restrictions:

- The first minimum in standard deviation, (with  $r \rightarrow r_{max}$ ) is used to define an initial estimate of the correlation dimension, where other possible scaling regions, even with lower deviations, are ignored, if the resulting correlation dimension estimates would be below this initial estimate ( $\pm$  the deviation).

- The size of the scaling region is fixed to  $\frac{1}{4}$  of the complete length of the evaluable attractor.

Although the latter restriction seems to be a rather coarse solution, it ensures that the scaling region will never lie within the depopulation region. Choosing a fixed scaling region also increases comparability between different calculations and also between different systems. The reliability and quality of this approach is indicated by the results provided in section B.6.

## B.5. Estimation of the Largest Lyapunov Exponent

Implementation of a method that is able to calculate the full or even a partial Lyapunov spectrum is problematic. While there are two existing methods, only the approach suggested by Wolf *et al.* (1985) is applicable to experimental data, as the other (Sano & Sawada, 1985) requires yet again a priori knowledge of the underlying system. Considering that both methods are as old as a quarter century and no more recent approach is available may give the reader a good impression of the complexity of the problem. Even if the time series is completely noise-free and the underlying dynamics are known, the amount of data points required to get results with acceptable accuracy is immense. If just one of these conditions is not met, even more data points are required. Without any a priori knowledge one is also limited to the spectrum of positive exponents. Due to these problems it is common to just calculate the largest Lyapunov exponent and I do so as well.

Most implementations of the calculation of the largest Lyapunov exponent evolve around the idea of forecasting. Normally, the data are separated into two sets of equal length, where one is used as a so-called prediction set and the other as the so-called validation set (Nehmzow, 2006). A point in the prediction set  $x_p$ , which is closest to a point in the validation set  $x_v$ , is then

used to predict the evolution of  $x_p$  in time. By repeating this procedure for all points in the validation set it is possible to calculate the so called prediction horizon, i.e. the point in time where any prediction based on previous data is as good as selecting a random point. From the prediction horizon or more precisely, from the increase in prediction error it is then possible to derive the largest Lyapunov exponent. The approach I implemented for calculating the largest Lyapunov exponent is basically similar, yet has several improvements over this rather crude method.

Unlike most implementations of forecasting, I decided to allow “post-diction”, meaning I do no longer care whether the closest point succeeds or precedes the original point. Consequently I no longer split up the data in a prediction and a validation set; assuming that the underlying process is continuous, it is really not important where the trajectories originate (Rosenstein *et al.*, 1993). By abandoning such a strict prediction scheme, the amount of usable data points has virtually doubled and calculations are in turn much more solid. In accordance with most algorithms used for the calculation of infinite time series, I stored the data in a pseudo-cyclic buffer. Therefore prediction does not stop, once the end of the time series is reached, but continues at the beginning of the time series, thus allowing every prediction-run to be performed for the complete data set. Besides allowing better use of the available data, slight trends, noisy parts and also partially non-stationary segments within the time series have less influence on the results. Assuming that the amount of data points affected by such events is small, their effect on the calculation is negligible.

It is, however, not sufficient to select only the closest point as a predictor; such an approach is statistically unsatisfying and can not serve the purpose of accurately approximating the true value of the largest Lyapunov exponent. When using only one point, accuracy is decreased due to spurious effects, like

convergence or stability that can occur if pseudo nearest neighbors, i.e. neighbors which have incorrect orientation within phase space, are selected. Selection of the closest neighbors is most commonly solved by defining an orbit  $\Omega$  and selecting all points within this orbit as neighbors (Rosenstein *et al.*, 1993; Wolf *et al.*, 1985). Usually the trajectories originating from these closest neighbors are followed for only a fixed evolution-time  $e$  after which the orbit has to be rescaled, i.e a new nearest neighbor with proper orientation need to be found. Yet there are no reliable guidelines as to how one should select an appropriate size for the orbit  $\Omega$  or the evolution-time  $e$ . In addition, the rescaling process is computationally intensive, error prone and difficult to implement. Although it has been suggested several times (Rosenstein *et al.*, 1993; Kantz & Schreiber, 1997) no one has yet implemented the idea of selecting a fixed number of closest neighbors. I now decided to apply this idea to my current approach and selected the 10 nearest neighbors as predictors. Besides being easier to implement and reducing time for calculation, this method ensures that the quality of calculation remains the same for all times, as the number of neighbors remains the same throughout the whole calculation.

While the prediction error  $pe$  is based on actual calculations, all previous approaches fail to apply some logic for selecting the largest Lyapunov exponent, ultimately resulting in biased results. I therefore felt the need to devise a method that would automatically select the largest Lyapunov exponent. In the current approach the actual value of the largest Lyapunov exponent was calculated from the highest steady increase in prediction error  $pe_t \rightarrow pe_{t+n}$ . In order to find this increase I performed multiple linear regressions. All prediction steps  $pe_t$  until the prediction horizon  $pe_{t=horizon}$ , but not more than the first 100 prediction steps, are used as possible starting points  $pe_t$  for these linear regressions. Each linear regression included initially the first two prediction steps. Additional prediction steps were added until the coefficient of determination dropped below a value

of 0.95. The next linear regression was then performed starting from  $pe_{t+1}$ . The linear segment with a coefficient of determination above 0.95, showing the highest increase in prediction error, was then selected as an appropriate choice to calculate the largest Lyapunov exponent. The reliability and quality of this approach is indicated by the results provided in section B.6.

## **B.6. Conclusion**

Results of the calculation of the correlation dimension and the largest Lyapunov exponent of four known chaotic deterministic systems are given in Table B.1. The slopes from which these results have been acquired are given in Figures B.3 to B.10. The figures for the correlation dimension show the dependency between the correlation dimension for three different embeddings and the distance interval  $r$ . The embedding dimensions that have been used are  $m - 1$  (green),  $m$  (orange) and  $m + 1$  (red), with  $m$  the embedding dimension as given in Table B.1. The figures for the largest Lyapunov exponent show the average increase in prediction error (red) and the average prediction horizon (blue).

It should be kept in mind that differences in results compared to those given in the literature may be the result of differences in the number of data points that were used. All calculations I performed were done with 4096 data points. Further differences can be simply attributed to the fact that I used objective criteria to define the slopes from which the results have been calculated, while the results given in the literature are all based on subjective criteria. In all four cases I could have simply selected a slope that would have corresponded to the expected correlation dimension and largest Lyapunov exponent (see Figures B.3 to B.10). Still the results are in most cases equivalent to those provide in the respective literature, showing that the calculations are reliable and that the objective selection criteria work.



**Table B.1.** – Correlation dimensions and largest Lyapunov exponents of known chaotic deterministic systems.

<b>System</b>	$\tau$	$m$	<b>expected</b> $d_2$	<b>calculated</b> $d_2$	<b>expected</b> $\lambda$	<b>calculated</b> $\lambda$
Logistic map	1	2	0.96 [1]	0.94	0.681[2] 0.693 [3]	0.609
Henon map	1	2	1.21 [1]	1.22	0.409 [2] 0.408 [4] 0.603 [5]	0.333
Lorenz equation	11	3	2.05 [1]	2.11	1.561 [2] 2.160[5] 1.630 [5]	1.500
Rössler equation	16	3	n.a.	1.17	0.087 [2] 0.130 [5] 0.096 [6]	0.240

The table includes the names of the systems, the embedding lag  $\tau$  the embedding dimension  $m$  the expected and the calculated values for the largest Lyapunov exponent  $\lambda$  and the correlation dimension  $d_2$ . The expected values are all according to those given in the respective literature: [1] - (Grassberger & Procaccia, 1983b), [2] - (Rosenstein *et al.*, 1993), [3] - (Eckmann & Ruelle, 1985), [4] - (Sano & Sawada, 1985), [5] - (Wolf *et al.*, 1985), [6] - (Zeng *et al.* (1991); values have been calculated in the presence of noise). The same variables and sampling times as in the cited literature were used.

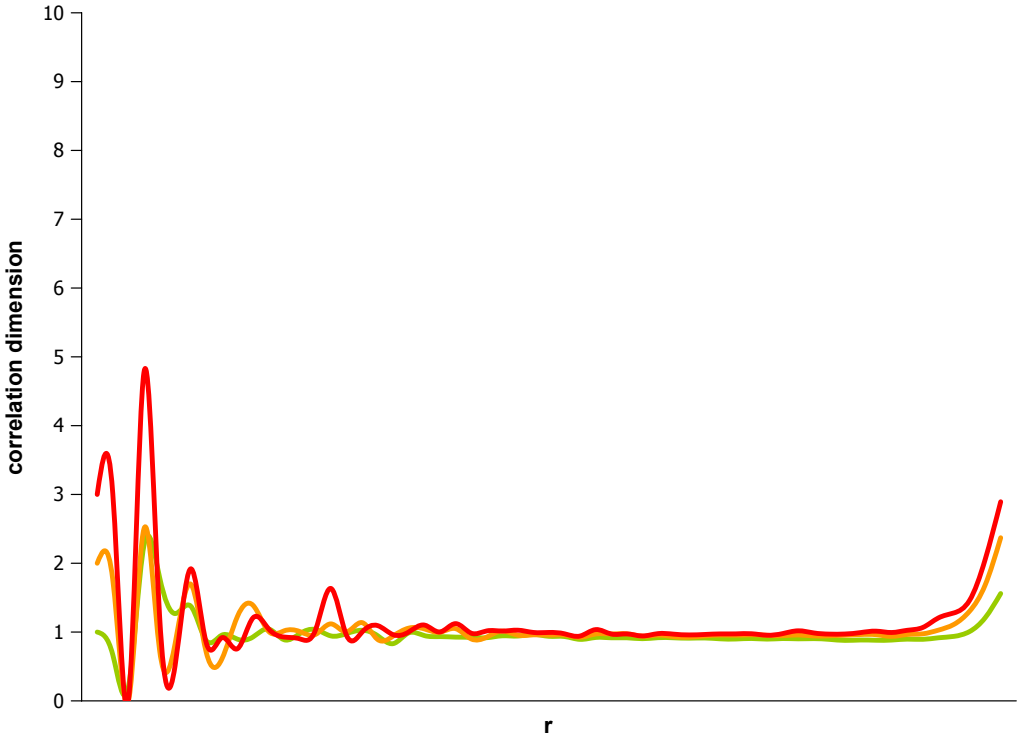


Figure B.3. – Correlation dimension of the Logistic map.

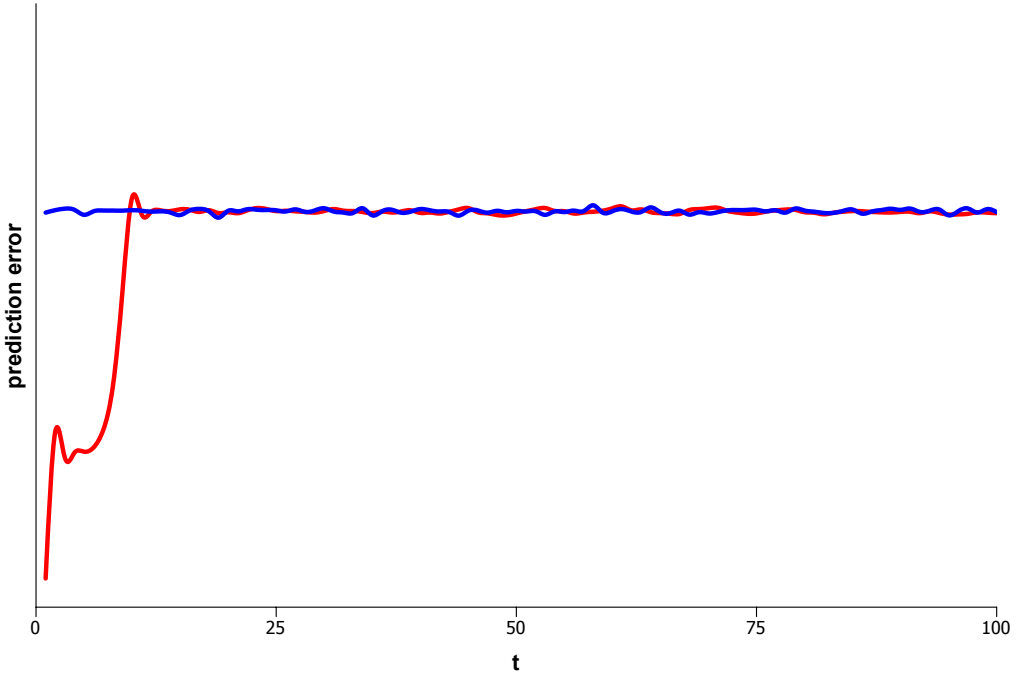


Figure B.4. – Increase in prediction error for the Logistic map.

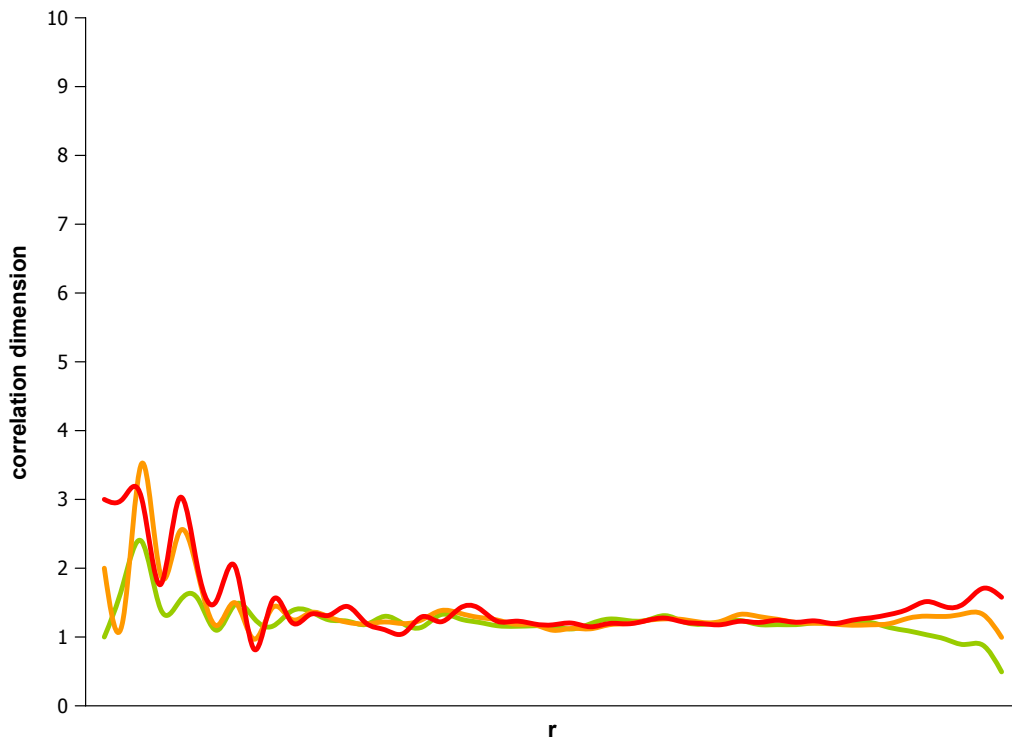


Figure B.5. – Correlation dimension of the Henon map.

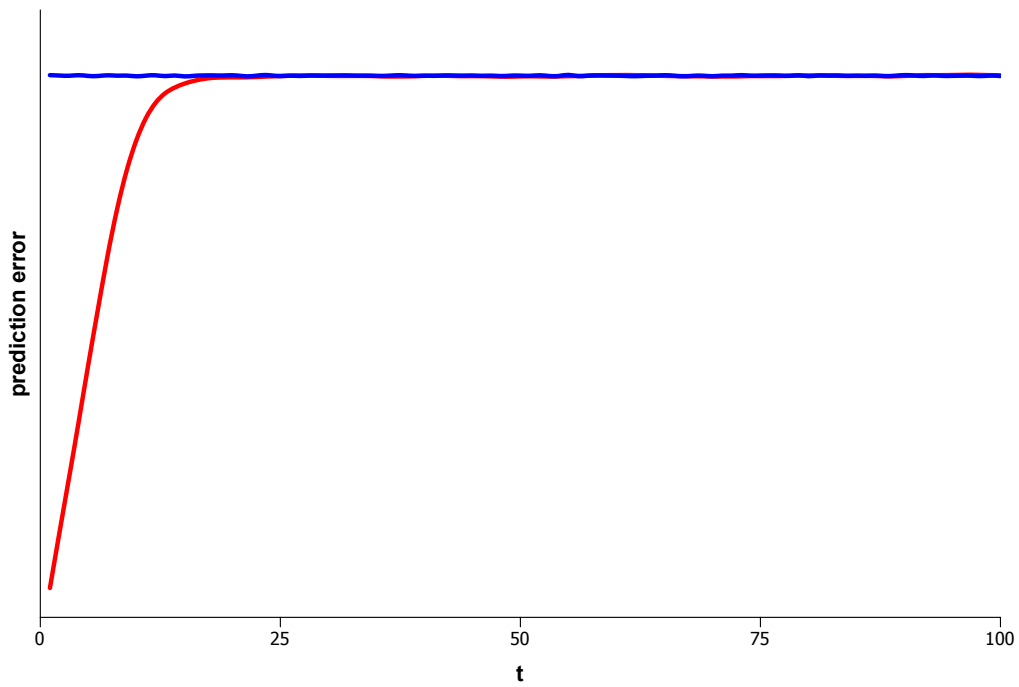


Figure B.6. – Increase in prediction error for the Henon map.

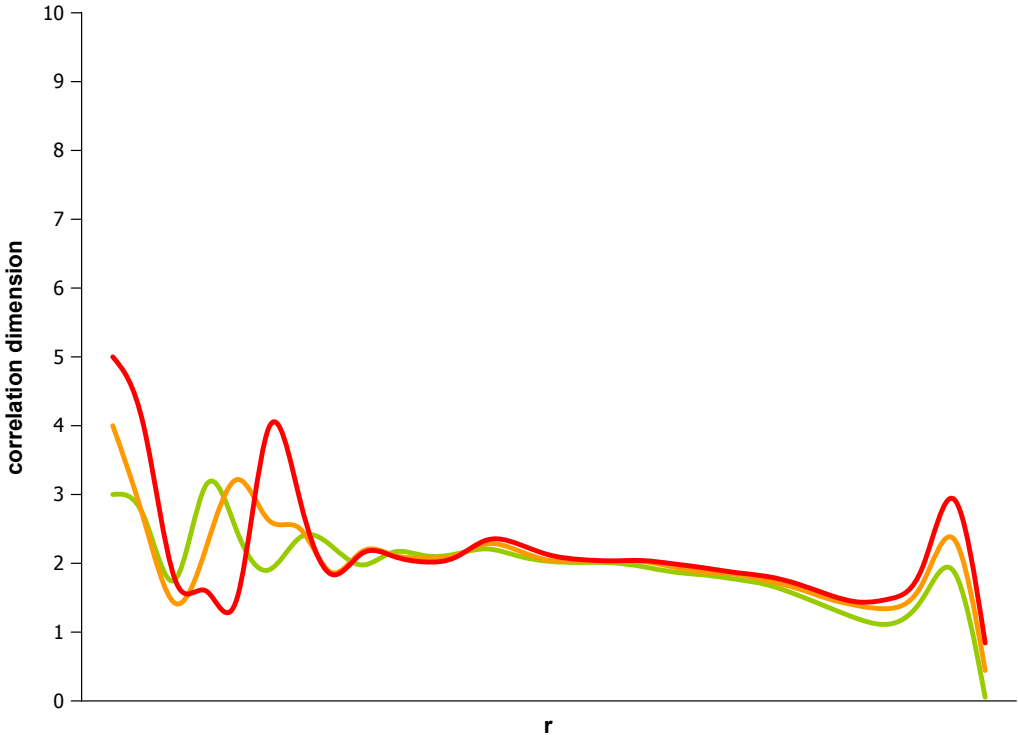


Figure B.7. – Correlation dimension of the Lorenz system.

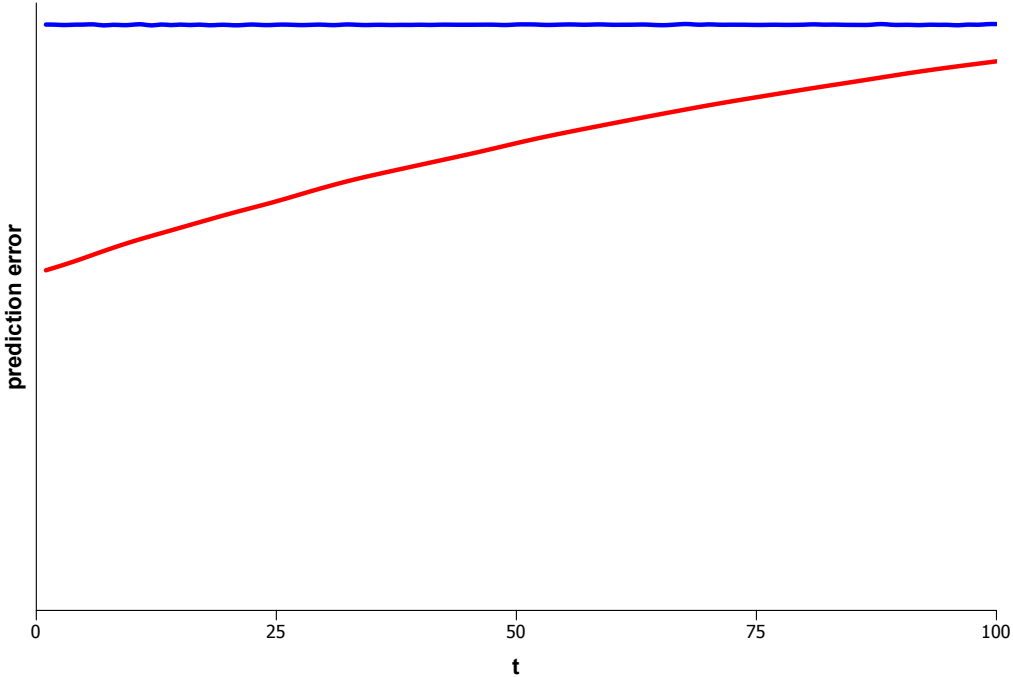


Figure B.8. – Increase in prediction error for the Lorenz system.

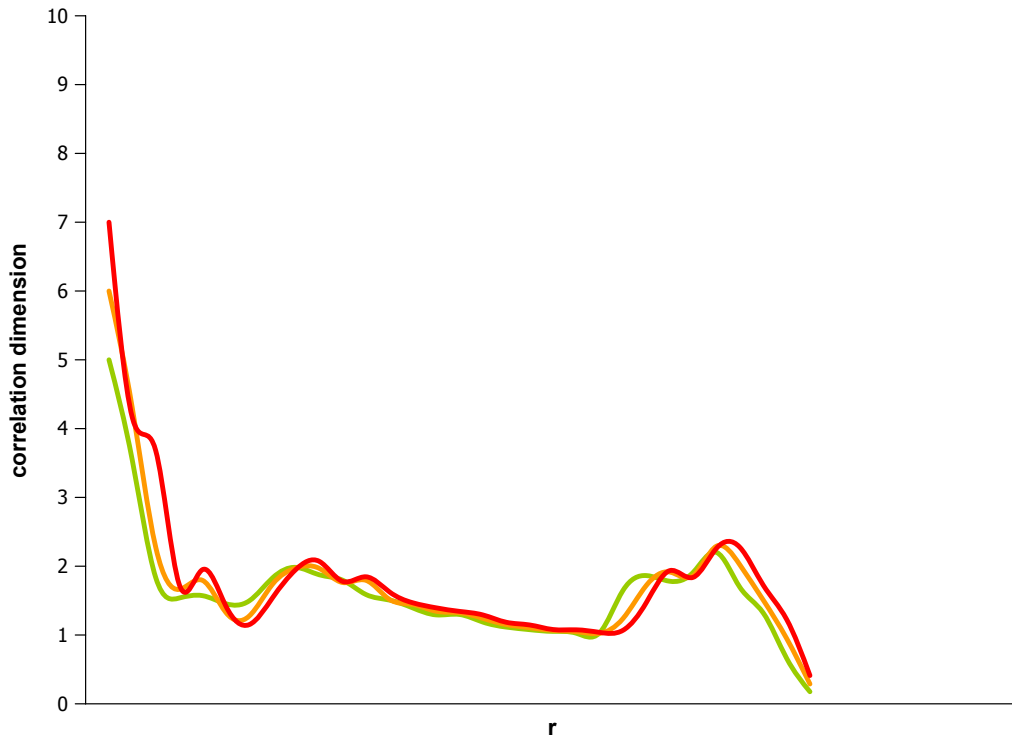


Figure B.9. – Correlation dimension of the Rössler system.

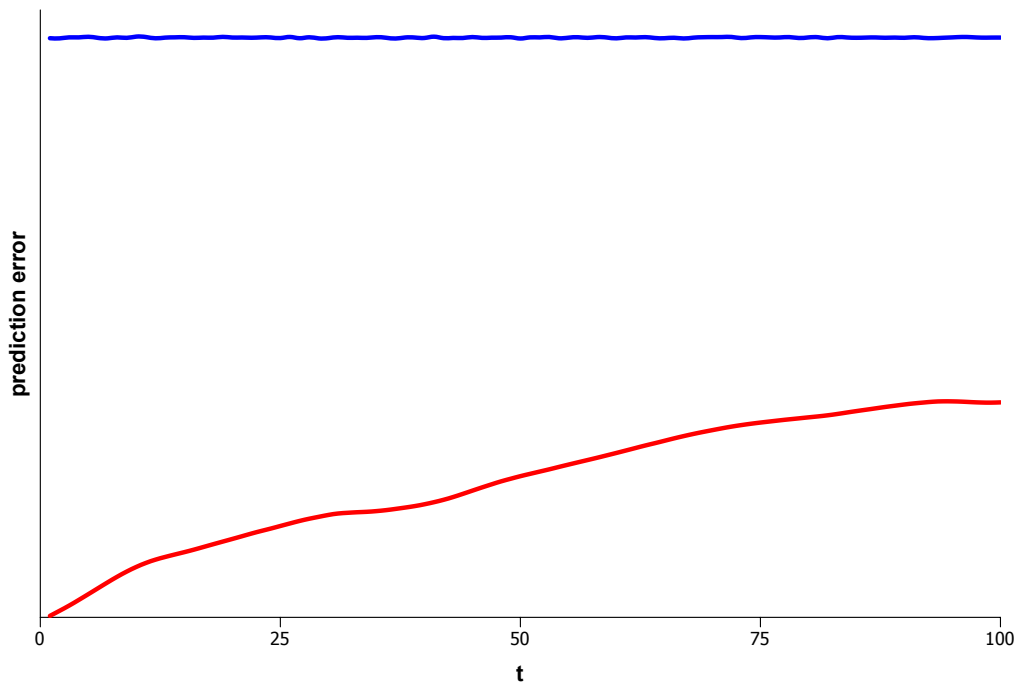


Figure B.10. – Increase in prediction error for the Rössler system.

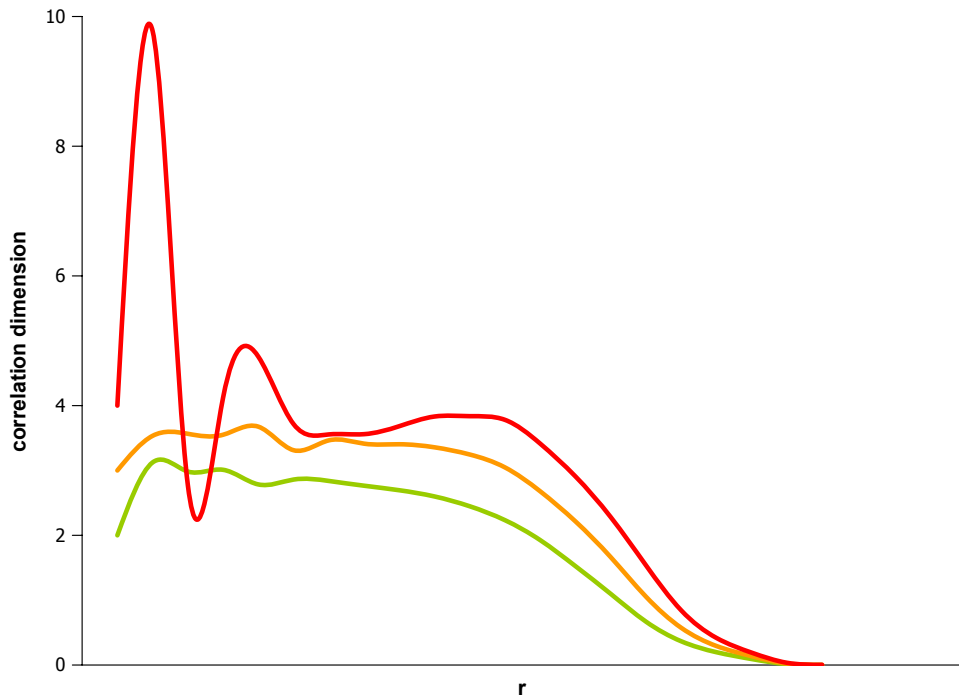
## Appendix B. Algorithms Explained

In order to show that the calculations are also valid for the experimental data, the tracks, or more specifically certain phases of the tracks of pigeons on their homing flight, I decided to include some of the samples used to estimate the correlation dimension and the largest Lyapunov exponent of the underlying navigational process. These samples are shown in Figures B.11 to B.22 - the respective values for the correlation dimension and the largest Lyapunov exponent are given in Table B.2. The samples are representative for all others and while they might not be as perfect as the examples for the known chaotic deterministic systems they prove that the approach is valid. The samples show that there are clear and well defined scaling regions for the estimation of the correlation dimension and that the behavior of the pigeon is clearly predictable.

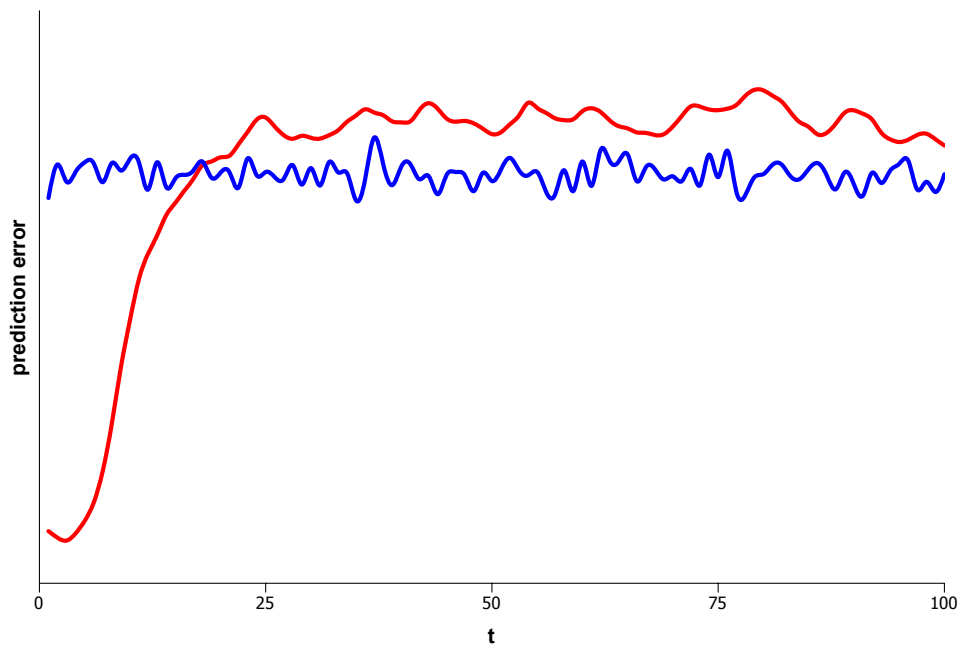
**Table B.2.** – Samples of the Correlation dimensions and largest Lyapunov exponents for the navigational process as calculated for individual pigeons.

ID	R	F. No.	P. No.	dp	$\tau$	$m$	$d_2$	$\lambda$
07-382	N30	12	6	1860	18	3	3.3	0.007
08-752	S30	4	6	2730	12	4	3.7	0.022
08-785	S30	4	6	1710	16	3	3.4	0.013
08-785	S60	1	4	2715	18	4	4.2	0.033
08-797	S60	1	2	2730	19	5	4.2	0.013
08-778	NE40	1	8	2880	10	3	3.7	0.018

The table includes the abbreviation for the release site R, the number of the flight from the respective release site F. No., the phase number P. No., the number of data points dp, the embedding lag  $\tau$  the embedding dimension  $m$  the calculated values for the largest Lyapunov exponent  $\lambda$  and the correlation dimension  $d_2$ .



**Figure B.11.** – Correlation dimension of the navigational process of pigeon 07-382 on its 12th flight from N30.



**Figure B.12.** – Increase in prediction error in the navigational process of pigeon 07-382 on its 12th flight from N30.

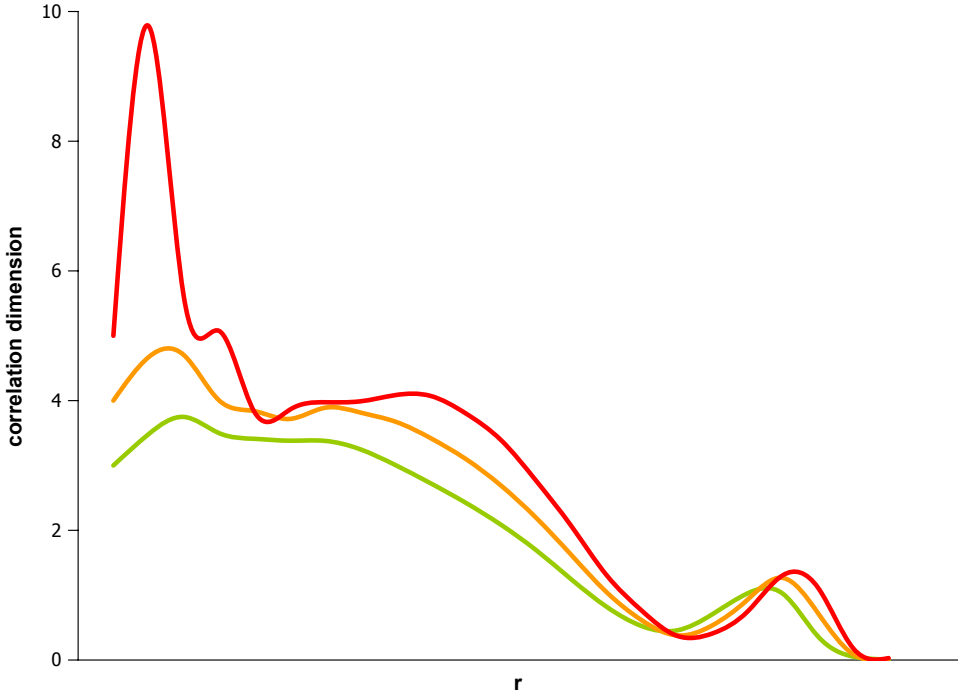


Figure B.13. – Correlation dimension of the navigational process of pigeon 08-752 on its 4th flight from S30.

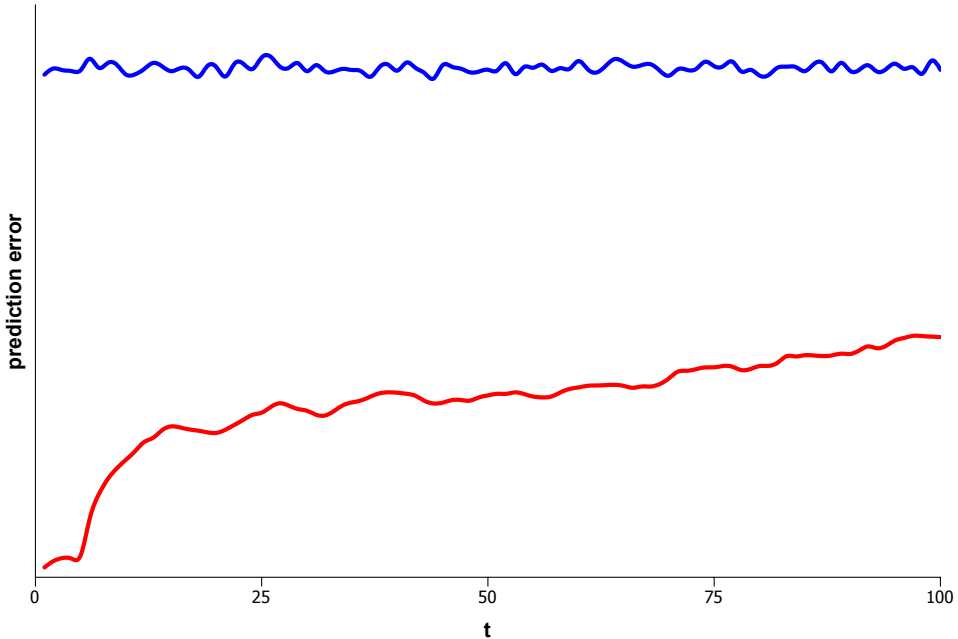
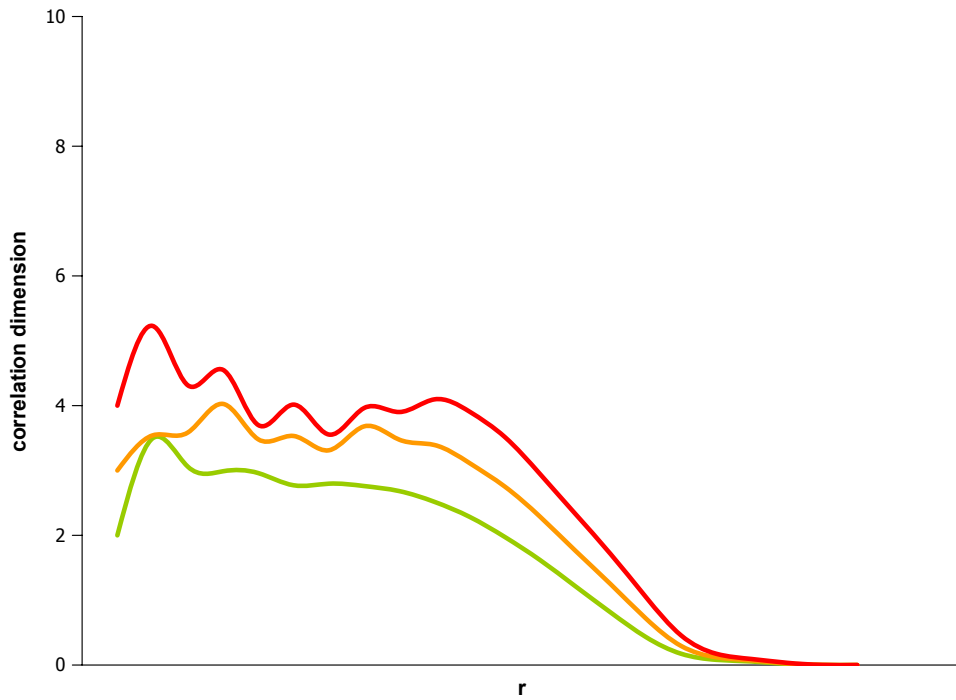
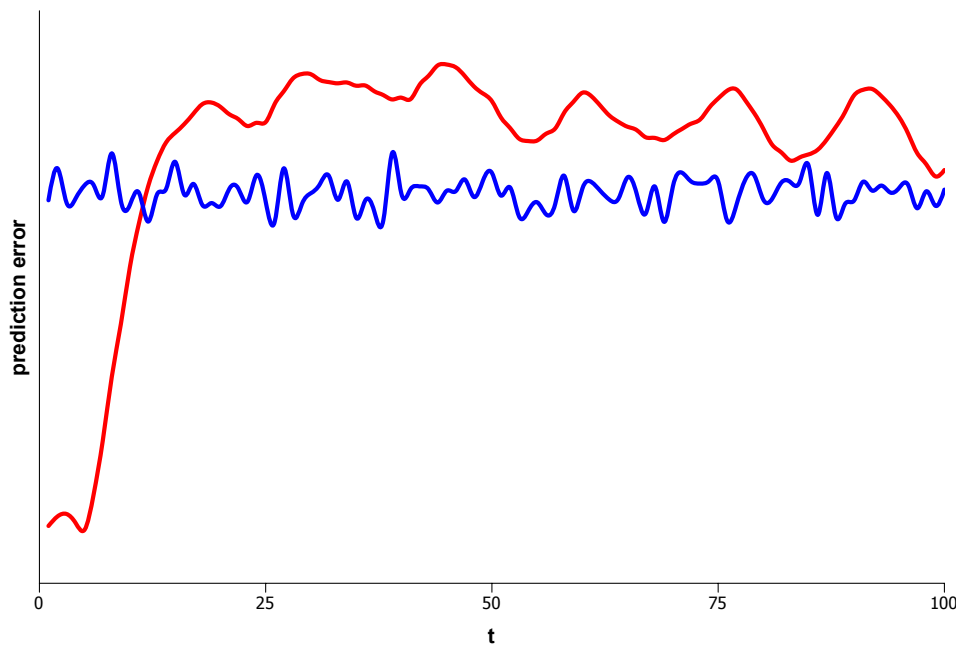


Figure B.14. – Increase in prediction error in the navigational process of pigeon 08-752 on its 4th flight from S30.





**Figure B.15.** – Correlation dimension of the navigational process of pigeon 08-785 on its 4th flight from S30.



**Figure B.16.** – Increase in prediction error in the navigational process of pigeon 08-785 on its 4th flight from S30.

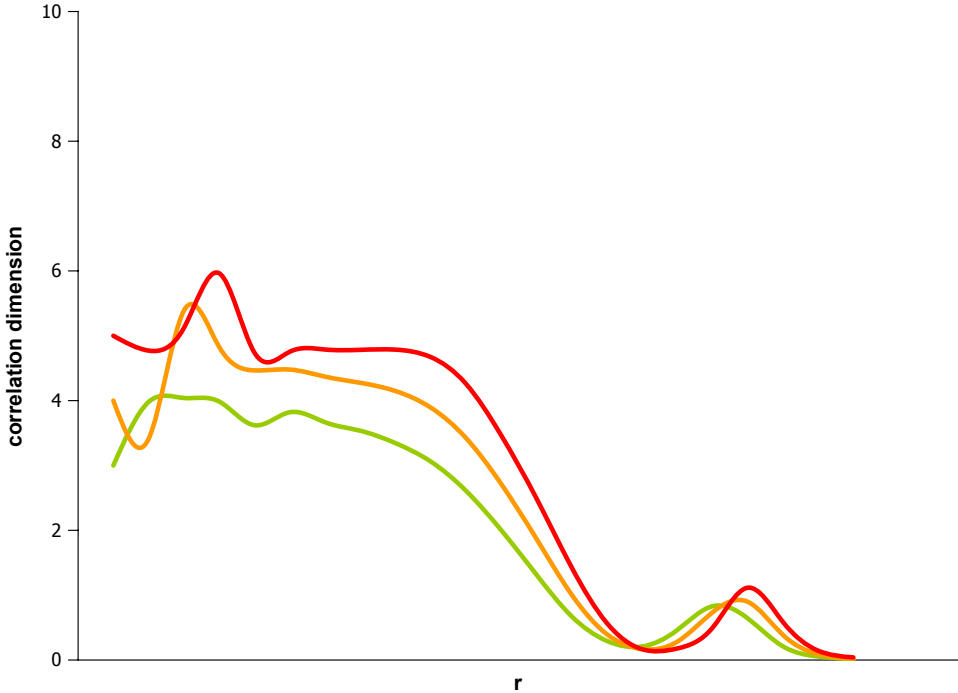


Figure B.17. – Correlation dimension of the navigational process of pigeon 08-785 on its flight from S60.

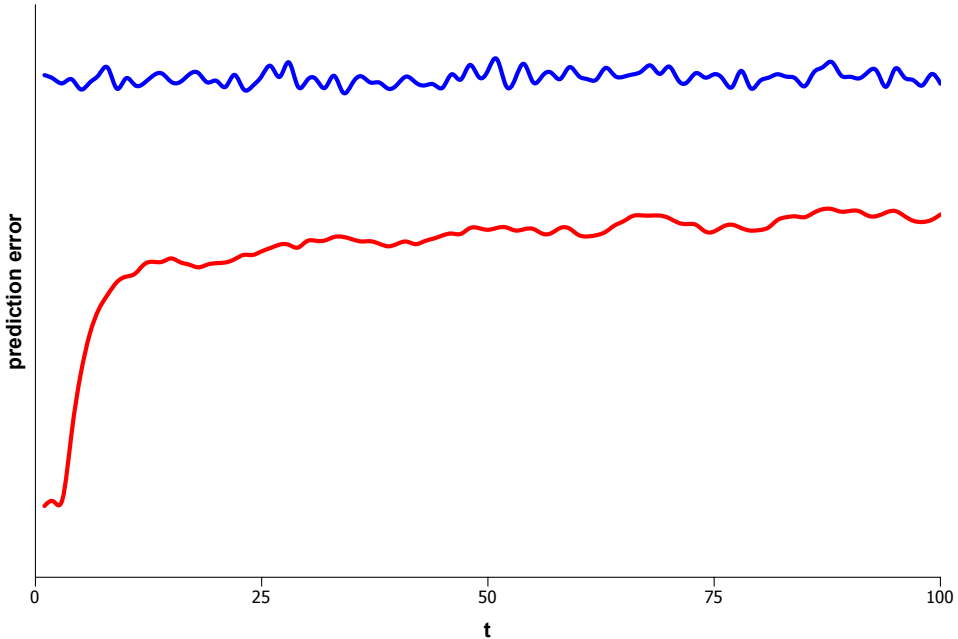
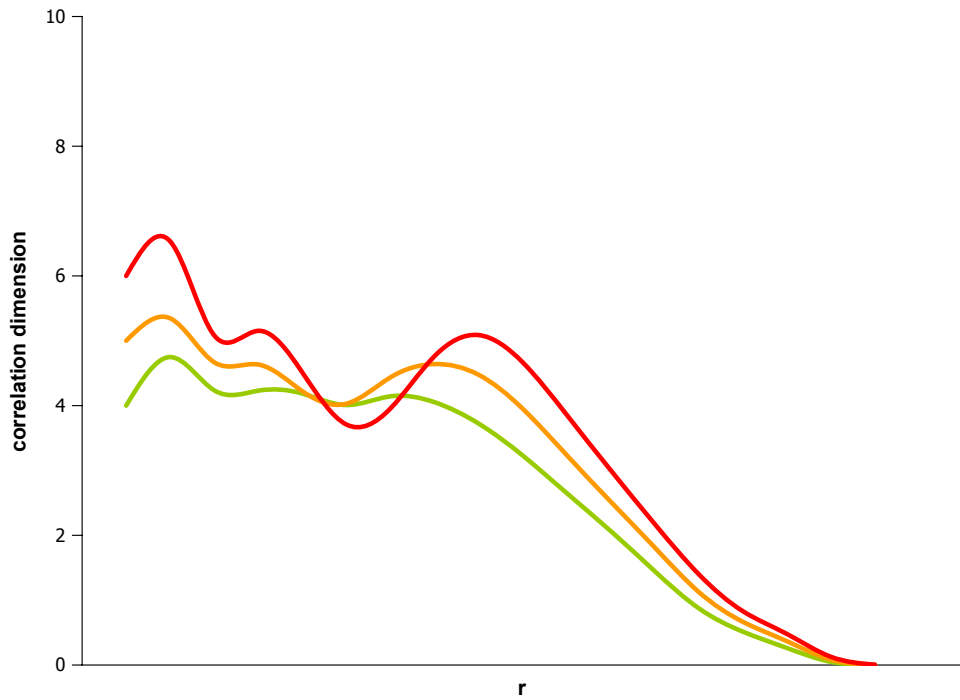
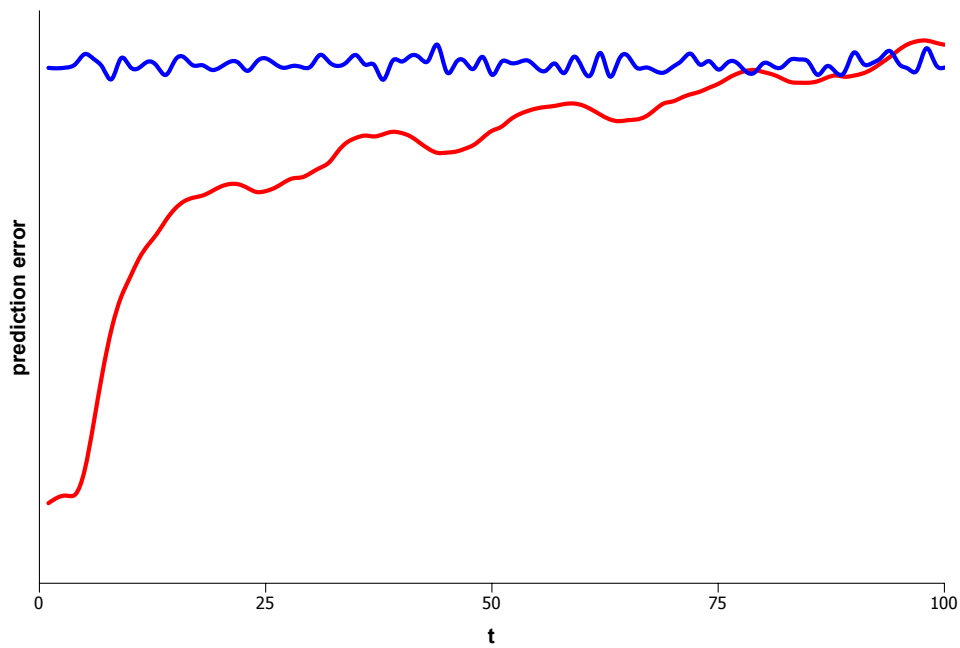


Figure B.18. – Increase in prediction error in the navigational process of pigeon 08-785 on its flight from S60.



**Figure B.19.** – Correlation dimension of the navigational process of pigeon 08-797 on its flight from S60.



**Figure B.20.** – Increase in prediction error in the navigational process of pigeon 08-797 on its flight from S60.

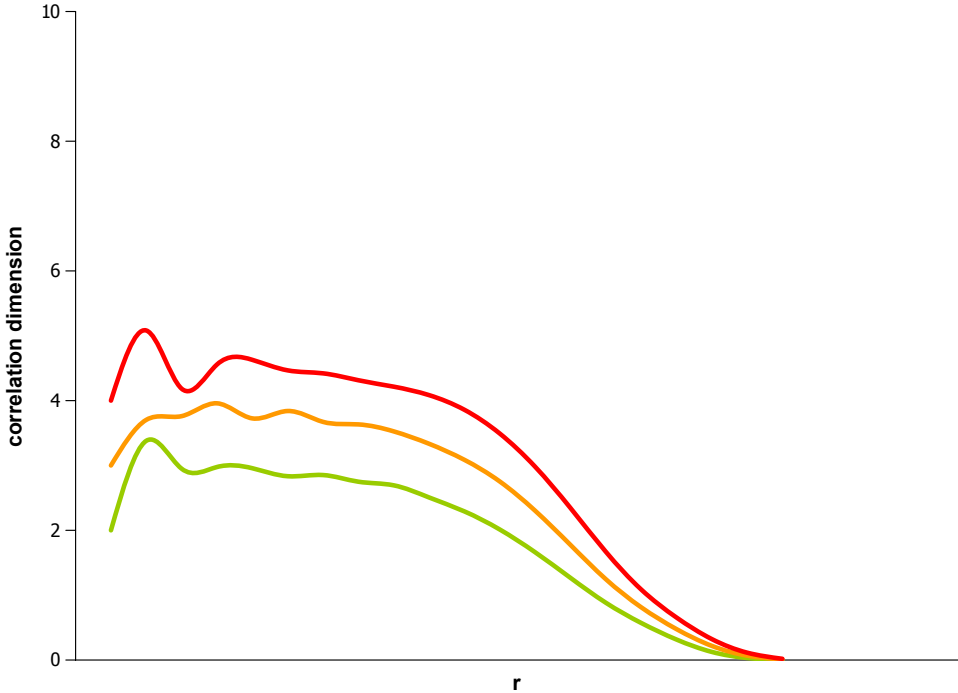


Figure B.21. – Correlation dimension of the navigational process of pigeon 08-778 on its flight from NE40.

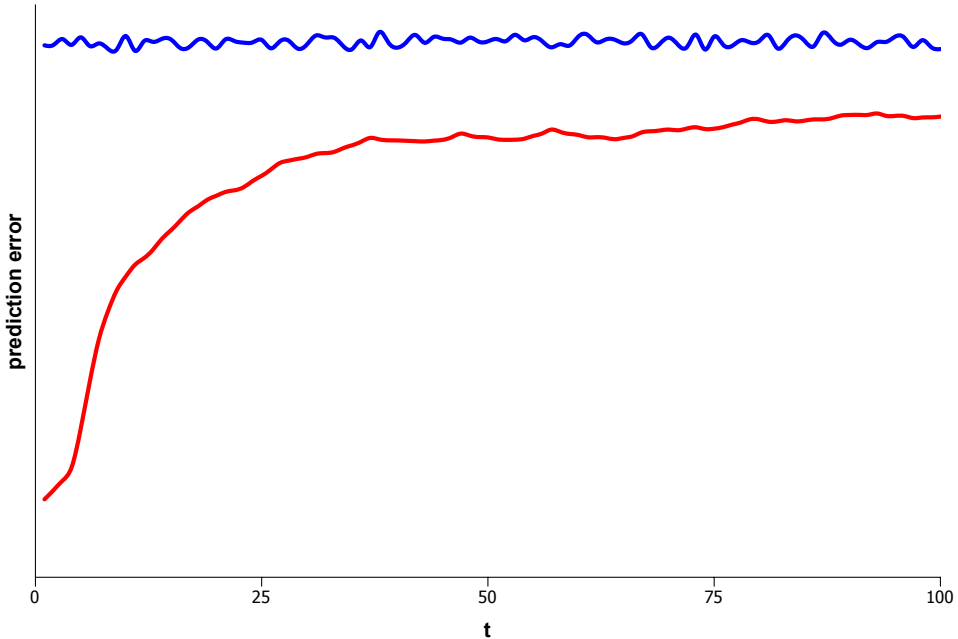
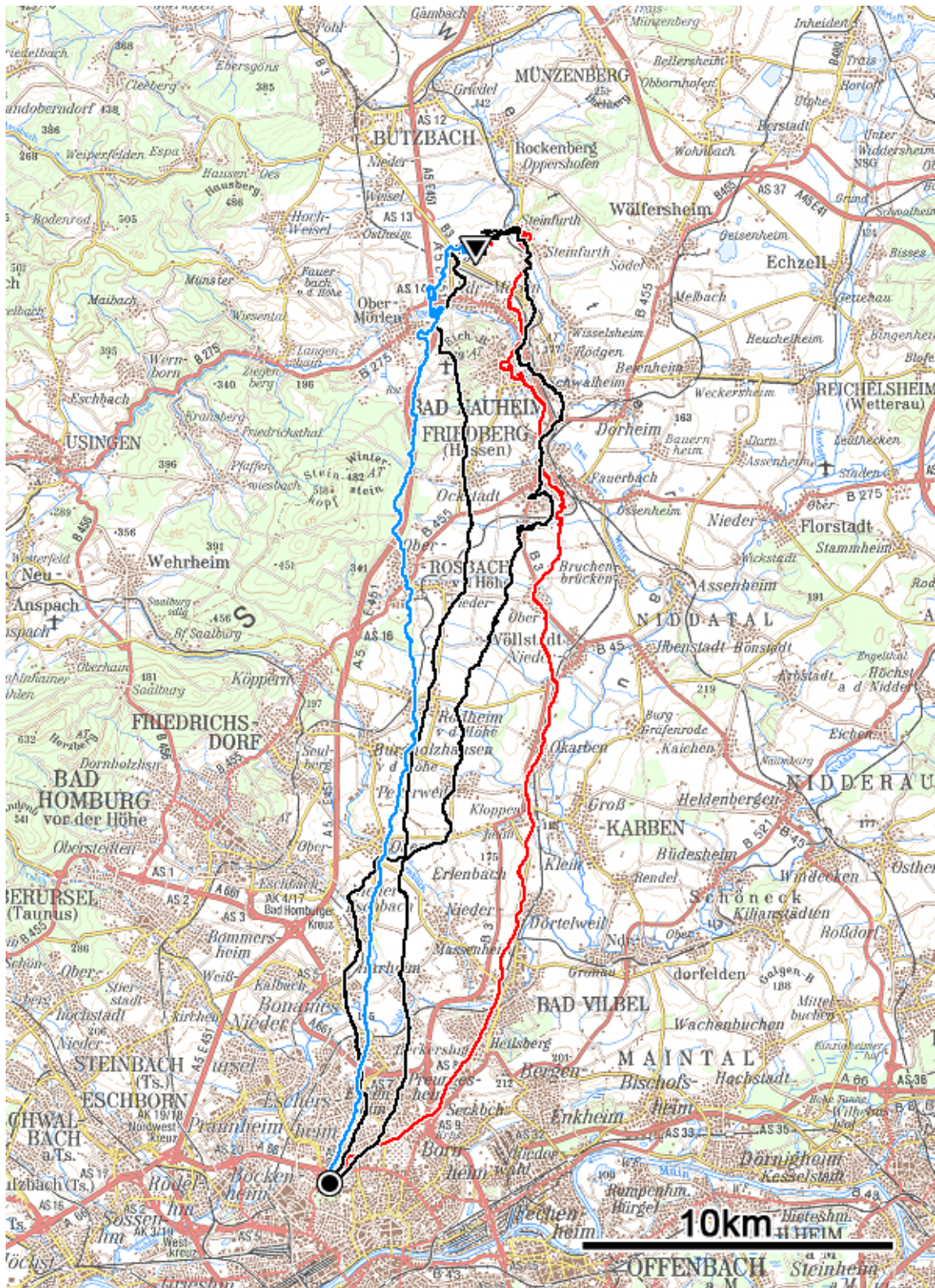


Figure B.22. – Increase in prediction error in the navigational process of pigeon 08-778 on its flight from NE40.

# Appendix C.

## Tracks of Individuals

The following appendix contains the flights of individual pigeons released at sites S30 and N30 plotted on ordnance survey maps. Only those individuals are shown, where at least two tracks from the same site were recorded. Additionally only those tracks are considered that cover a distance equivalent to at least 50% of the distance release site - home. The flights from the sites N60 and S60 are also included if available. The first recorded track is shown in red and the last recorded track in blue, all tracks in between are shown in black.



**Figure C.1.** – All flights (colored lines) of pigeon 07-351 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.





Figure C.2. – All flights (colored lines) of pigeon 07-357 from release sites N30 (black triangle) and N60 (black square) to its home loft (black circle). For color reference see text.



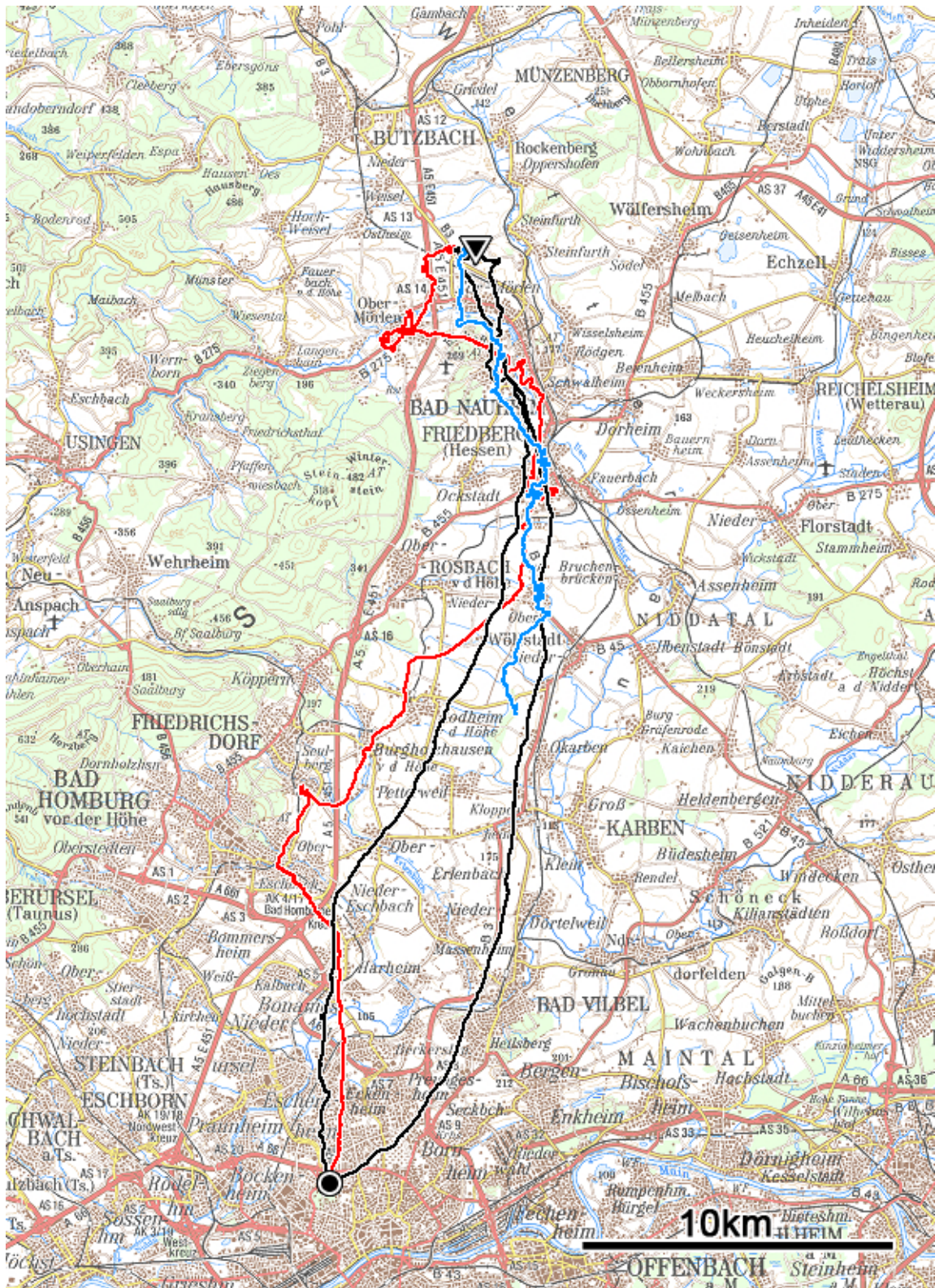


Figure C.3. – All flights (colored lines) of pigeon 07-364 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.





Figure C.4. – All flights (colored lines) of pigeon 07-366 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



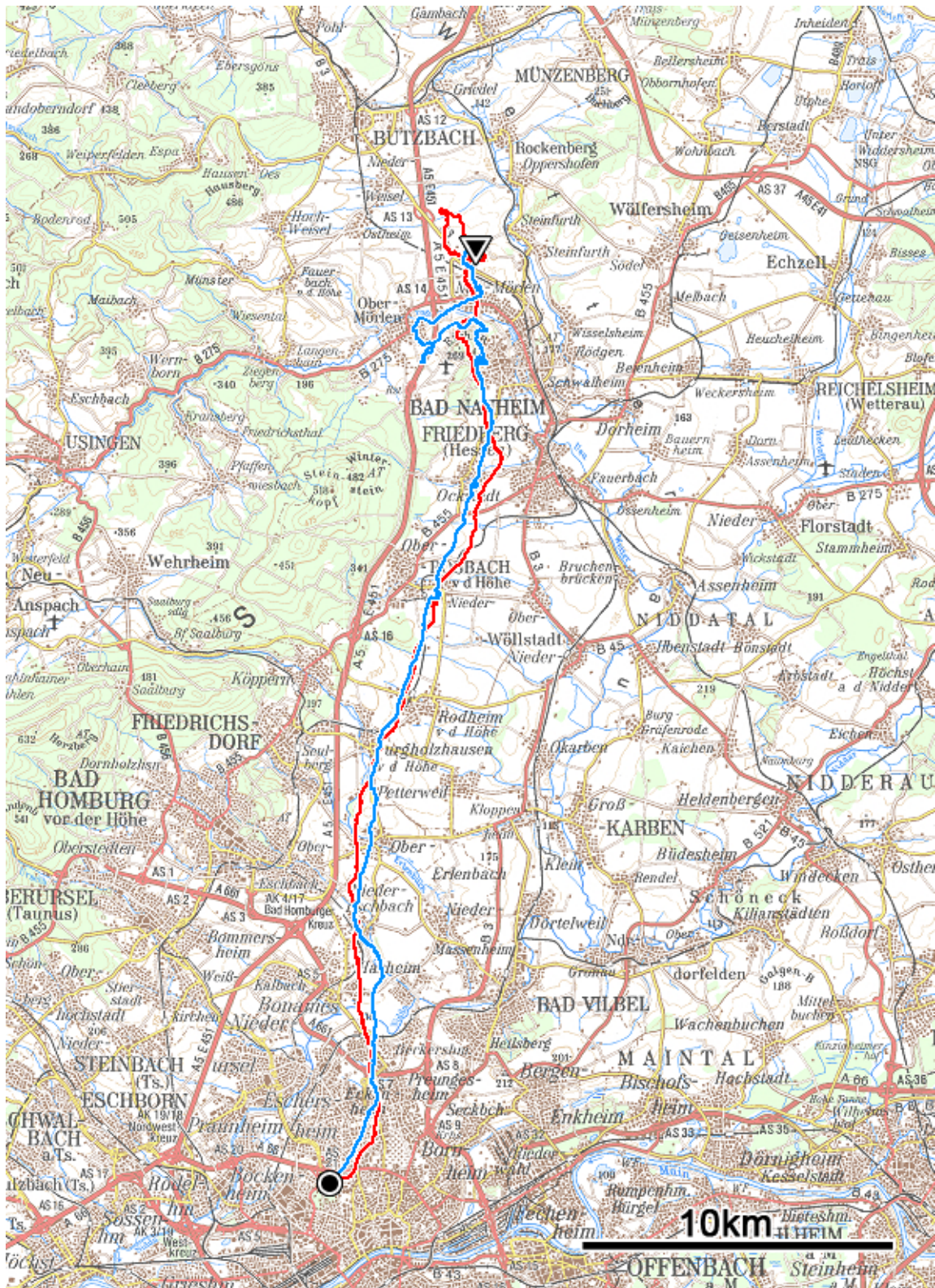


Figure C.5. – All flights (colored lines) of pigeon 07-367 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



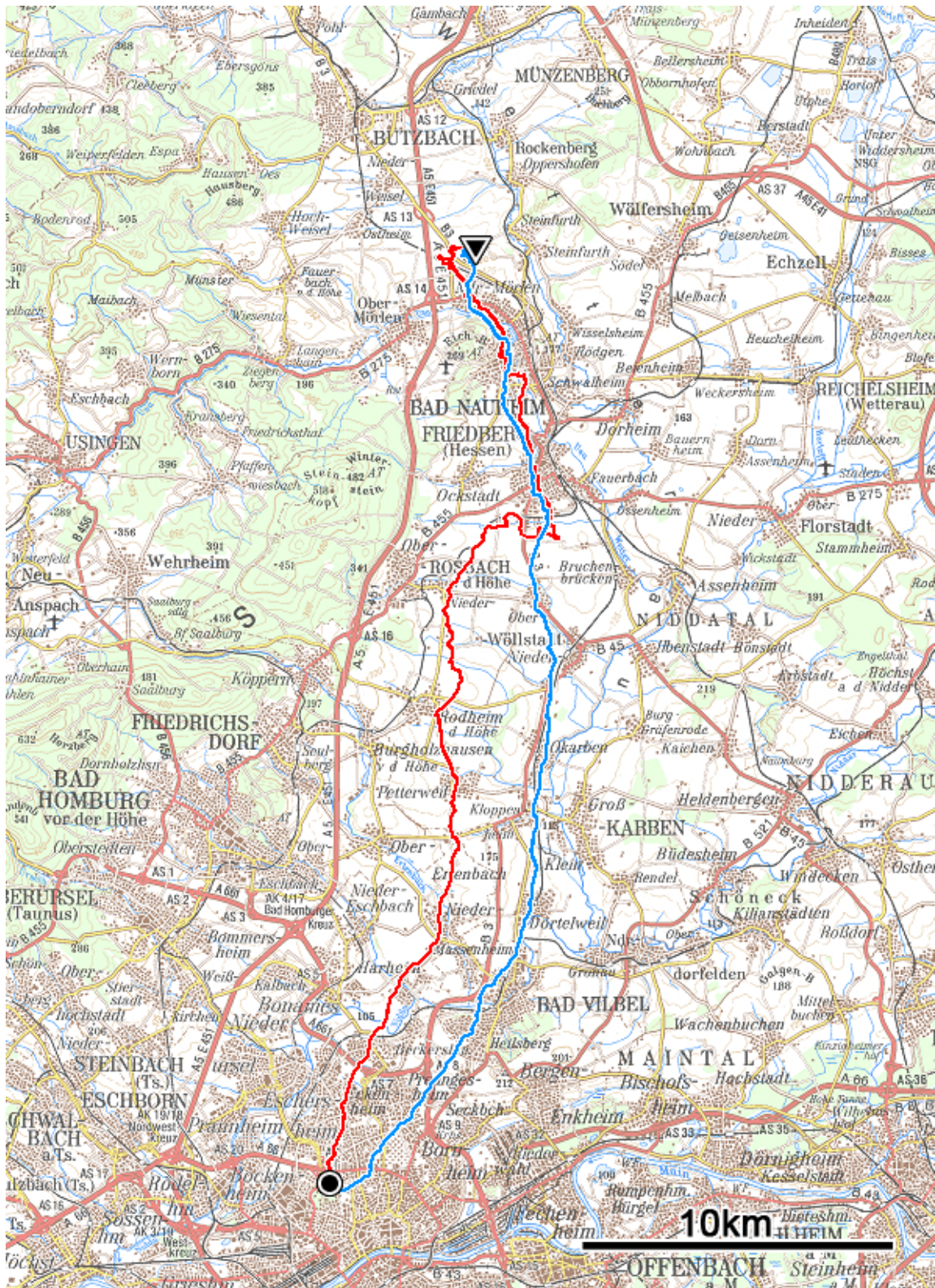


Figure C.6. – All flights (colored lines) of pigeon 07-371 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



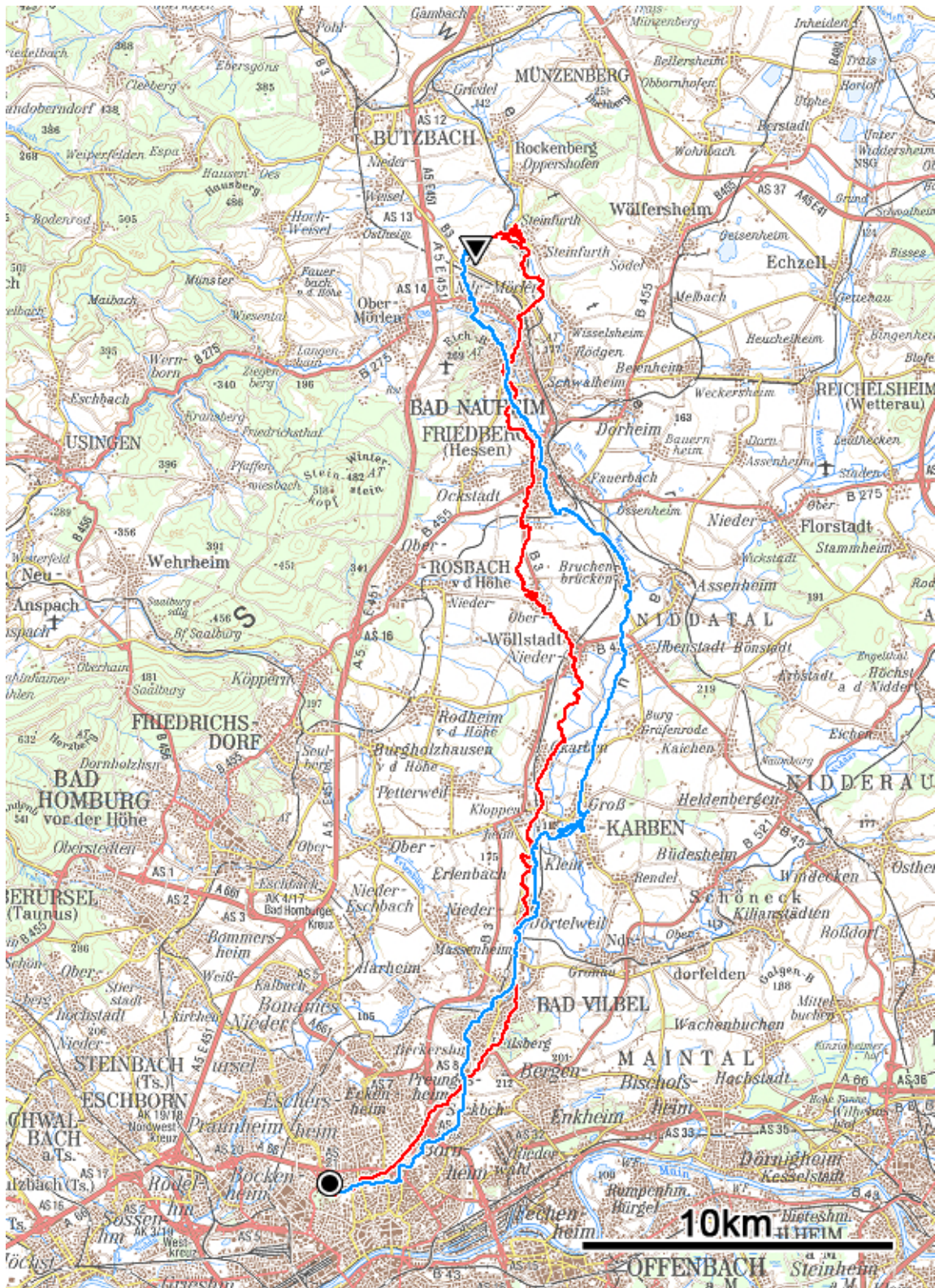


Figure C.7. – All flights (colored lines) of pigeon 07-375 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



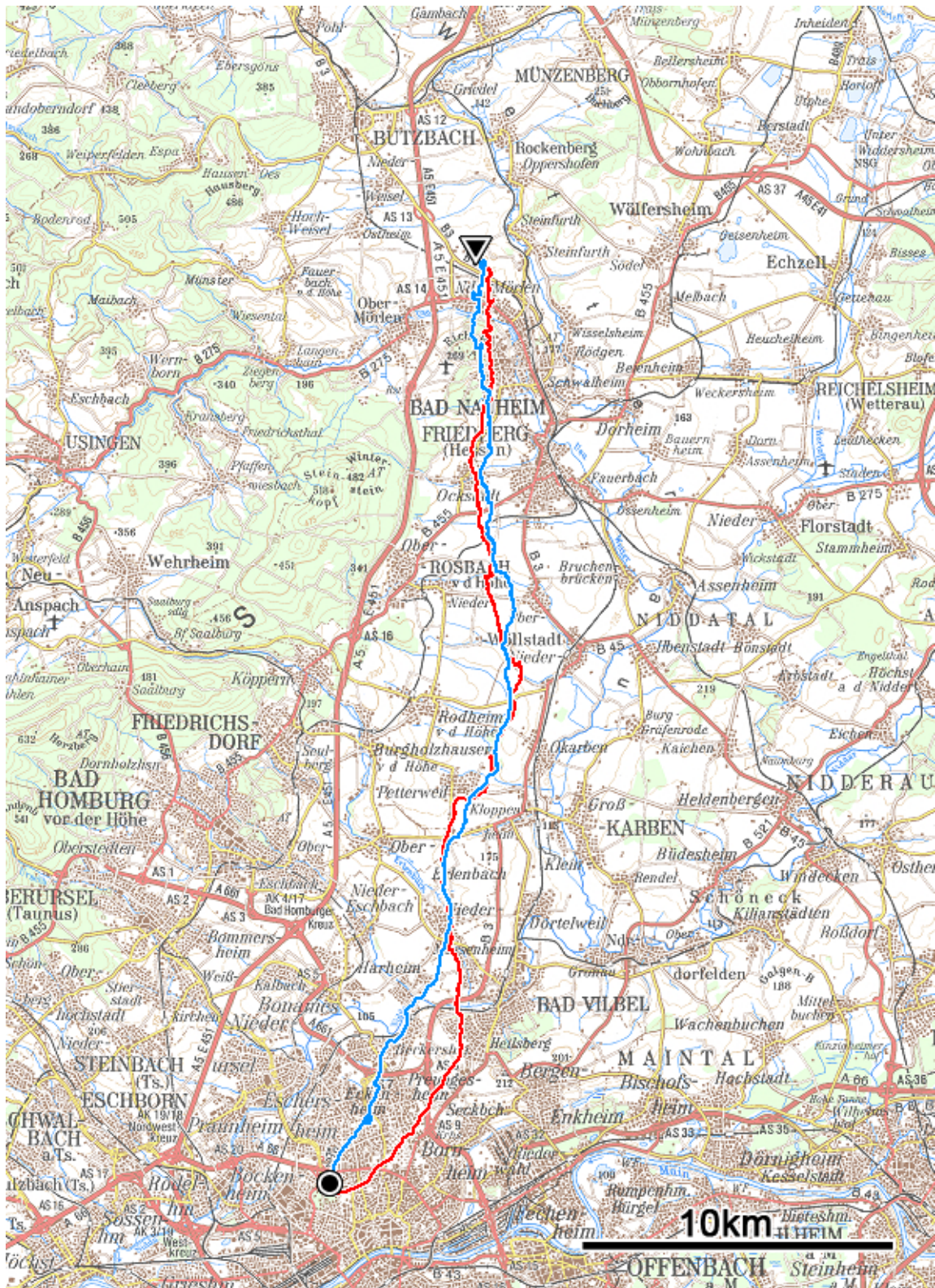


Figure C.8. – All flights (colored lines) of pigeon 07-377 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



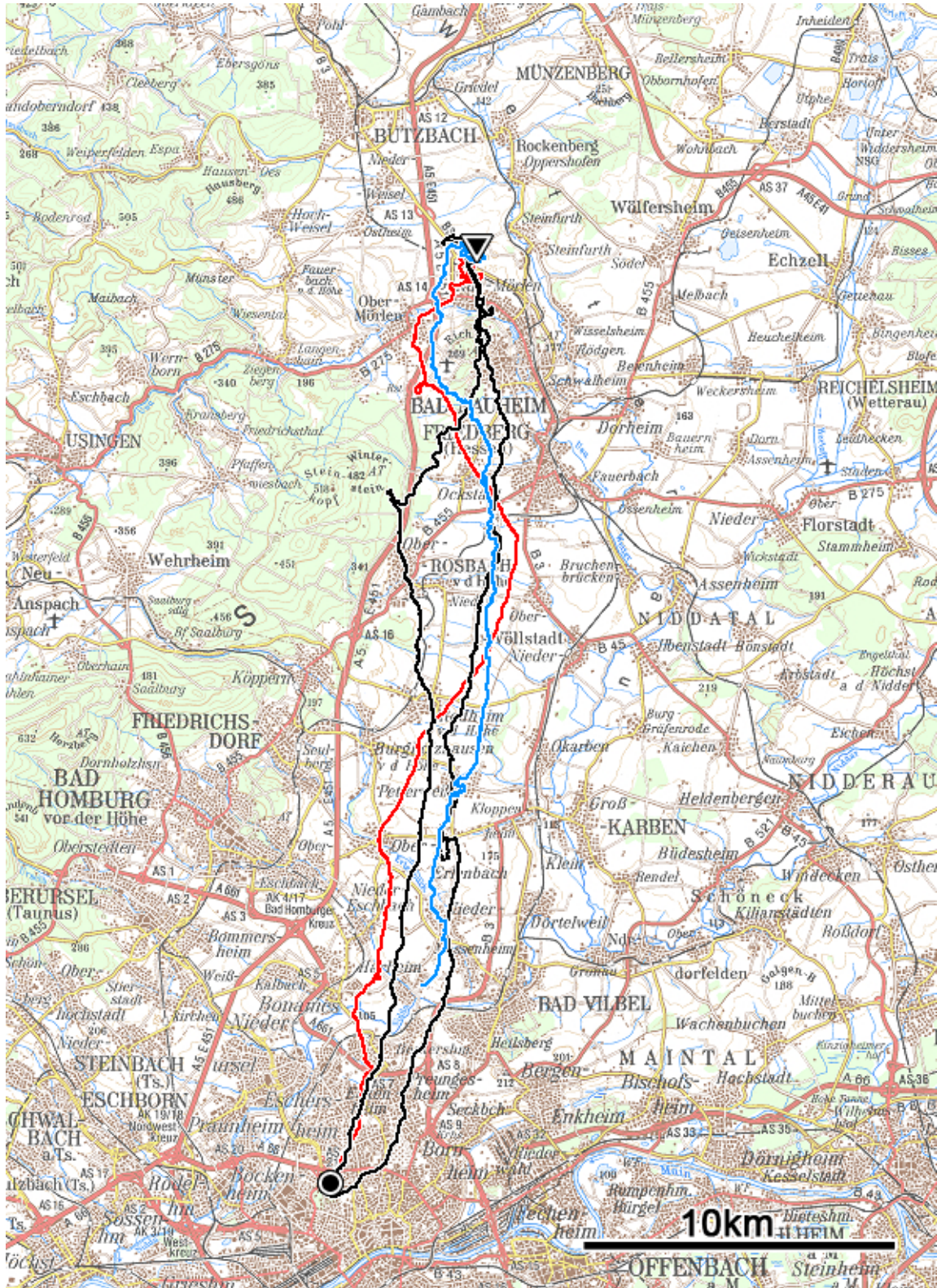


Figure C.9. – All flights (colored lines) of pigeon 07-379 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



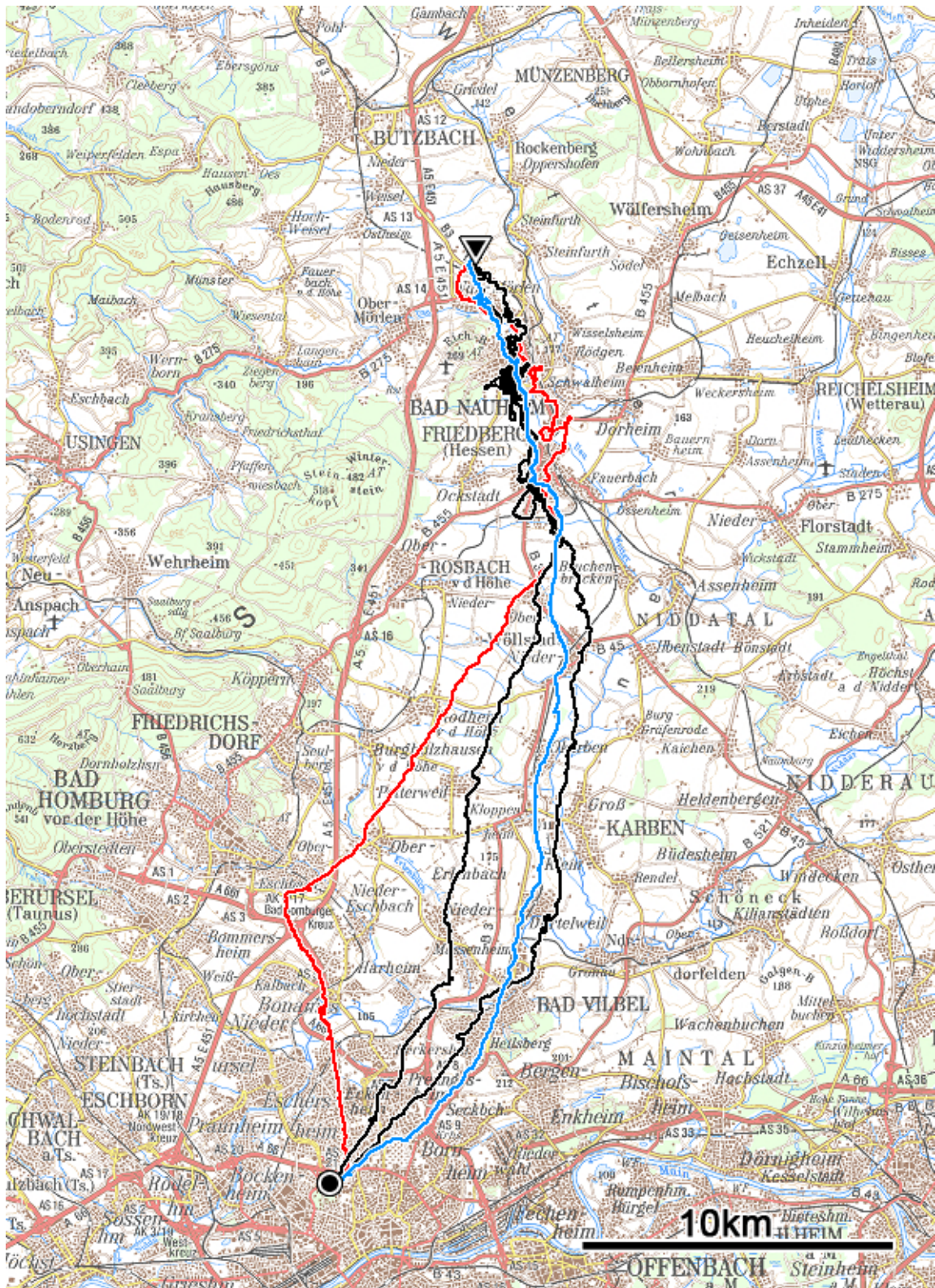


Figure C.10. – All flights (colored lines) of pigeon 07-382 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



Appendix C. Tracks of Individuals

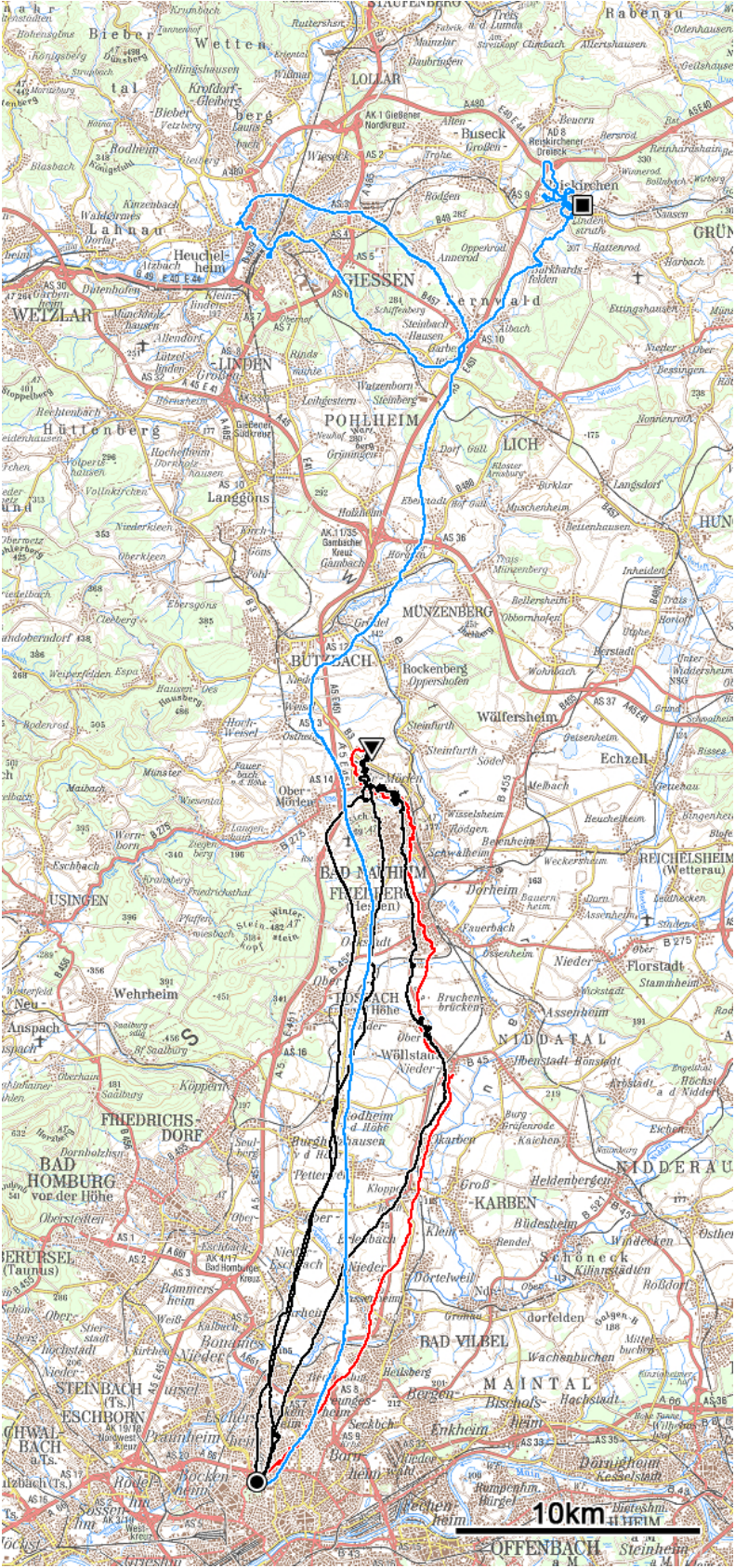


Figure C.11. – All flights (colored lines) of pigeon 07-386 from release sites N30 (black triangle) and N60 (black square) to its home loft (black circle). For color reference see text.



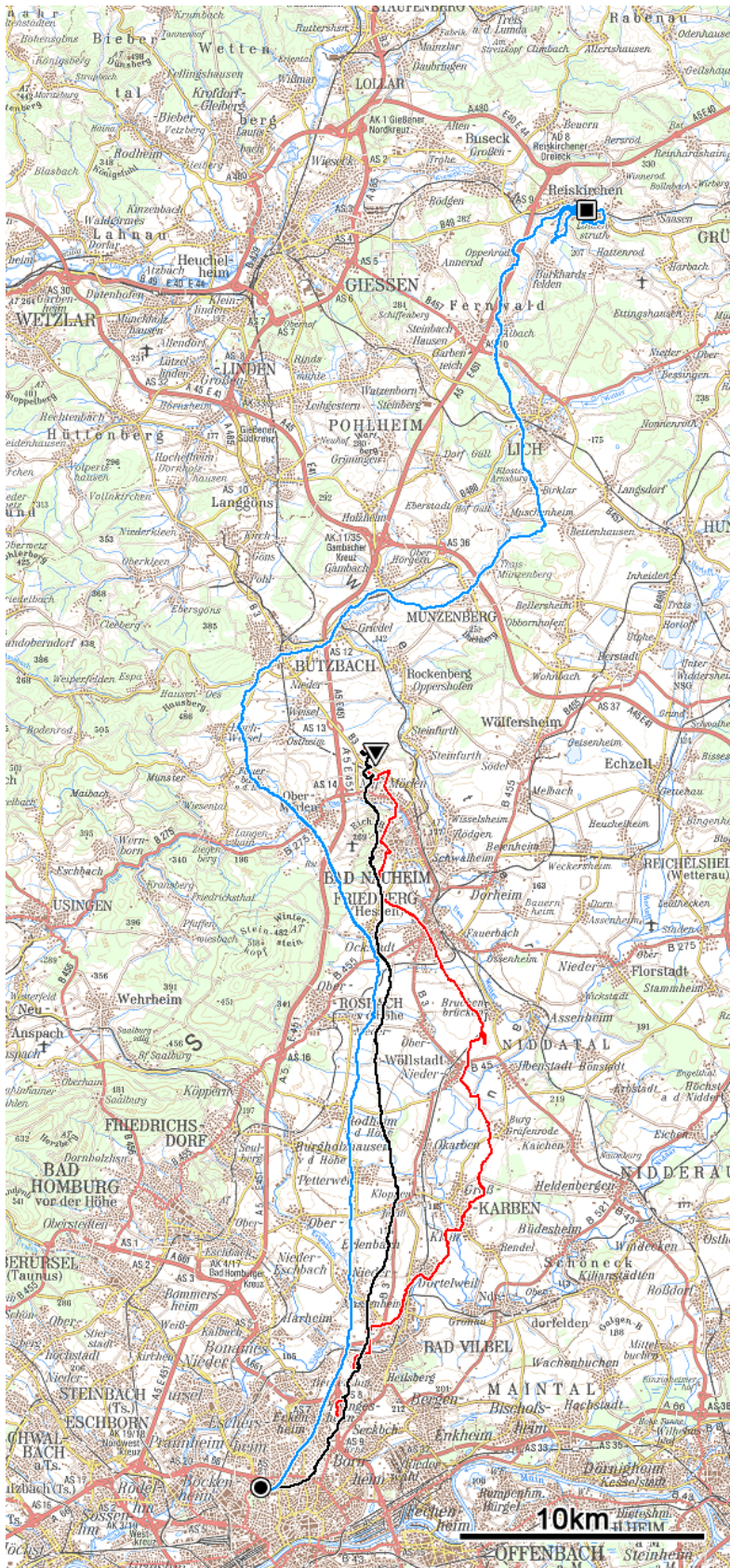


Figure C.12. – All flights (colored lines) of pigeon 07-387 from release sites N30 (black triangle) and N60 (black square) to its home loft (black circle). For color reference see text.



Appendix C. Tracks of Individuals

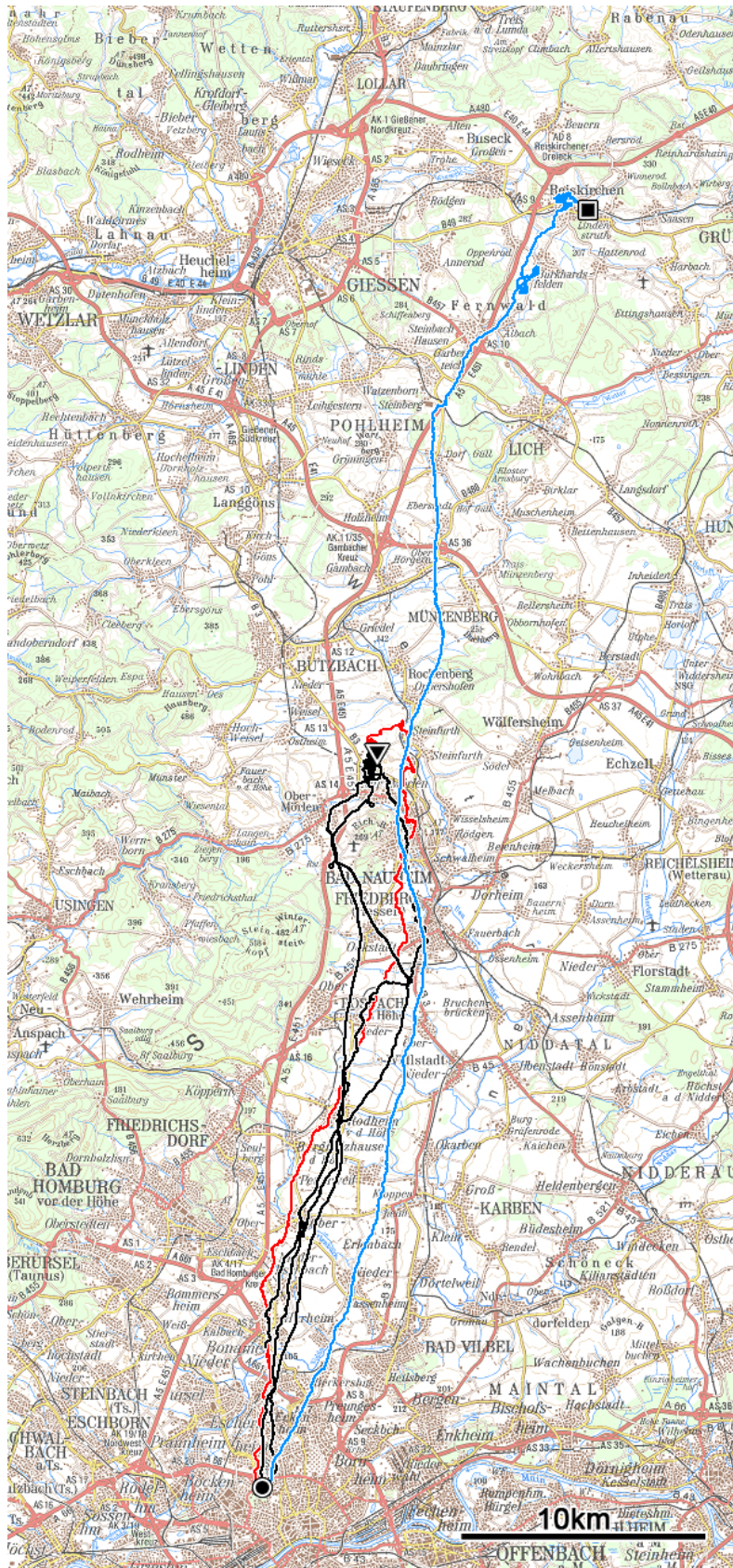


Figure C.13. – All flights (colored lines) of pigeon 07-389 from release sites N30 (black triangle) and N60 (black square) to its home loft (black circle). For color reference see text.





Figure C.14. – All flights (colored lines) of pigeon 07-392 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



Appendix C. Tracks of Individuals

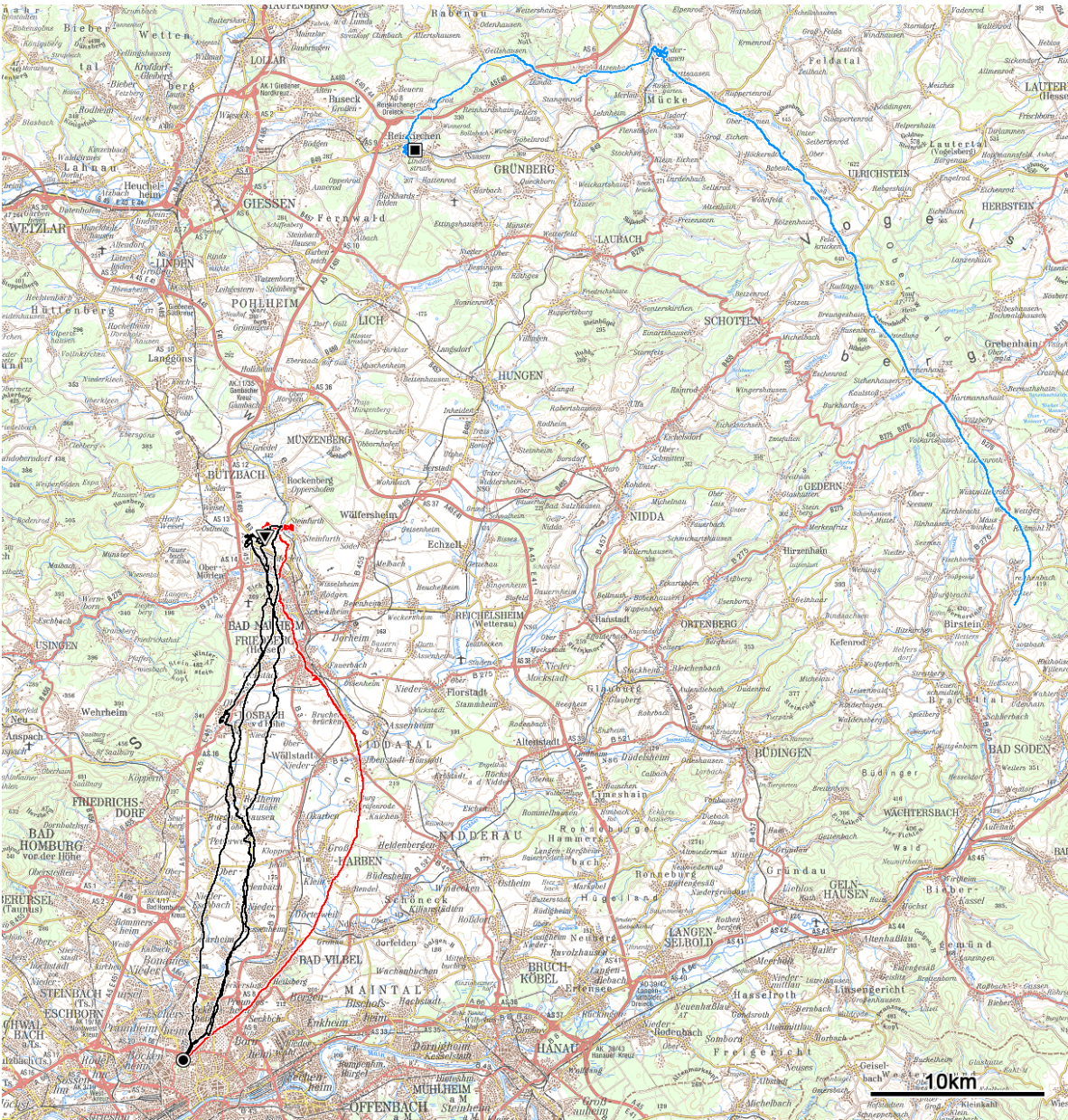


Figure C.15. – All flights (colored lines) of pigeon 07-393 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



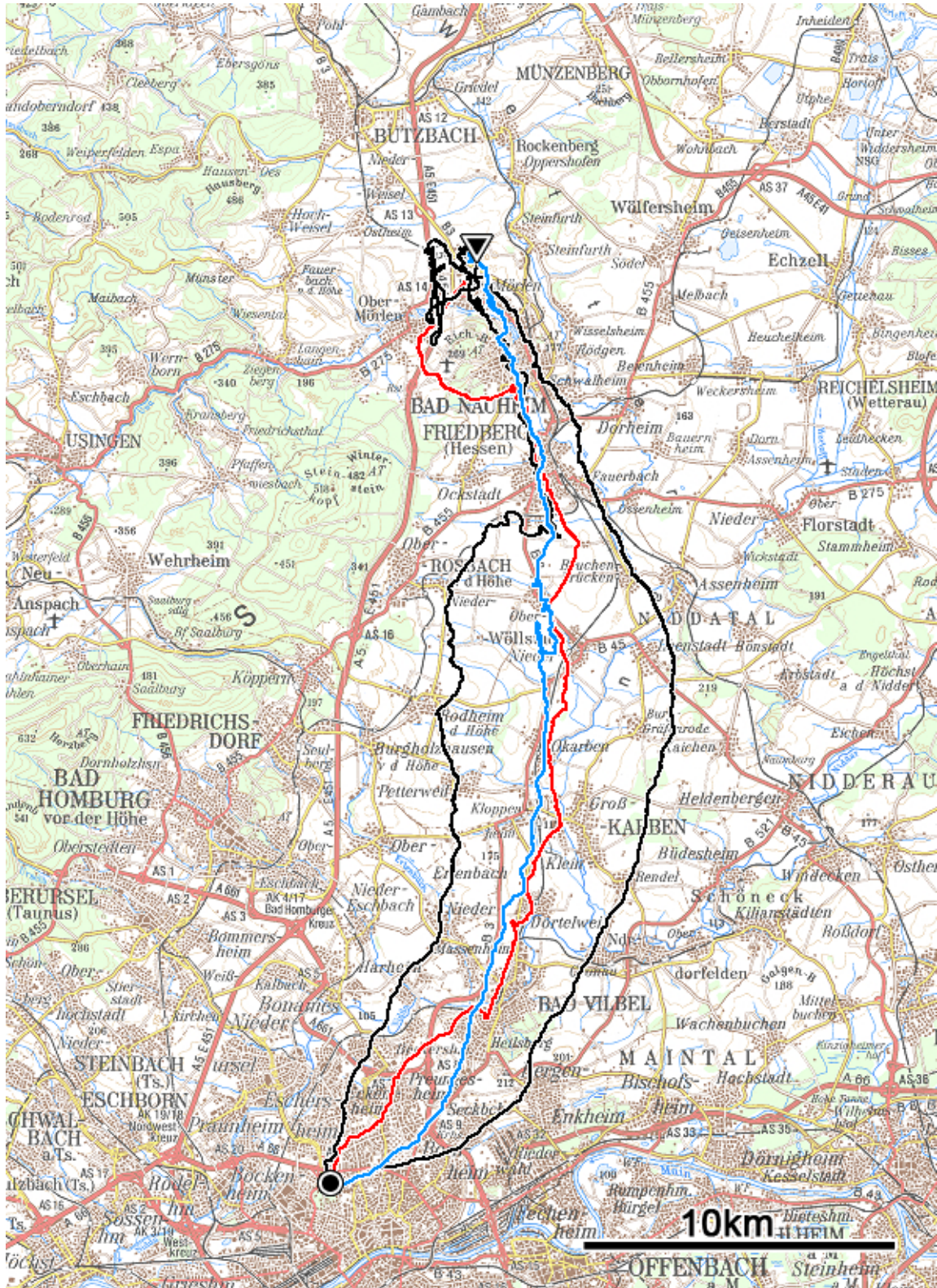


Figure C.16. – All flights (colored lines) of pigeon 07-399 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



Appendix C. Tracks of Individuals



Figure C.17. – All flights (colored lines) of pigeon 07-402 from release sites N30 (black triangle) and N60 (black square) to its home loft (black circle). For color reference see text.



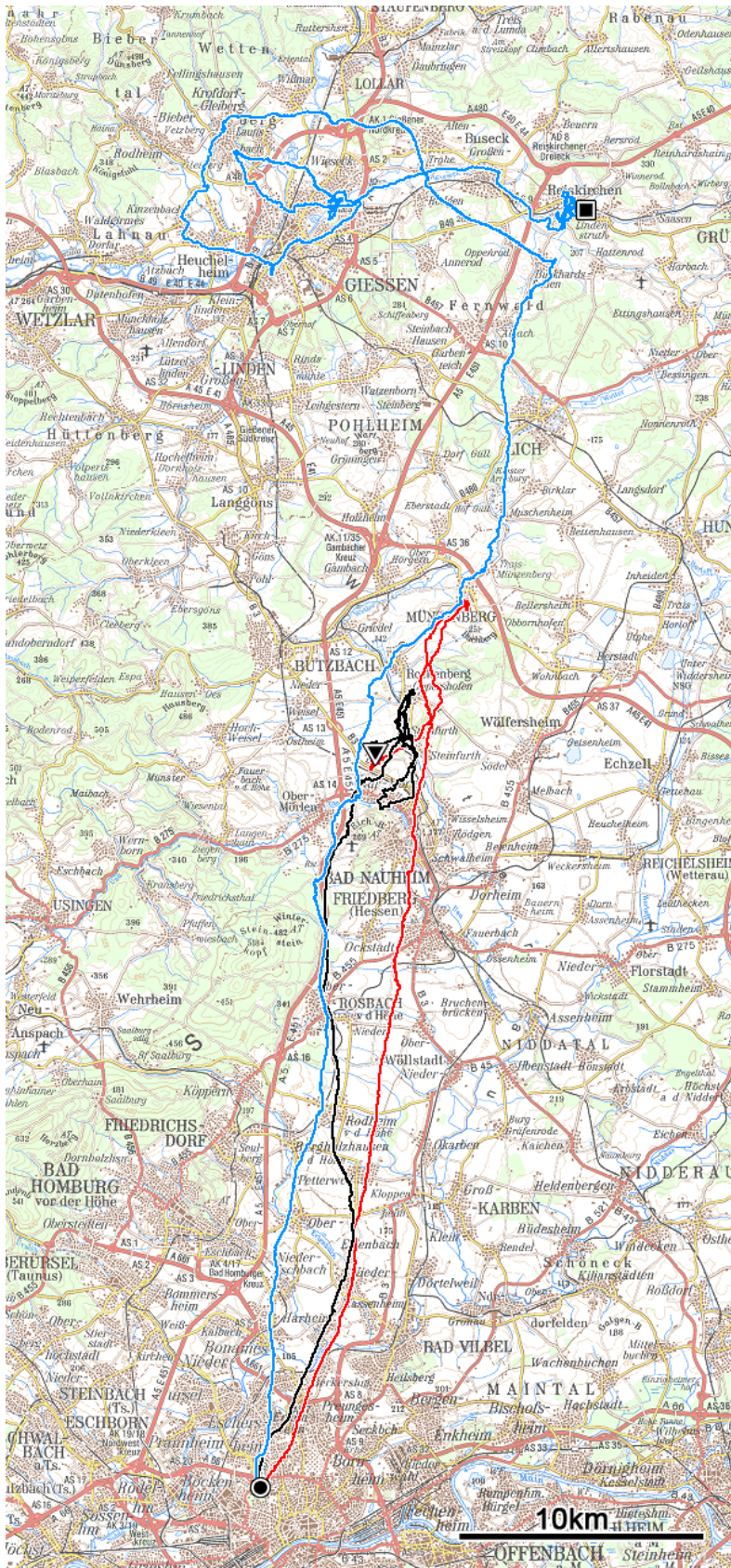


Figure C.18. – All flights (colored lines) of pigeon 07-405 from release sites N30 (black triangle) and N60 (black square) to its home loft (black circle). For color reference see text.



Appendix C. Tracks of Individuals

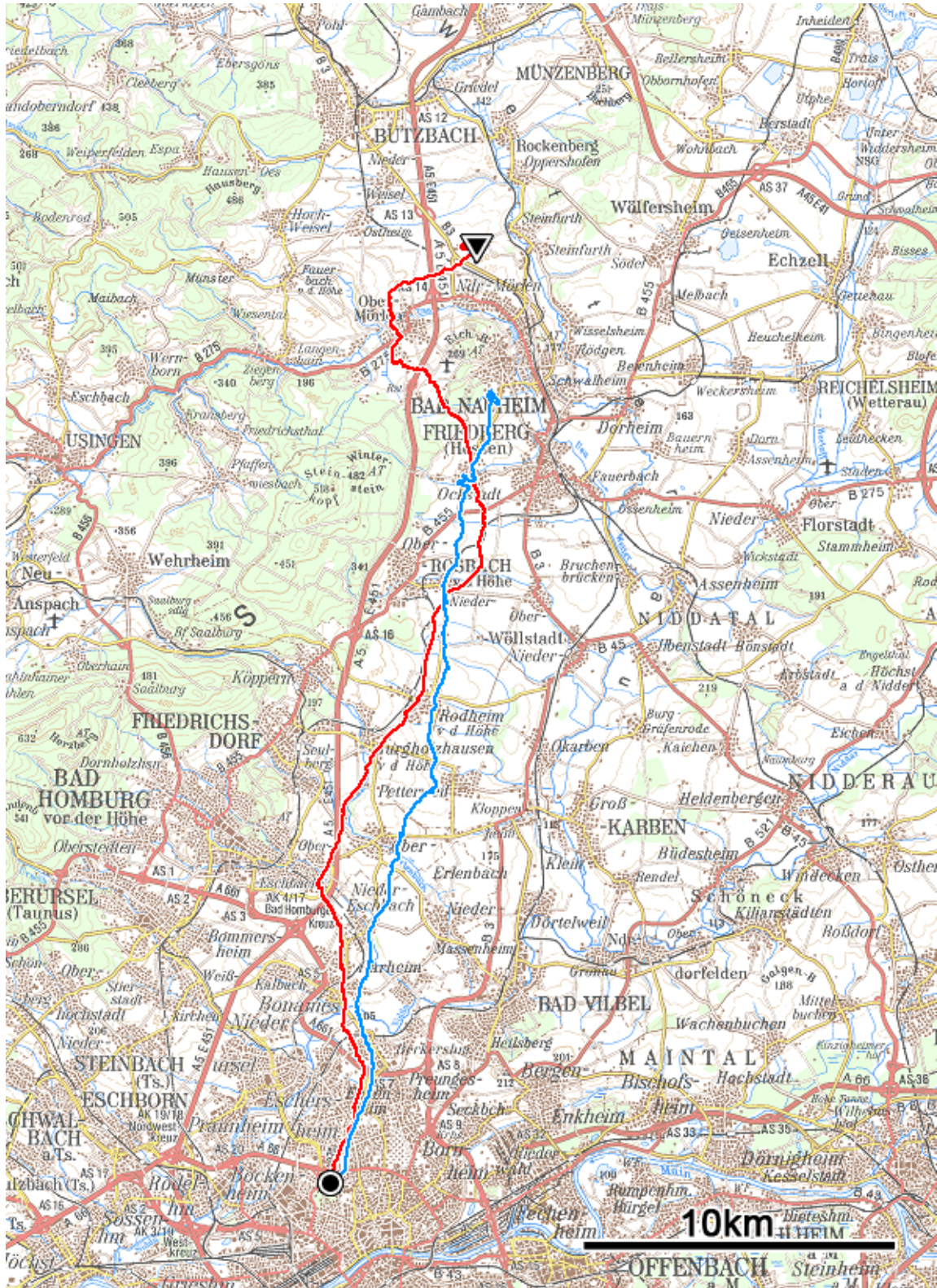


Figure C.19. – All flights (colored lines) of pigeon 07-407 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.



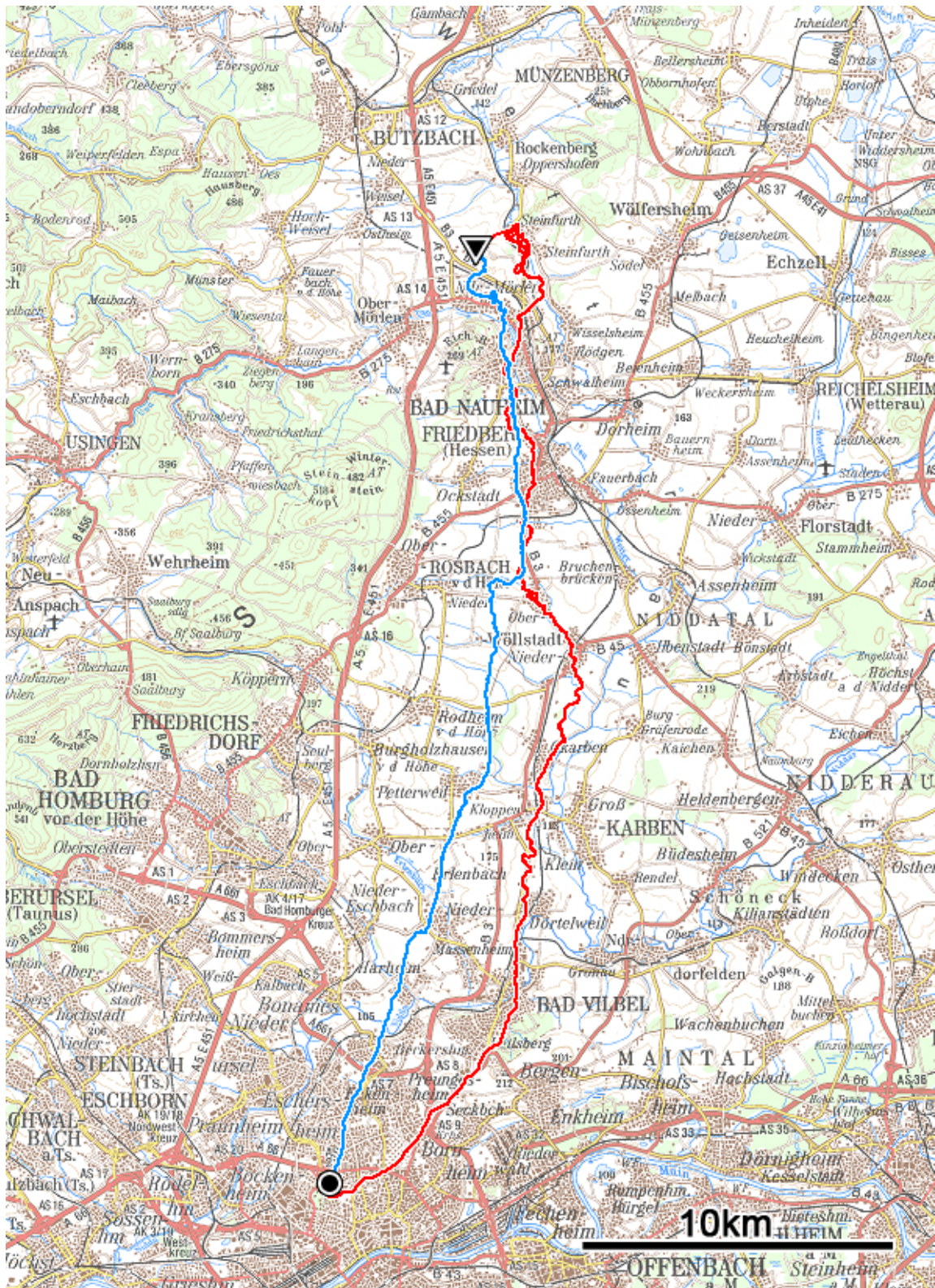


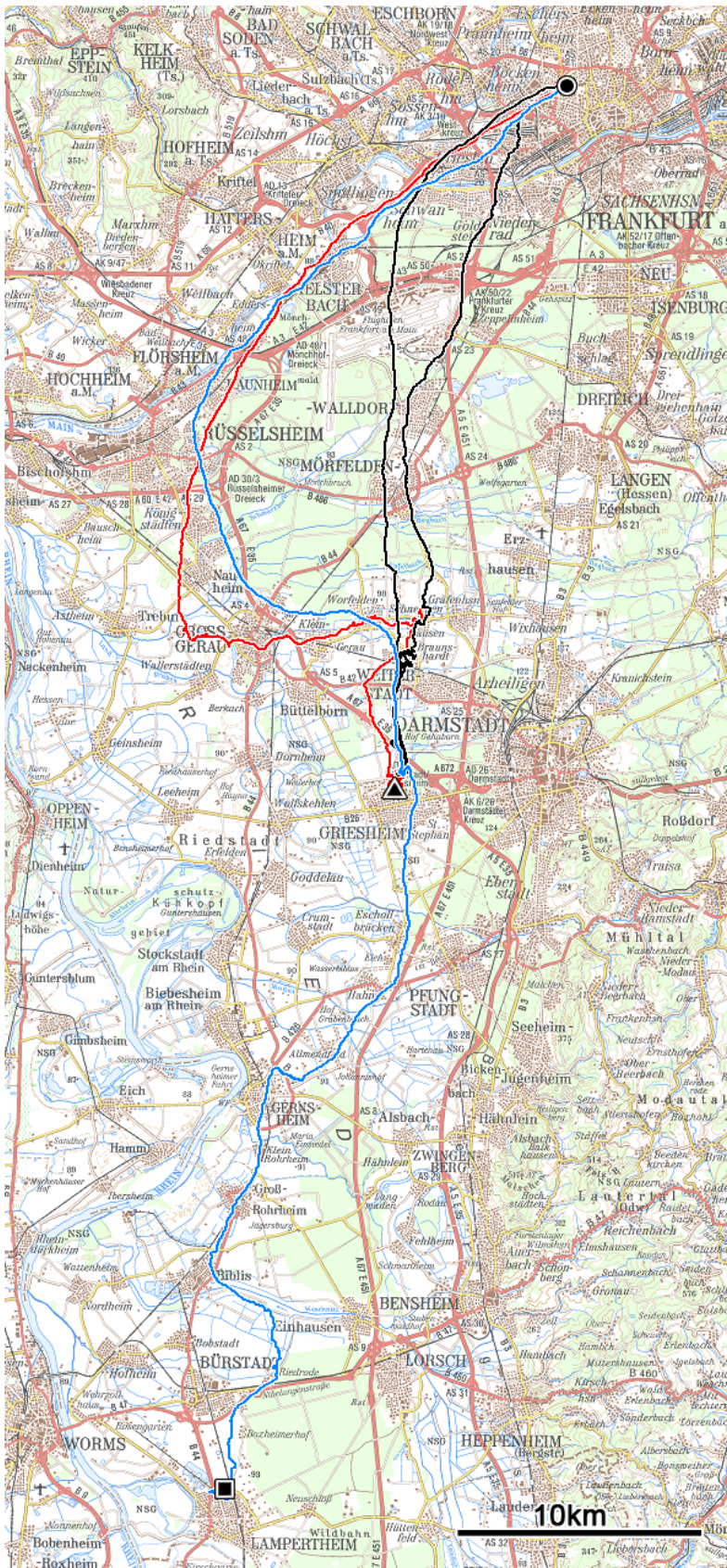
Figure C.20. – All flights (colored lines) of pigeon 07-408 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.





Figure C.21. – All flights (colored lines) of pigeon 07-410 from release site N30 (black triangle) to its home loft (black circle). For color reference see text.





**Figure C.22.** – All flights (colored lines) of pigeon 08-752 from release sites S30 (black triangle) and S60 (black square) to its home loft (black circle). For color reference see text.



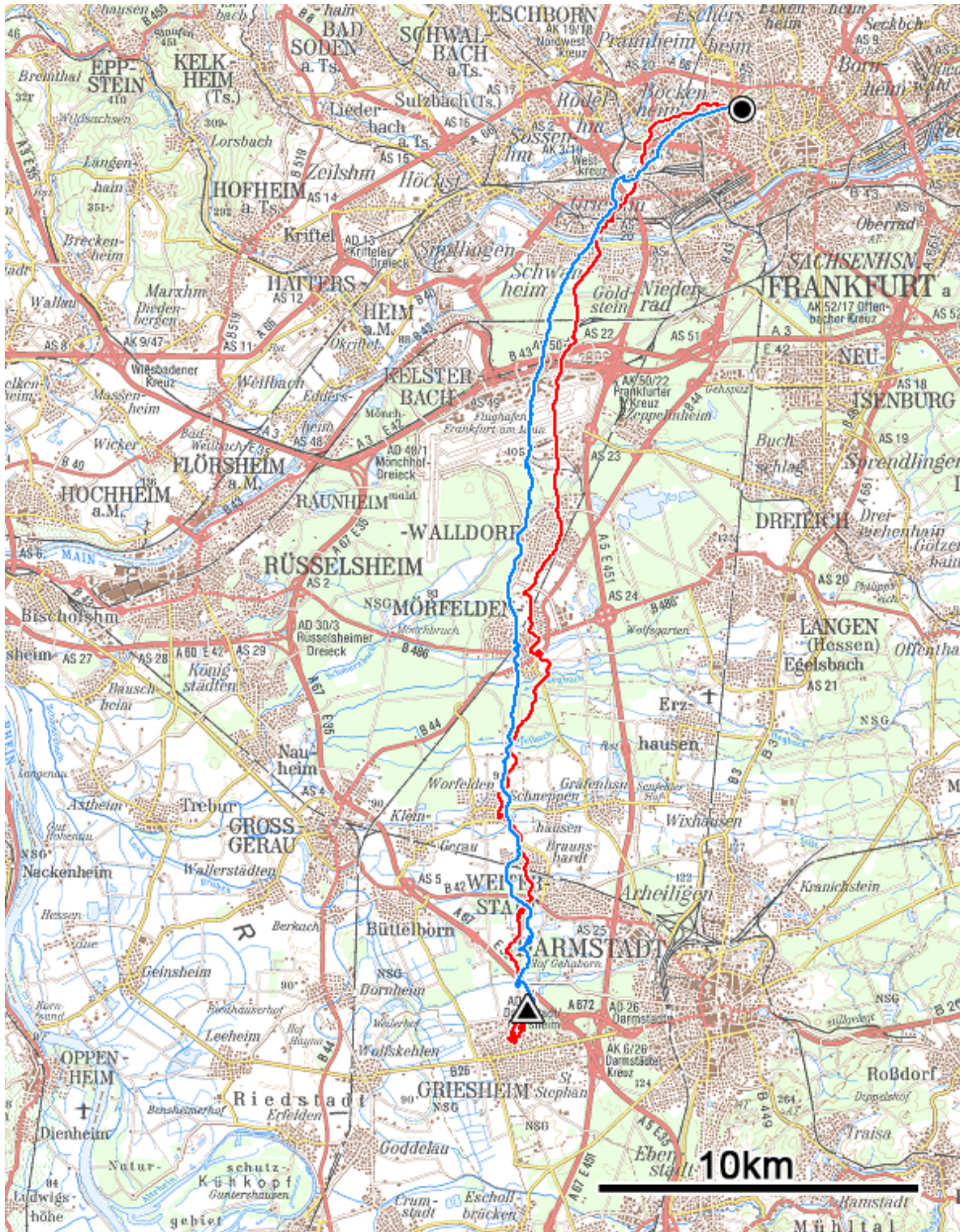
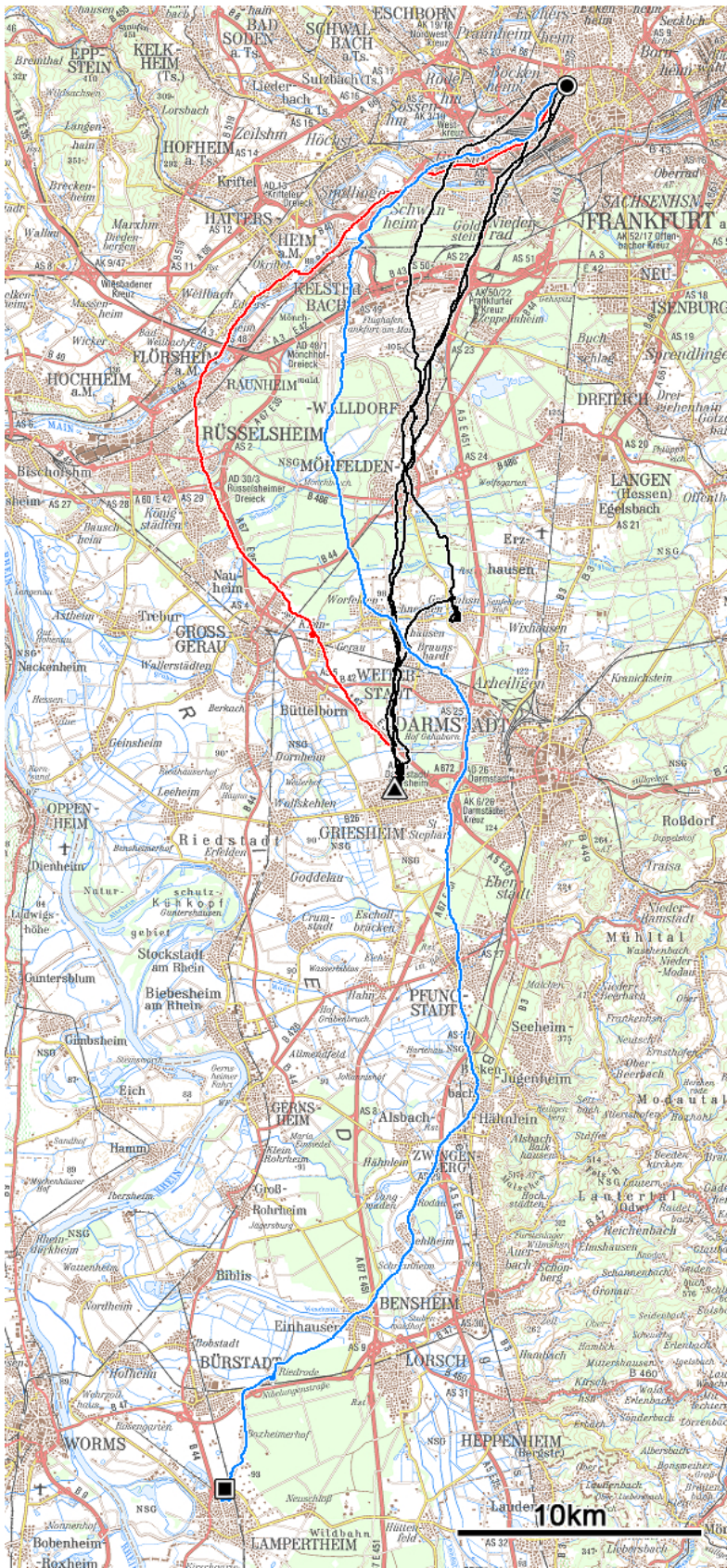


Figure C.23. – All flights (colored lines) of pigeon 08-755 from release site S30 (black triangle) to its home loft (black circle). For color reference see text.





**Figure C.24.** – All flights (colored lines) of pigeon 08-758 from release sites S30 (black triangle) and S60 (black square) to its home loft (black circle). For color reference see text.





Figure C.25. – All flights (colored lines) of pigeon 08-765 from release site S30 (black triangle) to its home loft (black circle). For color reference see text.



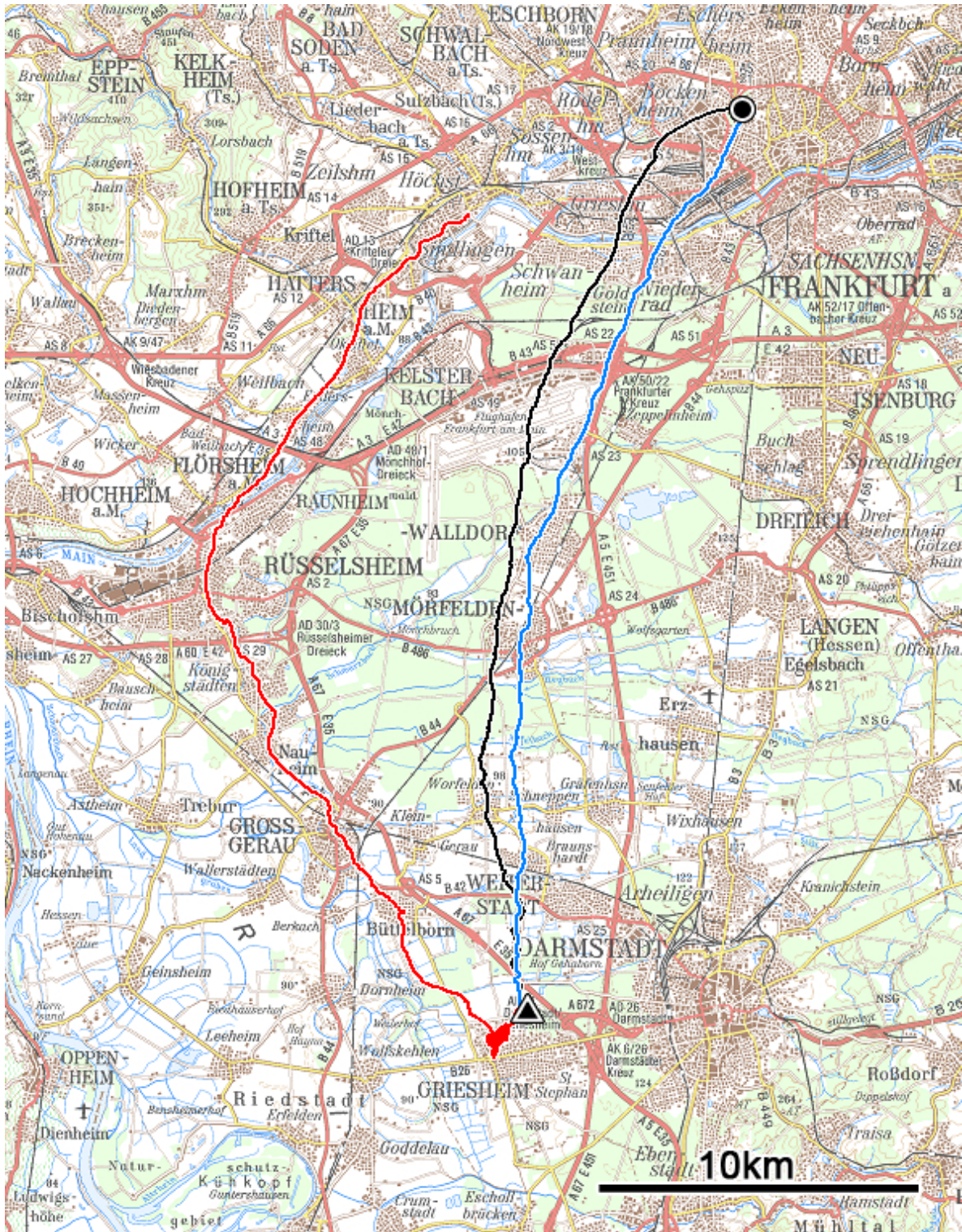


Figure C.26. – All flights (colored lines) of pigeon 08-771 from release site S30 (black triangle) to its home loft (black circle). For color reference see text.



Appendix C. Tracks of Individuals

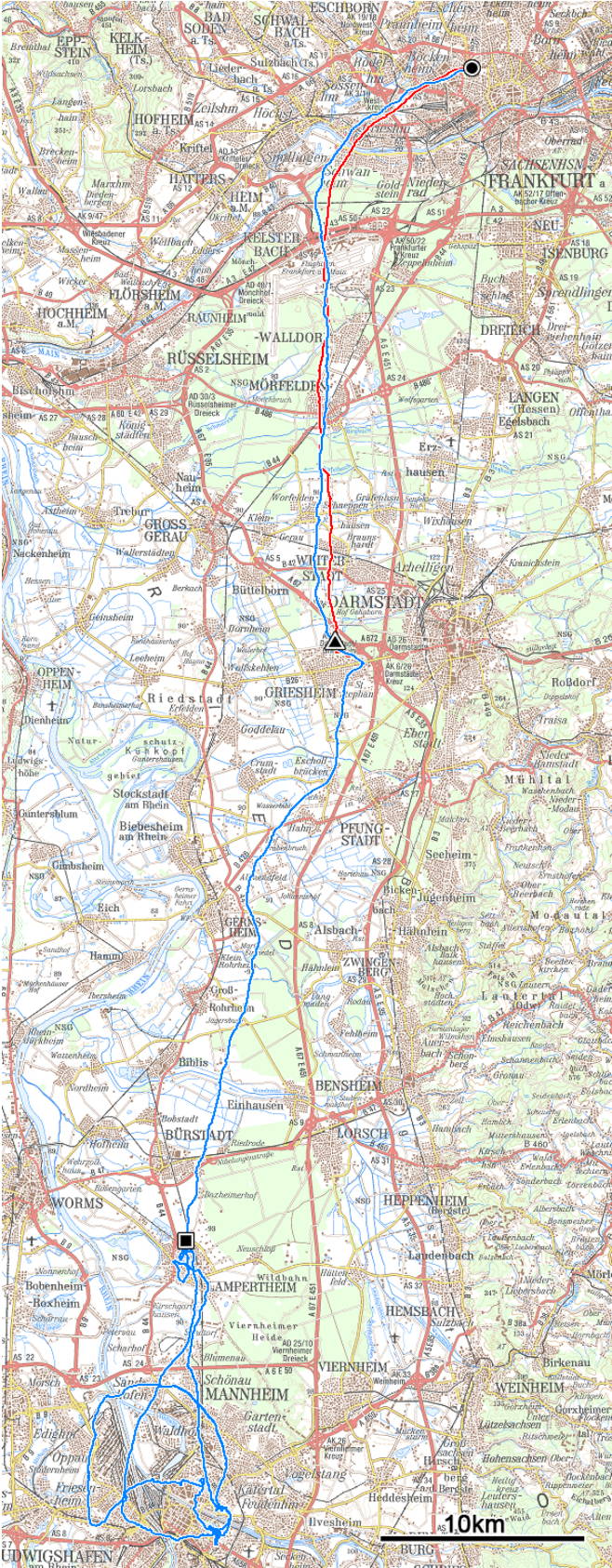


Figure C.27. – All flights (colored lines) of pigeon 08-778 from release sites S30 (black triangle) and S60 (black square) to its home loft (black circle). For color reference see text.





Figure C.28. – All flights (colored lines) of pigeon 08-779 from release site S30 (black triangle) to its home loft (black circle). For color reference see text.



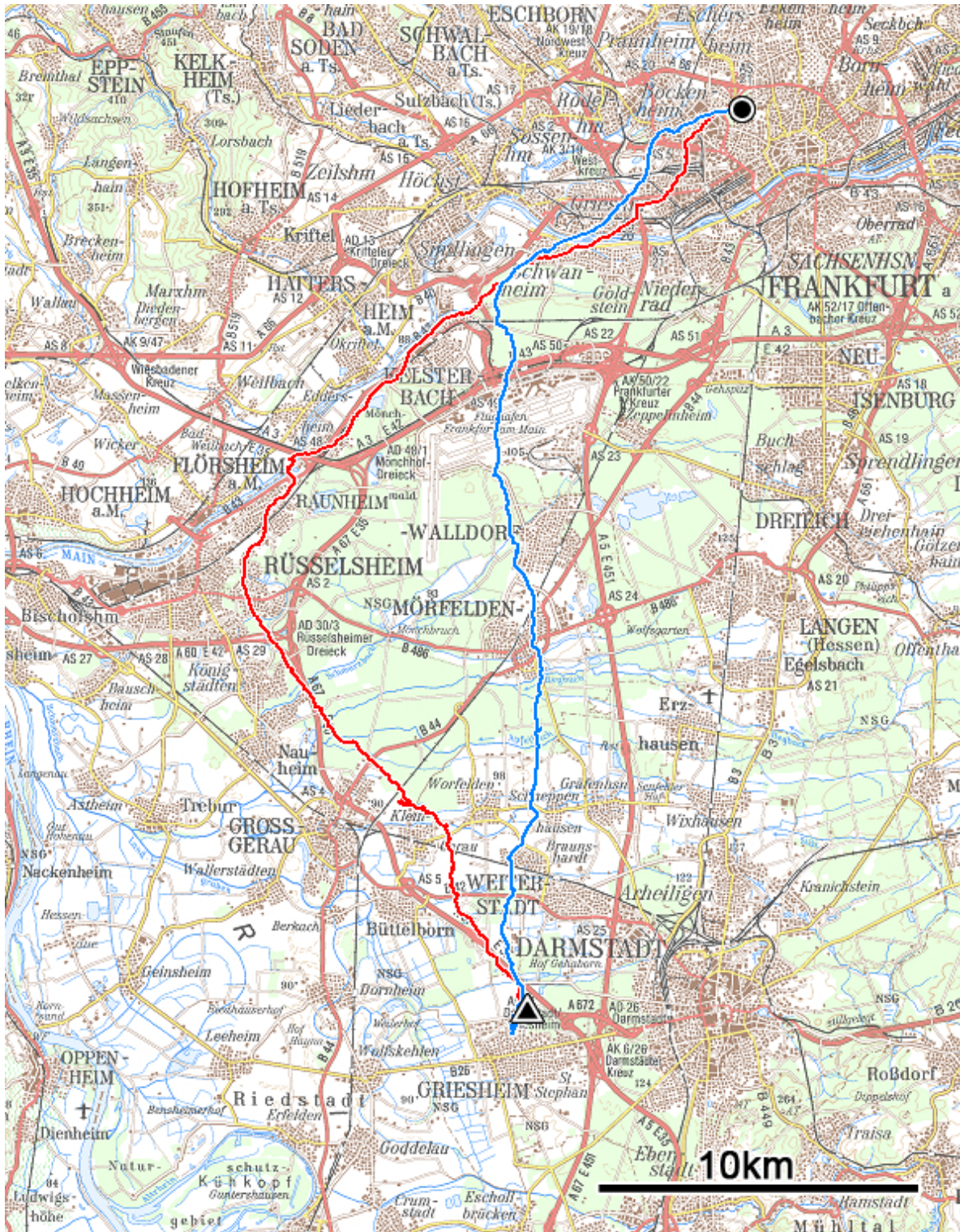
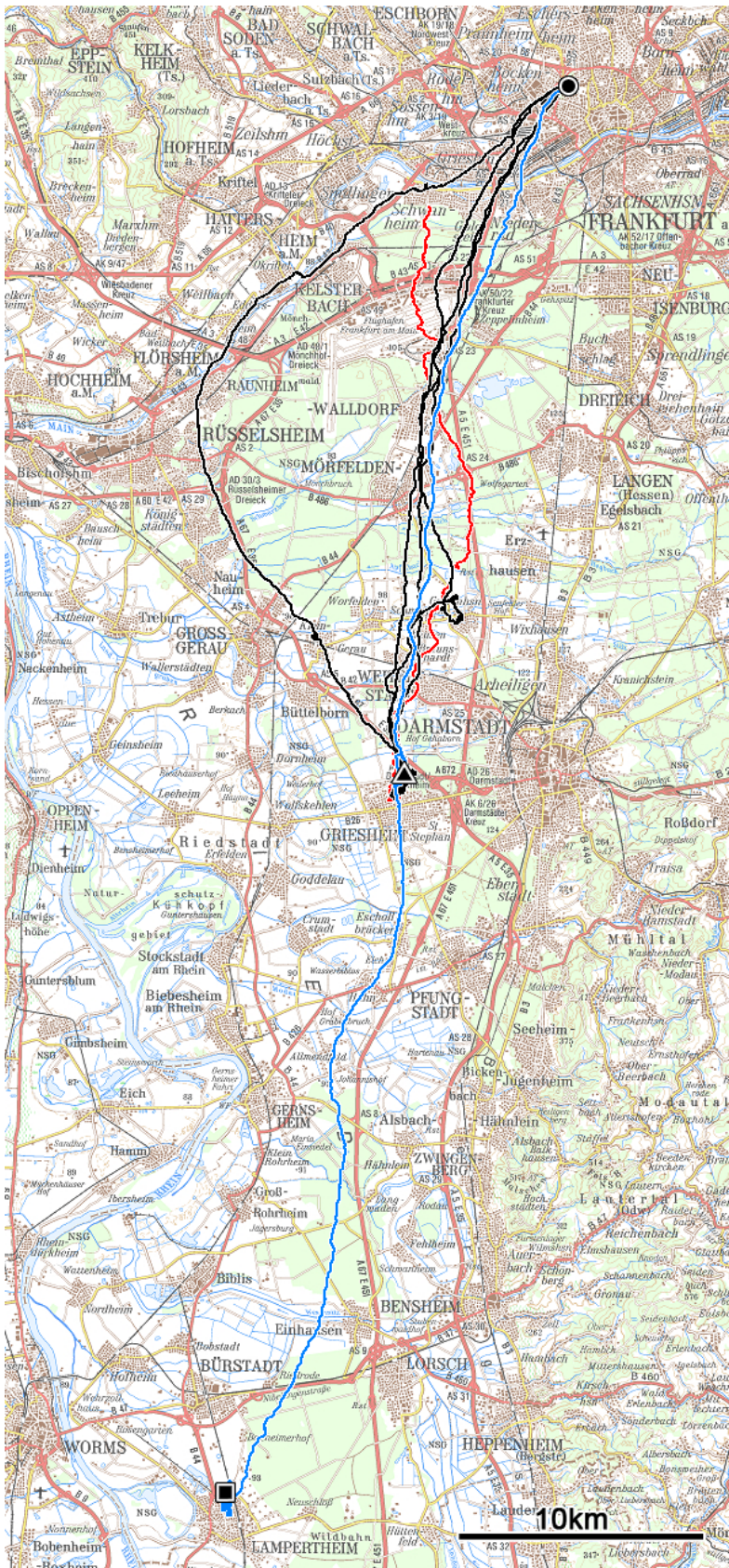


Figure C.29. – All flights (colored lines) of pigeon 08-783 from release site S30 (black triangle) to its home loft (black circle). For color reference see text.





**Figure C.30.** – All flights (colored lines) of pigeon 08-785 from release sites S30 (black triangle) and S60 (black square) to its home loft (black circle). For color reference see text.



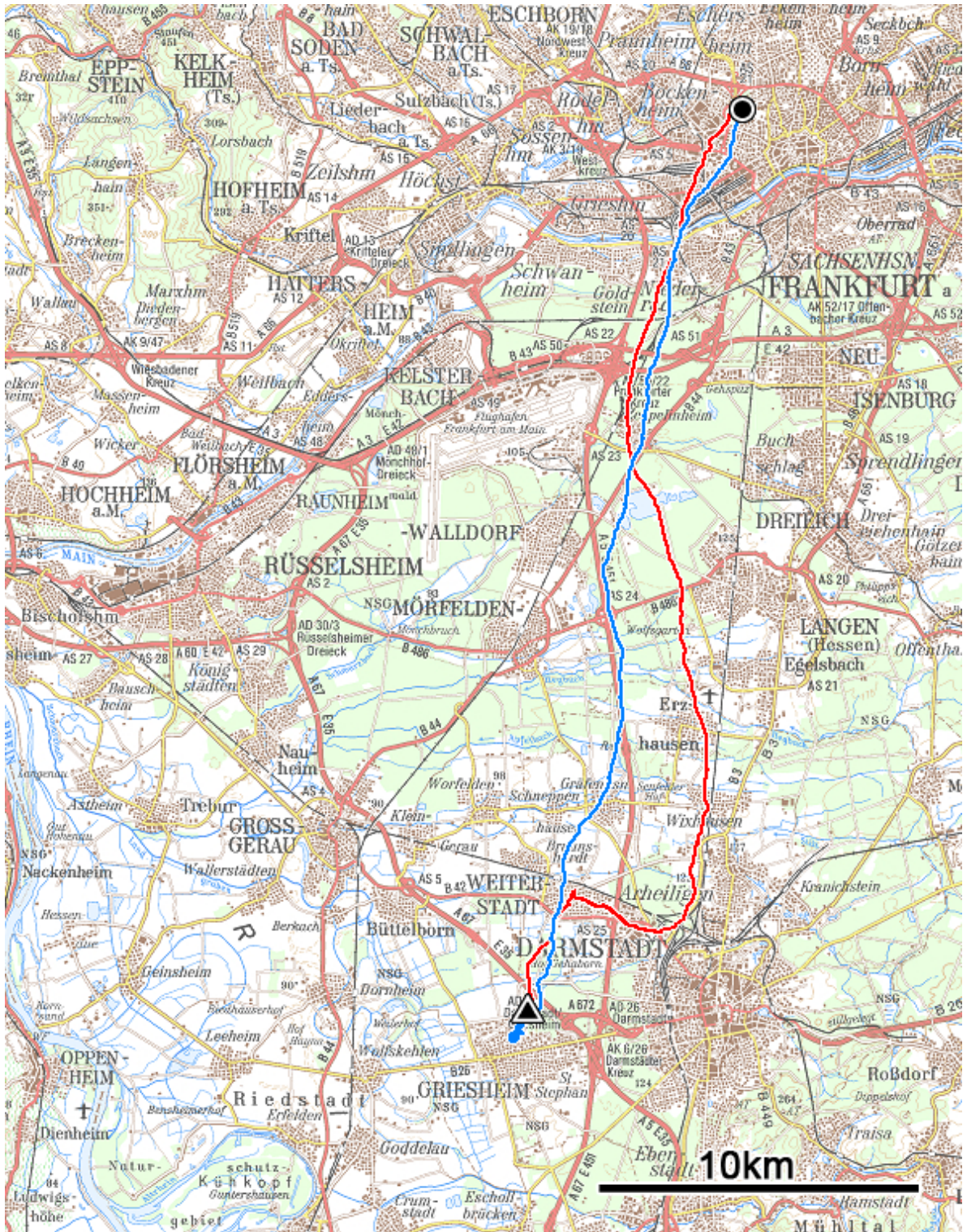
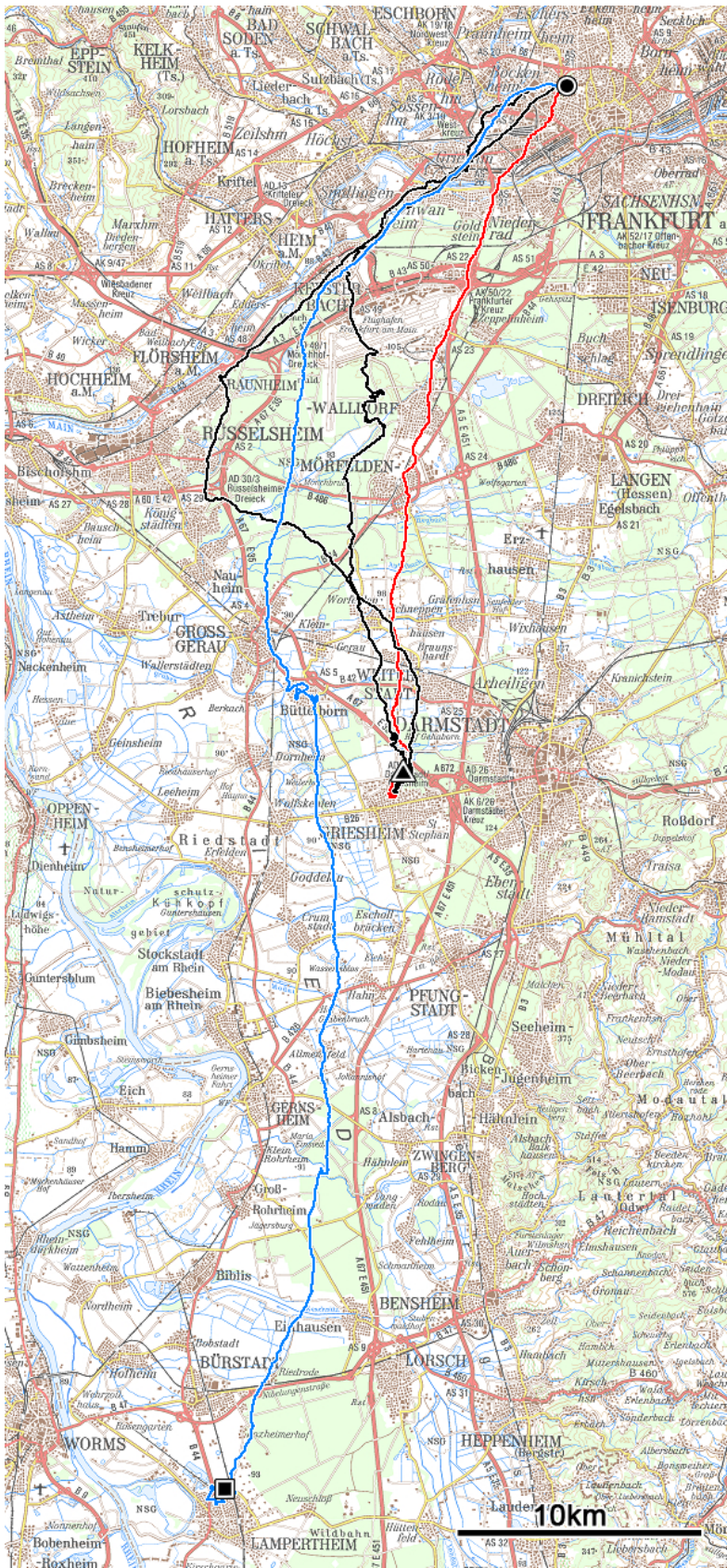


Figure C.31. – All flights (colored lines) of pigeon 08-787 from release site S30 (black triangle) to its home loft (black circle). For color reference see text.





**Figure C.32.** – All flights (colored lines) of pigeon 08-789 from release sites S30 (black triangle) and S60 (black square) to its home loft (black circle). For color reference see text.



Appendix C. Tracks of Individuals

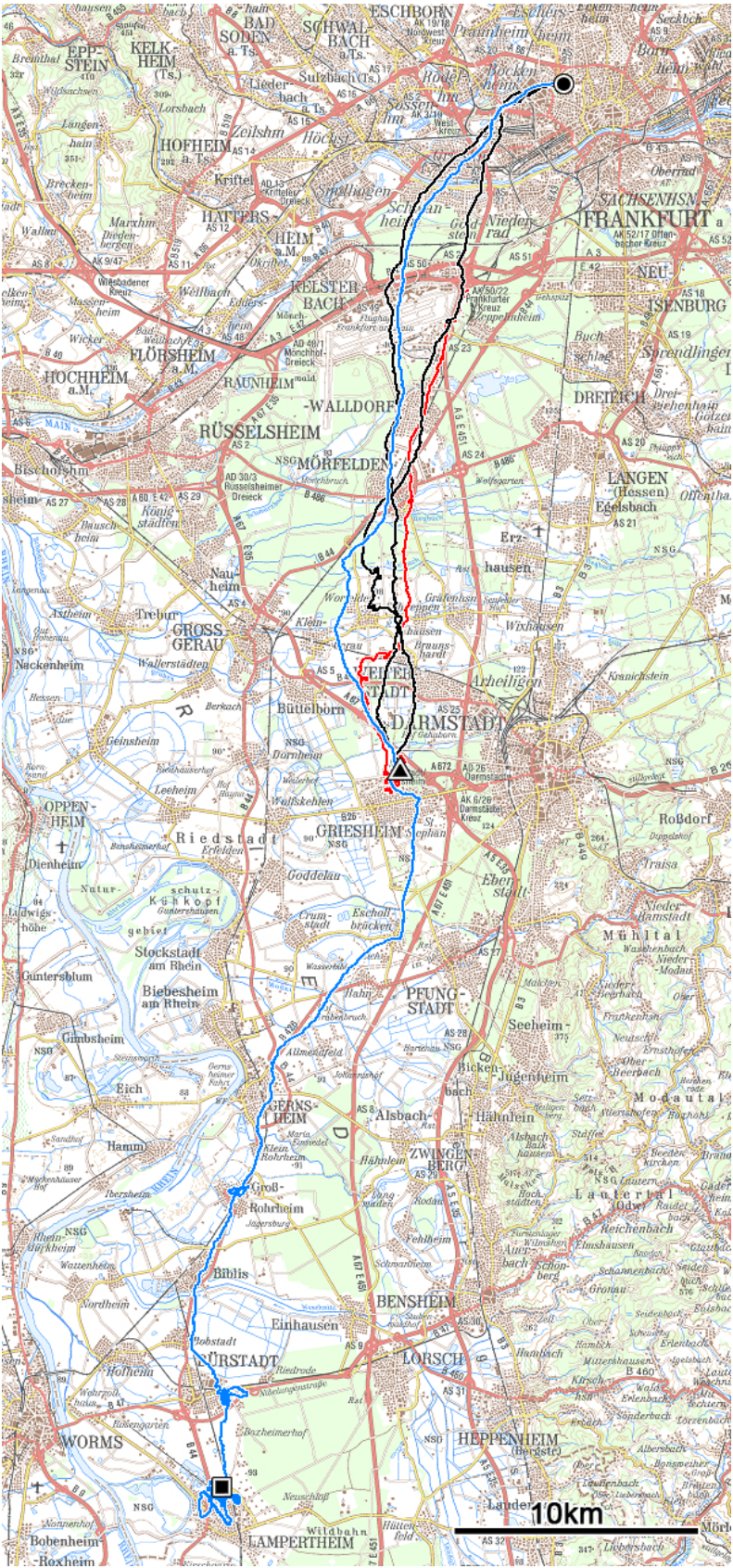
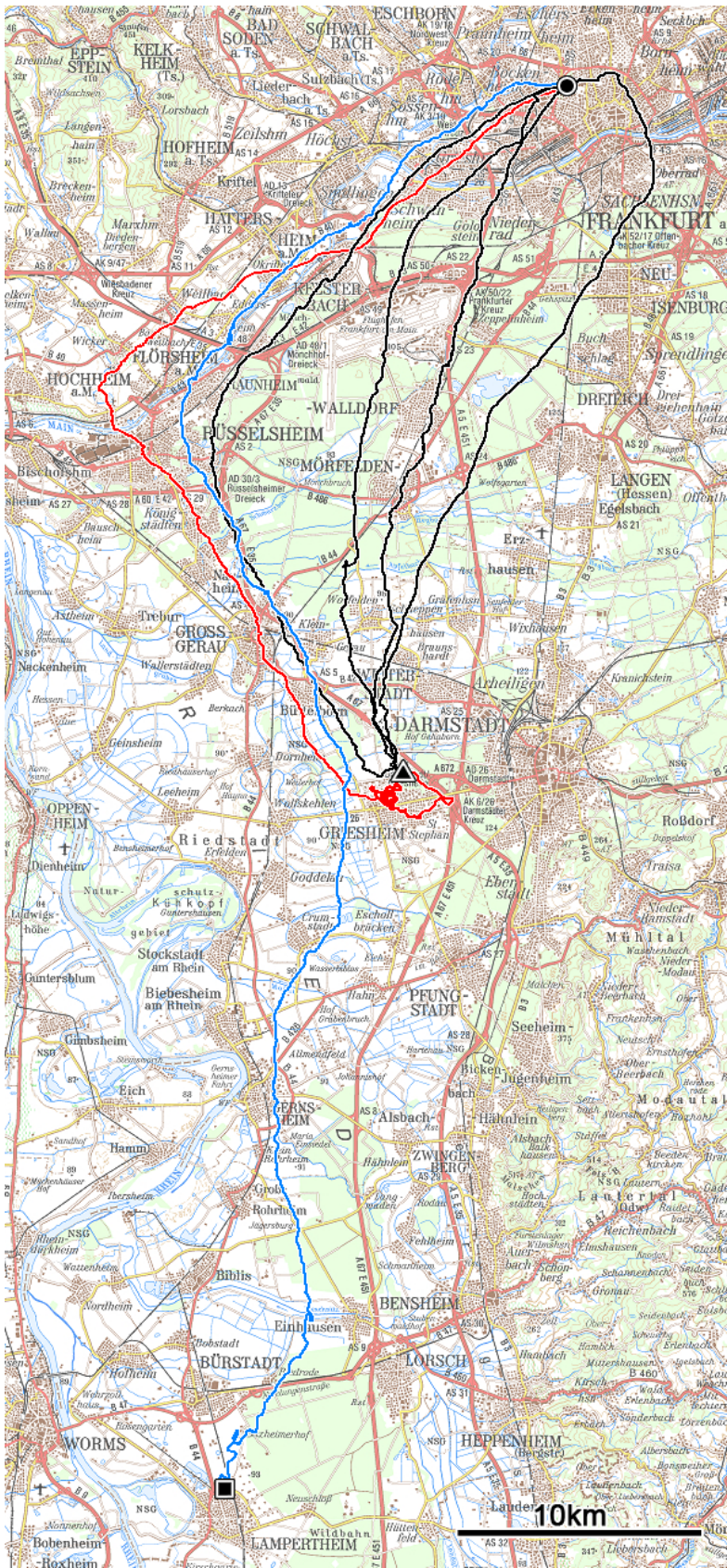


Figure C.33. – All flights (colored lines) of pigeon 08-790 from release sites S30 (black triangle) and S60 (black square) to its home loft (black circle). For color reference see text.





**Figure C.34.** – All flights (colored lines) of pigeon 08-797 from release sites S30 (black triangle) and S60 (black square) to its home loft (black circle). For color reference see text.





# Appendix D.

## Additional Tables

This appendix contains the data on abiotic factors for the two main series, as well as the individual results for each analysis step. Separate tables are given for each type of analysis and the data within each table is given in the same order as in the main text. At the beginning of each section I will give an explanation of the variables displayed in each table.

### D.1. Abiotic Data

The following table contains data on the abiotic factors during each release of the two main series. The table includes the average cloud cover, the average wind speed, the mean wind direction relative to the home direction, the average temperature and the magnetic variation, calculated as the deviation of the K-index over a 12 hour period starting with the first release of each experiment.

Table D.1. – Abiotic factors.

F. No.	Cloud Cover	Wind Speed	Wind Dir.	Temp.	Mag. Var.
N30-F1	4.3	0.0	0	19.8	0.417
N30-F4	3.7	3.4	44	18.7	0.452
N30-F8	3.2	3.0	-157	21.2	0.729
N30-F12	4.2	2.4	45	18.7	0.378
N30-F13	4.3	5.1	97	12.6	0.678
N30-F16	2.2	0.5	166	19.6	0.530
S30-F1	1.0	0.0	0	25.5	1.069
S30-F2	3.0	1.5	17	20.5	0.756
S30-F4	4.3	0.0	0	25.0	1.356
S30-F8	3.0	0.8	87	18.3	0.354
S30-F12	0.0	0.0	0	24.5	0.000

## D.2. Traditional Analysis

The following table contains the data for the traditional analysis, including the bearing after one minute  $h_{min}$ , the bearing after 2.5 km  $h_{2.5}$  and the respective time interval  $i_{2.5}$ , as well as the 2.5 km  $e_{2.5}$ , overland  $e_{ovl}$  and total  $e_{tot}$  efficiency.

Table D.2. – Traditional results

ID	$h_{min}$	$h_{2.5}$	$i_{2.5}$	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
<b>N30-F1</b>						
07-354	25	146	626	0.24	0.79	0.65
07-364	255	217	376	0.39	0.51	0.50
07-366	48	146	628	0.22	0.80	0.65
07-369	7	126	1561	0.10	0.72	0.47
07-382	202	154	223	0.60	0.62	0.62
07-386	248	150	453	0.35	0.81	0.72
07-388	78	142	556	0.31	0.62	0.56
07-392	244	175	284	0.53	0.88	0.83
07-399	162	207	217	0.64	0.71	0.71
07-400	259	187	327	0.50	-	-
07-402	3	209	285	0.52	-	-

Table D.2. – Traditional results

ID	$h_{min}$	$h_{2.5}$	$i_{2.5}$	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
07-403	240	153	285	0.56	0.57	0.55
07-410	246	213	249	0.58	0.61	0.59
<b>N30-F4</b>						
07-364	322	169	429	0.34	0.90	0.79
07-366	250	157	479	0.33	0.76	0.69
07-371	24	164	557	0.30	0.74	0.66
07-382	150	153	344	0.45	0.60	0.57
07-389	154	151	627	0.25	0.82	0.68
07-392	258	169	329	0.46	0.91	0.84
07-393	347	159	725	0.25	0.83	0.69
07-399	256	170	382	0.43	0.73	0.70
07-402	324	125	848	0.17	-	-
07-408	53	104	890	0.18	-	-
07-410	31	167	255	0.60	0.66	0.65
<b>N30-F8</b>						
07-354	12	189	827	0.19	0.88	0.67
07-364	218	161	270	0.53	0.90	0.85
07-366	243	159	410	0.41	0.78	0.71
07-367	145	189	594	0.27	0.89	0.74
07-371	295	169	377	0.41	0.87	0.79
07-377	147	169	241	0.70	0.84	0.81
07-379	282	176	600	0.26	0.80	0.67
07-386	-	158	-	-	0.74	-
07-389	223	159	372	0.45	0.82	0.76
07-393	237	176	257	0.64	0.90	0.87
07-399	160	214	271	0.52	0.71	0.53
07-402	253	101	727	0.22	-	-
07-407	298	240	339	0.44	0.82	0.74
07-410	226	175	308	0.51	0.56	0.56
<b>N30-F12</b>						
07-351	229	171	604	0.24	0.94	0.76
07-354	245	207	912	0.16	0.92	0.67
07-364	323	192	310	0.54	-	-

Table D.2. – Traditional results

ID	$h_{min}$	$h_{2.5}$	$i_{2.5}$	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
07-367	259	205	494	0.34	0.71	0.65
07-366	179	163	465	0.33	0.87	0.76
07-379	277	179	405	0.36	0.84	0.76
07-382	190	160	289	0.57	0.52	0.53
07-392	250	207	521	0.31	0.92	0.79
07-393	260	175	455	0.37	0.94	0.83
07-399	185	159	378	0.46	0.77	0.72
07-410	199	170	187	0.78	0.91	0.90
<b>N30-F13</b>						
07-354	49	134	619	0.24	0.74	0.62
07-357	71	181	645	0.24	0.89	0.72
07-375	13	118	619	0.23	0.76	0.60
07-377	154	180	360	0.45	0.84	0.79
07-381	-	117	-	-	0.86	-
07-382	157	162	618	0.26	-	-
07-386	189	197	220	0.61	0.96	0.91
07-389	-	197	-	-	0.95	-
07-392	259	182	518	0.31	0.90	0.77
07-393	357	163	507	0.36	0.77	0.70
07-402	235	151	294	0.59	0.76	0.73
07-405	177	63	652	0.26	0.70	0.53
07-408	53	118	718	0.23	0.77	0.61
07-410	190	166	566	0.25	0.88	0.73
<b>N30-F16</b>						
07-354	248	207	276	0.49	0.87	0.80
07-357	261	177	432	0.38	0.91	0.82
07-375	214	175	286	0.49	0.65	0.63
07-379	271	205	588	0.25	-	-
07-382	185	163	311	0.49	0.84	0.72
07-386	204	176	264	0.54	0.93	0.88
07-387	255	177	298	0.52	0.88	0.83
07-389	319	213	987	0.16	-	-
07-392	245	162	353	0.51	-	-

Table D.2. – Traditional results

ID	$h_{min}$	$h_{2.5}$	$i_{2.5}$	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
07-402	256	206	1204	0.12	0.89	0.59
07-405	310	31	562	0.30	0.89	0.48
07-408	227	158	1104	0.15	0.89	0.63
<b>S30-F1</b>						
08-752	199	103	1494	0.11	-	-
08-765	249	64	686	0.25	-	-
08-783	319	323	911	0.16	-	-
08-785	190	357	1328	0.14	-	-
08-787	221	219	727	0.21	-	-
08-797	127	263	1841	0.09	0.66	0.39
08-95	223	40	1141	0.14	-	-
<b>S30-F2</b>						
08-752	183	35	1255	0.14	-	-
08-758	251	325	512	0.32	0.71	0.63
08-765	209	313	1388	0.13	-	-
08-778	198	82	1913	0.09	-	-
08-779	248	329	298	0.57	0.64	0.61
08-783	331	331	203	0.81	0.63	0.63
08-785	205	325	960	0.18	0.71	0.55
08-787	241	19	320	0.54	0.79	0.76
08-797	190	304	689	0.26	0.77	0.62
<b>S30-F4</b>						
08-752	220	331	690	0.24	0.52	0.46
08-755	209	355	876	0.18	0.76	0.58
08-758	187	350	417	0.35	0.92	0.80
08-765	308	8	205	0.43	0.84	0.87
08-771	228	284	1585	0.10	-	-
08-783	191	343	539	0.27	0.81	0.68
08-785	197	357	1022	0.16	0.93	0.65
08-787	191	18	768	0.19	0.94	0.70
08-789	238	350	1095	0.14	0.92	0.61
08-790	203	331	1115	0.15	-	-
08-797	310	345	199	0.72	0.85	0.79



Table D.2. – Traditional results

ID	$h_{min}$	$h_{2.5}$	$i_{2.5}$	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
<b>S30-F8</b>						
08-752	46	354	269	0.58	0.90	0.85
08-755	152	3	421	0.36	0.83	0.73
08-758	-	347	-	-	0.73	-
08-765	234	350	558	0.32	0.91	0.77
08-771	339	350	196	0.82	0.91	0.88
08-778	268	354	549	0.29	0.90	0.75
08-779	61	350	505	0.31	0.94	0.78
08-785	288	347	228	0.71	0.75	0.74
08-789	197	13	214	0.62	0.68	0.67
08-790	231	339	532	0.33	0.80	0.69
08-797	333	332	165	0.92	0.87	0.86
<b>S30-F12</b>						
08-752	14	351	502	0.34	0.67	0.61
08-755	170	351	512	0.34	-	-
08-758	341	353	491	0.32	0.93	0.80
08-771	340	353	204	0.81	0.93	0.92
08-785	221	348	1533	0.12	0.93	0.58
08-789	193	346	754	0.20	0.67	0.55
08-790	277	14	318	0.60	0.86	0.82
08-797	325	331	195	0.83	0.91	0.87
<b>N60</b>						
07-354	354	227	1811	0.08	-	-
07-357	256	222	589	0.29	0.81	0.74
07-382	341	172	520	0.31	-	-
07-386	259	227	850	0.17	0.61	0.54
07-387	311	246	1202	0.14	0.78	0.63
07-389	315	239	757	0.20	0.81	0.70
07-393	304	16	594	0.31	-	-
07-402	83	227	1464	0.10	0.61	0.49
07-405	311	278	1090	0.15	0.43	0.38
<b>S60</b>						
08-752	233	7	559	0.32	0.73	0.69

Table D.2. – Traditional results

ID	$h_{min}$	$h_{2.5}$	$i_{2.5}$	$e_{2.5}$	$e_{ovl}$	$e_{tot}$
08-755	92	25	248	0.72	-	-
08-758	139	21	815	0.21	0.81	0.72
08-763	168	33	457	0.36	0.89	0.83
08-778	149	154	682	0.23	0.46	0.40
08-785	224	33	1475	0.12	0.79	0.63
08-789	203	25	491	0.34	0.82	0.76
08-790	215	359	1489	0.12	0.72	0.59
08-797	165	20	565	0.29	0.77	0.71
<b>NE40</b>						
07-393	313	248	398	0.39	-	-
08-758	105	81	1017	0.16	-	-
08-763	349	204	746	0.22	0.81	0.70
08-771	301	250	281	0.49	0.75	0.73
08-778	116	147	1399	0.12	-	-
08-779	308	233	500	0.31	0.91	0.82
08-785	261	100	2187	0.08	0.81	0.51
08-789	311	346	680	0.23	-	-
08-790	284	133	2991	0.06	-	-
<b>SW40</b>						
05-1012	86	92	584	0.29	0.87	0.72
05-1036	140	69	434	0.39	-	-
05-1044	263	84	509	0.32	-	-
05-1054	273	33	612	0.31	0.61	0.57
05-1067	77	98	283	0.54	-	-
05-1078	48	33	274	0.65	-	-
07-382	-	89	-	-	0.60	-
07-387	199	72	937	0.17	0.67	0.57
07-389	58	54	336	0.46	0.72	0.70
07-393	-	84	-	-	-	-
08-771	168	6	399	0.39	0.72	0.67
08-779	171	138	210	0.68	0.82	0.77

### D.3. Phases of the Flight I - First Point of Decision

The following table contains data on the behavior before and after the first point of decision. The variables given are as follows:

- First Point of Decision: The direction of the point of decision from the release site  $PoD_h$  and the respective distance from the release site  $PoD_{\Delta d}$  in meters.
- Initial Phase: The duration of the phase  $t_{ini}$  in seconds, i.e. the time until the first point of decision, the mean heading in relation to the home direction  $\Delta h_{ini}$ , the mean steadiness of the pigeon's flight  $s_{ini}$  and the average speed  $v_{ini}$  in km/h.
- Departure Phase: The duration of the phase  $t_{dep}$  in seconds, the mean heading in relation to the home direction  $\Delta h_{dep}$ , the mean steadiness of the pigeon's flight  $s_{dep}$  and the average speed  $v_{dep}$  in km/h.

**Table D.3.** – Behavior before and after the first point of decision

ID	$PoD_h$	$PoD_d$	$t_{ini}$	$\Delta h_{ini}$	$s_{ini}$	$v_{ini}$	$t_{dep}$	$\Delta h_{dep}$	$s_{dep}$	$v_{dep}$
<b>N30-F1</b>										
07-354	80	375	135	-125	0.18	54	90	-113	0.85	65
07-364	267	862	180	87	0.31	54	255	21	0.59	65
07-366	160	4729	885	-30	0.24	60	1530	-20	0.85	67
07-369	15	325	60	-172	0.30	58	45	-87	0.96	59
07-371	113	753	120	-89	0.37	55	75	-148	0.73	61
07-382	153	3015	255	-36	0.61	66	75	-30	0.89	66
07-386	180	1890	330	-11	0.36	56	930	-34	0.76	59
07-388	72	380	45	-114	0.60	44	75	-124	0.88	52
07-392	221	886	90	34	0.59	46	90	-18	0.94	62
07-399	193	218	75	-4	0.14	54	240	17	0.86	68
07-400	217	413	135	22	0.20	50	165	-20	0.80	55
07-402	343	267	45	161	0.33	53	345	19	0.72	59
07-403	150	4957	540	-41	0.56	55	105	-18	0.83	62
07-410	248	261	60	61	0.29	48	360	23	0.62	61

Table D.3. – Behavior before and after the first point of decision

ID	$PoD_h$	$PoD_d$	$t_{ini}$	$\Delta h_{ini}$	$s_{ini}$	$v_{ini}$	$t_{dep}$	$\Delta h_{dep}$	$s_{dep}$	$v_{dep}$
<b>N30-F4</b>										
07-364	235	617	300	50	0.11	54	1665	-22	0.91	68
07-366	230	901	120	49	0.60	49	75	-43	0.94	68
07-367	265	469	300	74	0.22	53	255	-75	0.39	65
07-371	244	957	270	32	0.33	52	120	-40	0.84	51
07-382	152	985	210	-4	0.30	54	105	-31	0.78	60
07-388	210	763	180	27	0.25	52	75	-35	0.99	66
07-389	328	633	150	118	0.32	49	105	-126	0.75	67
07-392	239	542	195	52	0.17	49	1635	-22	0.91	68
07-393	49	690	135	-144	0.42	45	105	-99	0.66	50
07-399	246	499	90	44	0.43	52	165	-21	0.73	50
07-402	264	616	360	24	0.18	52	375	-55	0.40	60
07-408	71	1540	255	-118	0.27	53	630	3	0.12	53
07-410	294	98	75	112	0.12	43	225	-27	0.86	62
<b>N30-F8</b>										
07-354	188	316	465	-56	0.08	52	135	-20	0.51	57
07-364	147	355	105	-61	0.24	54	1710	-3	0.87	70
07-366	215	627	165	8	0.22	54	90	-3	0.80	55
07-367	239	185	150	-25	0.07	51	90	145	0.84	62
07-371	204	380	210	-23	0.15	55	2025	-23	0.85	63
07-377	141	159	45	-56	0.36	43	750	-18	0.85	56
07-379	289	771	165	98	0.13	59	1680	-19	0.73	57
07-389	192	126	120	-77	0.09	49	810	-27	0.75	54
07-393	222	499	75	29	0.36	51	1095	-14	0.87	57
07-399	167	638	120	-29	0.39	54	165	30	0.72	68
07-402	298	540	315	-3	0.06	56	210	-139	0.56	54
07-407	213	567	225	-9	0.14	51	195	44	0.82	63
07-410	225	50	75	-8	0.02	39	405	-20	0.74	58
<b>N30-F12</b>										
07-351	136	223	270	2	0.01	57	90	-10	0.75	64
07-354	196	36	600	117	0.08	58	1935	-7	0.83	67
07-364	224	311	135	3	0.25	51	645	-30	0.74	53
07-366	171	1861	420	-19	0.24	57	300	-29	0.88	63

Table D.3. – Behavior before and after the first point of decision

ID	$PoD_h$	$PoD_d$	$t_{ini}$	$\Delta h_{ini}$	$s_{ini}$	$v_{ini}$	$t_{dep}$	$\Delta h_{dep}$	$s_{dep}$	$v_{dep}$
07-367	227	295	240	-7	0.20	49	435	10	0.58	54
07-379	247	304	210	116	0.13	52	675	10	0.71	60
07-382	160	3488	405	-31	0.64	52	45	-14	0.76	48
07-392	196	29	210	119	0.10	49	1935	-7	0.83	67
07-393	245	767	315	76	0.27	46	2055	-2	0.93	56
07-399	165	2132	345	-29	0.52	49	690	-24	0.87	54
07-410	196	743	75	11	0.65	52	345	-29	0.92	68
<b>N30-F13</b>										
07-354	166	8229	1170	-25	0.51	56	90	-42	0.70	51
07-357	59	425	105	-152	0.34	43	150	82	0.57	51
07-375	77	404	165	-32	0.07	54	120	-114	0.45	63
07-377	163	965	225	-16	0.37	51	2400	-9	0.85	53
07-382	166	1143	120	-17	0.64	54	30	-33	0.90	59
07-386	191	2116	195	8	0.5	66	1305	-1	0.94	83
07-392	190	251	270	106	0.07	47	1650	-19	0.87	73
07-393	348	250	180	80	0.22	42	90	-115	0.63	62
07-402	230	346	60	36	0.47	48	510	-35	0.80	50
07-405	137	505	495	161	0.11	50	585	-166	0.80	56
07-408	68	455	105	-98	0.29	48	165	-94	0.45	53
07-410	181	788	90	-2	0.49	55	60	-36	0.61	69
<b>N30-F16</b>										
07-354	258	518	75	78	0.45	52	90	27	0.75	70
07-357	187	1315	345	-5	0.18	51	1770	-17	0.92	61
07-375	212	651	150	26	0.22	58	1140	-34	0.83	67
07-379	258	309	420	153	0.07	56	345	-3	0.74	64
07-382	170	1946	270	-20	0.41	55	375	-30	0.86	61
07-386	179	2098	240	-9	0.48	58	450	-12	0.95	66
07-387	186	1303	210	-4	0.34	54	1500	-19	0.91	62
07-389	233	248	510	-37	0.04	52	105	0	0.64	52
07-392	251	419	90	53	0.32	46	135	-12	0.79	49
07-402	180	277	540	-166	0.05	54	75	-30	0.64	62
07-405	63	1417	450	-140	0.25	53	135	177	0.85	55
07-408	51	256	480	-124	0.08	43	60	3	0.58	54



Table D.3. – Behavior before and after the first point of decision

ID	$PoD_h$	$PoD_d$	$t_{ini}$	$\Delta h_{ini}$	$s_{ini}$	$v_{ini}$	$t_{dep}$	$\Delta h_{dep}$	$s_{dep}$	$v_{dep}$
<b>S30-F1</b>										
08-752	192	431	75	179	0.32	49	45	-165	0.60	63
08-765	210	205	315	19	0.02	45	75	-163	0.64	56
08-771	42	564	285	18	0.20	53	90	119	0.80	54
08-783	198	415	195	-145	0.07	55	45	-174	0.74	66
08-785	205	1000	570	-161	0.05	53	225	25	0.09	49
08-787	189	390	120	152	0.15	53	60	-174	0.78	66
08-797	237	93	405	-1	0.05	49	285	140	0.33	56
08-95	214	747	90	-154	0.49	52	60	139	0.68	62
<b>S30-F2</b>										
08-752	229	82	210	150	0.01	42	75	-173	0.68	52
08-758	332	112	345	1	0.11	49	1185	-56	0.90	58
08-765	231	293	225	-82	0.06	47	210	-50	0.08	51
08-778	188	533	90	173	0.38	46	15	165	0.86	56
08-779	216	148	105	-129	0.09	52	1170	-66	0.92	55
08-783	330	386	45	-40	0.57	48	315	-43	0.86	56
08-785	353	125	690	-1	0.14	46	1470	-49	0.83	58
08-787	201	237	105	-150	0.11	48	300	9	0.89	52
08-797	139	192	420	13	0.06	48	1440	-52	0.84	54
<b>S30-F4</b>										
08-752	205	55	150	-150	0.08	50	90	-174	0.71	51
08-755	202	472	135	-165	0.17	52	60	-176	0.42	61
08-758	225	451	240	-158	0.17	49	1755	-10	0.89	66
08-765	158	93	75	-110	0.02	44	105	-21	0.78	59
08-771	223	936	1305	-156	0.15	48	90	-157	0.53	51
08-778	169	810	285	162	0.19	53	90	97	0.74	60
08-783	225	155	180	-166	0.06	54	45	-164	0.84	59
08-785	215	445	180	-144	0.18	48	15	-176	0.95	53
08-787	195	464	135	-171	0.23	53	60	-140	0.52	58
08-789	216	420	90	-157	0.25	55	2595	-11	0.60	64
08-790	241	97	195	-83	0.06	48	465	-168	0.13	50
08-797	310	297	60	-72	0.32	55	1485	19	0.92	73
<b>S30-F8</b>										

Table D.3. – Behavior before and after the first point of decision

ID	$PoD_h$	$PoD_d$	$t_{ini}$	$\Delta h_{ini}$	$s_{ini}$	$v_{ini}$	$t_{dep}$	$\Delta h_{dep}$	$s_{dep}$	$v_{dep}$
08-752	28	244	135	-21	0.12	50	1470	-26	0.96	62
08-755	3	2276	405	-18	0.30	58	570	-22	0.84	65
08-765	129	95	105	156	0.06	47	75	-145	0.26	46
08-771	334	322	45	-39	0.52	48	1725	-21	0.90	65
08-778	136	447	240	165	0.11	48	30	126	0.97	60
08-779	212	351	240	-139	0.14	53	1845	-19	0.89	63
08-789	181	100	60	-144	0.14	54	390	-23	0.85	71
08-790	224	302	330	-134	0.12	47	495	-19	0.85	57
08-797	335	782	60	-42	0.86	54	405	-37	0.93	64
<b>S30-F12</b>										
08-752	356	1382	435	-7	0.26	49	210	-7	0.90	58
08-755	249	186	285	12	0.05	49	270	-19	0.80	51
08-758	308	195	315	-13	0.09	55	1965	-7	0.92	57
08-771	350	1712	150	-22	0.79	53	825	-16	0.95	58
08-785	271	163	585	19	0.10	47	105	-23	0.80	50
08-789	344	1742	705	-12	0.21	54	795	-31	0.79	55
08-790	281	129	105	-9	0.09	42	1965	-22	0.90	49
08-797	324	941	90	-46	0.69	53	210	-26	0.92	56
<b>N60</b>										
07-354	85	399	600	158	0.06	55	555	37	0.28	60
07-357	242	1281	495	61	0.23	49	2220	16	0.78	55
07-382	342	108	60	111	0.21	48	45	-82	0.86	62
07-386	289	1246	420	89	0.27	58	105	154	0.84	60
07-387	262	598	270	72	0.24	50	105	20	0.80	53
07-389	275	901	630	93	0.17	51	285	15	0.71	62
07-393	261	461	345	61	0.16	45	615	-150	0.79	59
07-402	80	385	255	-170	0.08	56	555	37	0.28	60
07-405	286	778	585	79	0.16	51	60	159	0.71	52
<b>S60</b>										
08-752	252	181	330	-85	0.09	48	690	1	0.79	50
08-755	86	251	60	70	0.20	49	1050	3	0.94	50
08-758	189	520	570	-54	0.01	51	2700	7	0.86	54
08-763	169	774	210	154	0.17	55	2235	1	0.92	53

Table D.3. – Behavior before and after the first point of decision

ID	$PoD_h$	$PoD_d$	$t_{ini}$	$\Delta h_{ini}$	$s_{ini}$	$v_{ini}$	$t_{dep}$	$\Delta h_{dep}$	$s_{dep}$	$v_{dep}$
08-778	179	652	360	166	0.08	52	90	168	0.88	61
08-785	167	760	1230	16	0.02	51	2250	1	0.92	53
08-789	59	333	315	4	0.08	53	2475	-9	0.93	51
08-790	241	505	285	-92	0.13	48	75	-171	0.85	58
08-797	19	2185	540	1	0.34	52	2730	-14	0.85	53
<b>NE40</b>										
07-393	327	1176	225	125	0.24	53	720	5	0.87	63
08-758	359	418	270	-146	0.13	53	60	102	0.53	65
08-763	16	425	480	-146	0.14	53	2985	-30	0.83	62
08-771	292	192	45	37	0.16	45	60	60	0.69	69
08-778	43	212	120	-140	0.19	50	420	-94	0.34	52
08-779	2	944	285	-177	0.23	52	3015	-4	0.90	61
08-785	295	356	360	-116	0.08	49	780	-148	0.15	48
08-789	347	2606	690	159	0.18	57	120	157	0.76	64
08-790	309	178	135	-170	0.04	45	345	-139	0.44	47
<b>SW40</b>										
05-1012	73	810	150	9	0.49	43	60	8	0.83	47
05-1036	140	374	90	55	0.27	54	1035	2	0.79	52
05-1044	274	57	60	-34	0.03	49	105	68	0.74	50
05-1054	217	259	75	148	0.15	48	315	-45	0.54	46
05-1067	100	769	135	29	0.43	54	330	29	0.69	56
05-1078	46	952	150	-11	0.51	46	270	-9	0.81	54
07-387	193	282	60	133	0.27	51	90	97	0.64	61
07-389	56	2239	315	-14	0.46	54	555	-1	0.83	56
08-771	121	233	210	68	0.01	53	645	-57	0.88	61
08-779	132	1654	150	73	0.65	59	195	54	0.82	67

## D.4. Phases of the Flight II - Last Point of Decision

The following table contains data on the behavior after the last point of decision. The variables given are as follows:

- Last Point of Decision: The direction of the point of decision from the release site  $PoD_h$  and the respective distance from the release site  $PoD_{\Delta d}$  in meters.
- Final Homing Phase: The duration of the phase  $t_{home}$  in seconds, the mean heading in relation to the home direction  $\Delta h_{home}$ , the mean steadiness of the pigeon's flight  $s_{home}$  and the average speed  $v_{home}$  in km/h.

**Table D.4.** – Behavior after the last point of decision

ID	PoD's	$PoD_h$	$PoD_d$	$t_{home}$	$\Delta h_{home}$	$s_{home}$	$v_{home}$
<b>N30-F1</b>							
07-354	2	159	4763	1515	-20	0.85	67
07-364	4	197	18646	765	-9	0.86	66
07-366	1	160	4729	1530	-20	0.85	67
07-369	2	77	1581	3585	-5	0.52	56
07-382	3	191	24980	345	-16	0.83	70
07-386	2	167	14208	1005	-11	0.93	61
07-388	4	183	17888	1155	18	0.79	50
07-392	2	196	2046	1605	4	0.87	65
07-399	4	180	24468	540	9	0.86	58
07-403	4	170	11865	1245	-23	0.83	67
07-410	3	196	11080	1470	11	0.86	56
<b>N30-F4</b>							
07-364	1	235	617	1665	-22	0.91	68
07-366	4	174	11952	1350	3	0.90	57
07-371	3	165	9563	2070	2	0.80	50
07-382	5	175	22327	495	-4	0.83	53
07-389	2	153	3309	2040	9	0.84	57
07-392	1	239	542	1635	-22	0.91	68
07-393	2	159	8799	1740	-20	0.86	56

Table D.4. – Behavior after the last point of decision

ID	PoD's	$PoD_h$	$PoD_d$	$t_{home}$	$\Delta h_{home}$	$s_{home}$	$v_{home}$
07-399	3	165	9569	2070	2	0.80	50
07-410	4	179	11185	1275	11	0.87	63
<b>N30-F8</b>							
07-354	2	209	1204	2025	-10	0.85	61
07-364	1	147	355	1710	-3	0.87	70
07-366	3	169	11425	1335	-23	0.87	62
07-367	2	314	1217	2175	-10	0.85	60
07-371	1	204	380	2025	-23	0.85	63
07-377	4	182	18115	945	-26	0.86	56
07-379	2	182	19043	870	-22	0.85	58
07-386	2	188	28489	135	-8	0.84	67
07-389	2	182	10498	1410	-2	0.89	57
07-393	2	182	17310	990	-9	0.92	53
07-399	3	274	1209	2580	-34	0.75	56
07-407	2	207	4442	2010	-6	0.84	55
07-410	4	183	7270	1920	9	0.71	59
<b>N30-F12</b>							
07-351	2	147	763	1665	-10	0.94	68
07-354	1	196	36	1935	-7	0.83	67
07-366	2	165	6459	1410	7	0.92	68
07-367	2	179	3817	2280	-3	0.87	49
07-379	2	198	8601	1425	-9	0.91	61
07-382	3	165	8540	1860	-8	0.84	52
07-392	1	196	29	1935	-7	0.83	67
07-393	1	245	767	2055	-2	0.93	56
07-399	2	171	12473	1425	-20	0.89	53
07-407	2	180	16872	915	-5	0.90	56
07-410	2	171	7601	1215	6	0.94	64
<b>N30-F13</b>							
07-354	3	189	20358	855	-5	0.88	49
07-357	2	177	2308	1365	-20	0.93	78
07-375	3	170	11492	1635	-21	0.79	56
07-377	1	163	965	2400	-9	0.85	53



Table D.4. – Behavior after the last point of decision

ID	PoD's	$PoD_h$	$PoD_d$	$t_{home}$	$\Delta h_{home}$	$s_{home}$	$v_{home}$
07-381	3	166	8813	1170	-23	0.92	67
07-386	1	191	2116	1305	-1	0.94	83
07-389	2	193	2157	1305	-1	0.93	83
07-392	1	190	251	1650	-19	0.87	73
07-393	3	191	10391	1980	-13	0.82	45
07-402	3	170	8898	2070	-12	0.82	48
07-405	2	32	6977	2115	-4	0.90	70
07-408	2	113	1529	2910	-19	0.70	54
07-410	2	165	1058	1575	3	0.85	77
<b>N30-F16</b>							
07-354	2	210	2551	1755	-4	0.89	64
07-357	1	187	1315	1770	-17	0.92	61
07-375	2	170	18867	1065	-19	0.66	60
07-379	1	199	4759	1785	-8	0.86	61
07-382	2	164	7914	1290	-23	0.90	62
07-386	2	182	10507	1185	-1	0.95	64
07-387	1	186	1303	1500	-19	0.91	62
07-402	2	243	303	1890	-8	0.86	66
07-405	4	31	2513	2340	-3	0.88	57
07-408	2	91	128	2190	-9	0.82	61
<b>S30-F1</b>							
08-797	4	336	20807	1320	2	0.93	51
<b>S30-F2</b>							
08-758	2	350	20740	945	4	0.92	53
08-779	2	324	17812	1740	-8	0.86	51
08-783	3	338	18652	1245	-2	0.88	56
08-785	2	2	23888	585	-1	0.92	47
08-787	2	28	3895	2085	-5	0.82	54
08-797	2	349	19647	885	-12	0.93	50
<b>S30-F4</b>							
08-752	3	6	6662	2730	-44	0.43	57
08-755	2	1	3410	1740	-23	0.79	64
08-758	1	225	451	1755	-10	0.89	66

Table D.4. – Behavior after the last point of decision

ID	PoD's	$PoD_h$	$PoD_d$	$t_{home}$	$\Delta h_{home}$	$s_{home}$	$v_{home}$
08-765	1	158	93	105	-21	0.78	59
08-783	2	330	302	1590	-27	0.83	62
08-785	3	281	145	1710	-12	0.91	66
08-787	2	192	648	1725	-3	0.91	67
08-789	1	216	420	2595	-11	0.60	64
08-797	1	310	297	1485	19	0.92	73
<b>S30-F8</b>							
08-752	1	28	244	1470	-26	0.96	62
08-755	2	359	11679	795	-25	0.91	71
08-758	2	18	6884	1485	-26	0.80	65
08-765	2	192	150	1785	-21	0.89	65
08-771	1	334	322	1725	-21	0.90	65
08-778	2	10	80	1695	-24	0.92	62
08-779	1	212	351	1845	-19	0.89	63
08-785	2	17	6530	1350	-20	0.87	68
08-789	3	336	17719	1005	-5	0.95	69
08-790	2	6	18509	645	-24	0.90	59
08-797	3	7	24820	270	3	0.88	72
<b>S30-F12</b>							
08-752	3	5	4859	1905	-11	0.85	53
08-758	1	308	195	1965	-7	0.92	57
08-771	2	9	23229	135	-3	0.96	58
08-785	3	211	592	2280	-9	0.86	54
08-789	3	358	22082	630	-12	0.83	53
08-790	1	281	129	1965	-22	0.90	49
08-797	2	7	17051	750	-13	0.94	56
<b>N60</b>							
07-357	2	190	46930	495	-19	0.90	61
07-386	4	269	13745	3660	-13	0.81	63
07-387	4	195	34334	1185	-14	0.94	63
07-389	2	222	3167	3300	-3	0.92	60
07-402	5	269	13733	3675	-14	0.81	63
07-405	4	283	15067	5550	-5	0.70	51

Table D.4. – Behavior after the last point of decision

ID	PoD's	$PoD_h$	$PoD_d$	$t_{home}$	$\Delta h_{home}$	$s_{home}$	$v_{home}$
<b>S60</b>							
08-752	5	7	36081	1470	-41	0.71	50
08-758	2	7	51639	315	-6	0.95	54
08-763	2	14	29931	2265	-15	0.90	51
08-778	5	16	29718	2415	-24	0.84	52
08-785	2	14	29969	2715	-8	0.71	53
08-789	2	6	32422	1845	-27	0.77	50
08-790	6	3	12021	3990	-13	0.84	51
08-797	2	2	36698	735	-52	0.81	60
<b>NE40</b>							
08-763	1	16	425	2985	-30	0.83	62
08-771	5	220	30144	1080	-16	0.79	62
08-779	1	2	944	3015	-4	0.90	61
08-785	4	201	15713	2070	-14	0.85	62
<b>SW40</b>							
05-1012	3	82	2185	2940	7	0.90	55
05-1054	5	68	25113	1620	-7	0.80	48
07-382	3	36	20730	1275	-15	0.84	61
07-387	4	35	24858	1395	-18	0.88	60
07-389	3	47	22451	1485	-7	0.91	56
08-771	6	57	28982	960	-17	0.86	58
08-779	3	61	30850	810	-2	0.90	55

## D.5. Time Series Analysis I - Correlation Dimension

The following table contains data on the calculation of the correlation dimension, including the number of the phase P. No., the number of data points  $dp$ , the embedding lag  $\tau$ , the embedding dimension  $m$ , as well as the correlation dimension of the original time series  $d_2$  and the two sub samples  $d_{21}$  and  $d_{22}$ .

**Table D.5.** – Correlation dimension estimates

ID	P. No.	dp	$\tau$	$m$	$d_2$	$d_{21}$	$d_{22}$
<b>N30-F1</b>							
07-366	2	1530	14	4	3.3	2.5	3.2
07-382	4	1155	9	5	3.9	3.4	3.7
07-392	4	1605	15	5	3.7	3.0	3.5
07-399	4	1095	10	5	3.7	3.3	3.1
07-410	6	1470	11	9	3.7	3.2	3.2
<b>N30-F4</b>							
07-364	2	1665	9	3	3.6	3.0	3.6
07-366	8	1350	8	4	4.1	3.5	3.8
07-389	4	2040	10	3	3.5	3.3	3.2
07-393	4	1740	6	3	3.7	3.5	3.7
07-410	8	1275	10	3	3.3	2.8	3.2
<b>N30-F8</b>							
07-364	2	1710	15	5	3.4	3.5	3.4
07-366	6	1335	12	3	3.3	2.9	3.0
07-367	4	2175	15	4	3.7	3.1	3.6
07-371	2	2025	13	3	3.4	3.0	3.3
07-379	2	1680	12	3	3.3	2.9	3.2
07-389	4	1410	7	6	4.1	3.2	4.0
07-393	2	1095	12	3	3.3	2.8	3.2
07-399	6	2580	8	5	4.4	4.1	4.2
07-407	4	2010	7	4	4.1	3.6	3.4
07-410	8	1920	21	5	3.7	3.2	3.6
<b>N30-F12</b>							
07-351	4	1665	12	4	3.8	3.4	3.6

Table D.5. – Correlation dimension estimates

ID	P. No.	dp	$\tau$	$m$	$d_2$	$d_{21}$	$d_{22}$
07-354	2	1935	10	4	3.9	3.3	3.8
07-366	4	1410	24	3	3.2	3.3	2.8
07-382	4	1185	13	3	2.6	1.9	2.6
07-382	6	1860	18	3	3.3	3.1	2.9
07-392	2	1935	16	3	3.3	2.8	3.3
07-393	2	2055	15	4	4.1	3.6	4.1
07-410	4	1215	13	5	3.9	3.7	3.8
<b>N30-F13</b>							
07-375	4	1065	14	3	2.9	2.4	2.9
07-377	2	2400	14	8	3.7	4.2	4.5
07-381	6	1170	6	3	3.6	3.3	3.6
07-386	2	1305	9	4	3.7	3.2	3.4
07-393	6	1980	9	5	4.8	4.6	4.7
07-402	6	2070	15	3	3.6	3.3	3.6
07-408	4	2910	25	3	3.4	2.9	3.4
07-410	4	1575	10	5	4.2	3.7	3.9
<b>N30-F16</b>							
07-354	4	1755	10	3	3.4	3.1	3.5
07-357	2	1770	18	6	3.3	3.4	4.0
07-375	4	1065	13	3	3.0	2.3	2.9
07-375	2	1140	9	4	3.5	3.1	3.3
07-382	4	1290	8	3	3.3	3.0	3.4
07-386	4	1185	9	4	4.0	3.3	3.6
07-387	2	1500	12	5	3.8	2.8	3.6
07-389	4	1470	18	5	3.3	2.7	3.3
07-405	8	2340	6	6	5.1	4.7	5.2
<b>S30-F1</b>							
08-785	4	2175	13	6	4.8	4.9	4.3
08-797	6	1470	13	3	3.3	3.2	3.2
<b>S30-F2</b>							
08-779	4	1740	12	3	3.5	3.2	3.3
08-779	2	1170	5	5	4.5	4.2	4.1
08-783	6	1245	7	4	4.2	4.1	3.7



Table D.5. – Correlation dimension estimates

ID	P. No.	dp	$\tau$	$m$	$d_2$	$d_{21}$	$d_{22}$
08-785	2	1470	8	4	3.8	3.6	3.6
08-787	4	2085	11	4	4.6	3.5	4.3
08-797	2	1440	13	4	4.0	3.5	3.6
<b>S30-F4</b>							
08-752	6	2730	12	4	3.7	3.3	3.7
08-755	4	1740	10	3	3.1	2.7	3.0
08-758	2	1755	9	4	3.8	3.1	3.5
08-771	1	1305	5	3	2.5	2.3	2.3
08-771	4	1830	16	4	3.4	3.1	3.4
08-783	4	1590	8	3	3.6	3.1	3.0
08-785	6	1710	16	3	3.4	3.1	3.2
08-790	6	1020	13	4	3.7	3.0	3.5
08-797	2	1485	11	3	3.2	3.5	3.0
<b>S30-F8</b>							
08-752	2	1470	13	5	4.2	3.9	3.8
08-758	4	1485	15	5	3.9	3.5	3.7
08-765	4	1785	10	5	4.1	3.4	4.0
08-771	2	1725	10	4	4.2	3.5	3.8
08-778	4	1695	13	4	3.9	3.8	3.5
08-779	2	1845	5	3	3.3	3.6	3.5
08-785	4	1350	9	5	4.1	3.3	4.0
<b>S30-F12</b>							
08-752	6	1905	7	6	4.2	4.4	3.5
08-790	2	1965	8	2	2.5	2.5	2.8
<b>N60</b>							
07-354	6	1410	19	3	2.6	2.4	2.6
07-357	2	2220	23	3	3.2	2.9	2.8
07-357	3	1260	9	3	3.3	2.9	3.1
07-386	8	3660	13	3	3.4	3.2	3.8
07-387	4	1500	9	4	3.5	3.0	3.3
07-389	4	3300	7	4	4.6	4.2	4.3
07-402	10	3675	11	5	4.4	3.5	4.4
07-405	6	1125	16	3	3.0	2.7	2.8

Table D.5. – Correlation dimension estimates

ID	P. No.	dp	$\tau$	$m$	$d_2$	$d_{21}$	$d_{22}$
07-405	8	5550	7	4	4.4	4.0	4.3
<b>S60</b>							
08-752	6	1035	9	5	3.8	3.5	3.7
08-752	10	1470	9	6	4.5	4.5	4.3
08-755	2	1050	12	4	3.2	2.8	3.1
08-763	2	2235	15	5	4.2	3.7	3.8
08-778	7	1230	7	3	3.3	3.1	3.2
08-778	10	2415	18	3	3.4	2.8	3.2
08-778	9	3585	13	4	4.3	3.9	3.9
08-785	2	2250	11	4	4.0	3.7	3.8
08-785	4	2715	18	4	4.2	3.6	4.3
08-789	2	2475	17	3	3.5	3.1	3.4
08-789	4	1845	13	4	3.9	3.3	3.9
08-790	12	3990	6	4	4.5	4.3	4.4
08-797	2	2730	19	5	4.2	3.8	3.7
<b>NE40</b>							
08-785	7	1740	11	6	3.1	2.8	2.5
08-771	10	1080	11	5	3.5	3.2	3.2
08-771	6	1500	13	4	3.7	3.2	3.5
08-778	8	2880	10	3	3.7	3.5	3.3
08-785	8	2070	17	7	3.7	4.2	3.9
08-763	2	2985	15	5	4.4	3.8	4.0
08-779	2	3015	18	6	4.5	3.8	4.4
<b>SW40</b>							
05-1054	9	1650	14	3	3.0	2.8	2.6
05-1054	10	1620	14	5	3.4	2.8	3.0
08-779	3	1140	8	3	3.5	2.8	2.9
07-382	6	1275	10	4	3.8	3.3	3.4
07-382	2	1005	8	6	3.9	4.3	3.4
07-387	4	1605	10	9	3.4	2.8	2.9
07-387	8	1395	10	4	3.6	3.4	3.0

## D.6. Time Series Analysis II - Largest Lyapunov Exponent

The following table contains data on the calculation of the largest Lyapunov exponent, including the number of the phase P. No., the number of data points  $dp$ , the embedding lag  $\tau$ , the embedding dimension  $m$ , the largest Lyapunov exponent for the original time series  $\lambda$  and the two sub-samples  $\lambda_1$  and  $\lambda_2$ .

**Table D.6.** – Largest Lyapunov exponents

ID	P. No.	dp	$\tau$	$m$	$\lambda$	$\lambda_1$	$\lambda_2$
<b>N30-F1</b>							
07-364	4	915	11	4	0.016	0.021	0.022
07-369	4	3585	8	4	0.026	0.026	0.027
07-386	2	930	9	4	0.016	0.017	0.018
07-392	4	1605	15	5	0.010	0.010	0.008
07-399	4	1095	10	5	0.027	0.031	0.028
07-410	4	690	13	3	0.017	0.006	0.010
07-410	6	1470	11	9	0.022	0.024	0.020
<b>N30-F4</b>							
07-366	8	1350	8	4	0.026	0.026	0.031
07-371	4	690	8	3	0.017	0.014	0.018
07-382	8	945	8	3	0.028	0.024	0.022
07-389	4	2040	10	3	0.025	0.025	0.024
07-393	4	1740	6	3	0.045	0.043	0.042
07-399	4	630	10	3	0.019	0.027	0.028
<b>N30-F8</b>							
07-354	4	2025	14	7	0.011	0.011	0.010
07-366	6	1335	12	3	0.020	0.021	0.025
07-367	4	2175	15	4	0.014	0.017	0.016
07-389	4	1410	7	6	0.016	0.019	0.018
07-389	2	810	9	4	0.020	0.021	0.018
07-393	2	1095	12	3	0.018	0.026	0.022
07-407	4	2010	7	4	0.012	0.012	0.014
07-410	4	510	16	3	0.012	0.042	0.012

Table D.6. – Largest Lyapunov exponents

ID	P. No.	dp	$\tau$	$m$	$\lambda$	$\lambda_1$	$\lambda_2$
07-410	8	1920	21	5	0.020	0.023	0.021
<b>N30-F12</b>							
07-351	4	1665	12	4	0.012	0.013	0.010
07-354	1	600	8	4	0.019	0.025	0.022
07-379	2	675	13	4	0.006	0.010	0.005
07-382	6	1860	18	3	0.007	0.007	0.008
07-382	4	1185	13	3	0.018	0.025	0.020
07-399	2	690	11	4	0.024	0.024	0.026
07-407	4	915	15	4	0.010	0.007	0.007
07-407	2	810	6	4	0.025	0.023	0.021
07-410	4	1215	13	5	0.018	0.016	0.017
<b>N30-F13</b>							
07-354	1	1170	10	4	0.017	0.022	0.020
07-354	6	855	7	3	0.017	0.023	0.024
07-375	4	1065	14	3	0.013	0.011	0.016
07-377	2	2400	14	8	0.016	0.016	0.015
07-386	2	1305	9	4	0.023	0.029	0.026
07-392	2	1650	11	8	0.014	0.013	0.014
07-393	6	1980	9	5	0.032	0.035	0.037
07-408	4	2910	25	3	0.022	0.020	0.023
07-410	4	1575	10	5	0.017	0.015	0.014
<b>N30-F16</b>							
07-357	2	1770	18	6	0.016	0.014	0.019
07-375	4	1065	13	3	0.013	0.016	0.018
07-375	2	1140	9	4	0.018	0.020	0.019
07-379	4	675	8	3	0.022	0.018	0.018
07-382	4	1290	8	3	0.029	0.034	0.031
07-386	4	1185	9	4	0.015	0.019	0.015
07-387	2	1500	12	5	0.015	0.015	0.017
07-389	4	1470	18	5	0.005	0.007	0.010
07-402	4	1890	15	6	0.014	0.017	0.015
07-405	8	2340	6	6	0.028	0.024	0.019
<b>S30-F1</b>							

Table D.6. – Largest Lyapunov exponents

ID	P. No.	dp	$\tau$	$m$	$\lambda$	$\lambda_1$	$\lambda_2$
08-785	4	2175	13	6	0.010	0.010	0.010
08-785	1	570	8	4	0.028	0.022	0.022
<b>S30-F2</b>							
08-758	2	1185	14	4	0.019	0.022	0.019
08-779	4	1740	12	3	0.023	0.020	0.024
08-779	2	1170	5	5	0.023	0.016	0.021
08-785	2	1470	8	4	0.012	0.009	0.013
08-785	4	585	10	4	0.025	0.029	0.027
08-797	2	1440	13	4	0.024	0.017	0.019
<b>S30-F4</b>							
08-752	4	570	10	9	0.016	0.019	0.015
08-755	4	1740	10	3	0.012	0.010	0.014
08-755	3	855	5	4	0.018	0.018	0.021
08-771	1	1305	5	3	0.022	0.020	0.023
08-783	4	1590	8	3	0.013	0.016	0.015
08-789	2	2595	9	7	0.029	0.034	0.029
08-790	6	1020	13	4	0.023	0.022	0.026
<b>S30-F8</b>							
08-752	2	1470	13	5	0.009	0.011	0.009
08-758	4	1485	15	5	0.013	0.015	0.011
08-771	2	1725	10	4	0.019	0.018	0.023
08-778	4	1695	13	4	0.023	0.026	0.021
08-779	2	1845	5	3	0.027	0.027	0.032
08-785	4	1350	9	5	0.023	0.020	0.025
08-797	4	825	11	3	0.021	0.024	0.022
<b>S30-F12</b>							
08-752	6	1905	7	6	0.020	0.023	0.026
08-771	3	615	5	4	0.037	0.034	0.032
08-789	6	630	9	4	0.012	0.006	0.003
08-789	2	795	9	4	0.025	0.023	0.028
08-790	2	1965	8	2	0.013	0.014	0.016
08-797	4	750	5	3	0.030	0.034	0.032
<b>N60</b>							



Table D.6. – Largest Lyapunov exponents

ID	P. No.	dp	$\tau$	$m$	$\lambda$	$\lambda_1$	$\lambda_2$
07-354	6	1410	19	3	0.011	0.019	0.017
07-354	1	600	12	3	0.016	0.007	0.012
07-357	2	2220	23	3	0.011	0.015	0.011
07-386	8	3660	13	3	0.011	0.012	0.014
07-389	4	3300	7	4	0.014	0.013	0.016
07-402	10	3675	11	5	0.013	0.014	0.017
07-405	6	1125	16	3	0.016	0.016	0.016
<b>S60</b>							
08-752	6	1035	9	5	0.012	0.016	0.012
08-752	4	795	8	3	0.016	0.022	0.024
08-763	2	2235	15	5	0.014	0.013	0.017
08-778	9	3585	13	4	0.014	0.011	0.010
08-778	10	2415	18	3	0.025	0.027	0.025
08-785	4	2715	18	4	0.033	0.034	0.031
08-789	2	2475	17	3	0.011	0.010	0.014
08-790	12	3990	6	4	0.020	0.021	0.019
08-797	2	2730	19	5	0.013	0.012	0.014
<b>NE40</b>							
08-763	2	2985	15	5	0.017	0.014	0.017
08-771	10	1080	11	5	0.023	0.022	0.027
08-778	8	2880	10	3	0.018	0.019	0.019
08-779	2	3015	18	6	0.035	0.038	0.037
08-785	8	2070	17	7	0.012	0.014	0.017
<b>SW40</b>							
05-1054	6	795	7	5	0.013	0.010	0.011
05-1054	9	1650	14	3	0.018	0.008	0.007
05-1054	10	1620	14	5	0.009	0.009	0.010
07-382	2	1005	8	6	0.011	0.013	0.011
07-382	5	735	8	4	0.027	0.018	0.014
07-387	4	1605	10	9	0.005	0.009	0.012
07-387	8	1395	10	4	0.015	0.006	0.009
07-389	4	600	5	5	0.022	0.020	0.024
07-389	6	1485	10	3	0.019	0.015	0.012

Table D.6. – Largest Lyapunov exponents

ID	P. No.	dp	$\tau$	$m$	$\lambda$	$\lambda_1$	$\lambda_2$
07-393	2	630	5	4	0.028	0.019	0.018
07-393	6	1665	19	3	0.022	0.012	0.010
08-771	6	585	6	3	0.029	0.014	0.019
08-771	12	960	14	5	0.009	0.006	0.009



# Bibliography

- ABLE, K.P., GERGITS, W.F., CHERRY, J.D., & TERRILL, S.B. 1984. Homing behavior of wood thrushes (*Hyalocichla mustelina*). *Behavioral ecology and sociobiology*, **15**(1), 39–43.
- ALERSTAM, T., HAKE, M., & KJELLÉN, N. 2006. Temporal and spatial patterns of repeated migratory journeys by ospreys. *Animal behaviour*, **71**(3), 555–566.
- ANDERSON, T.W., & DARLING, D.A. 1952. Asymptotic theory of certain "goodness of fit" criteria based on stochastic processes. *The annals of mathematical statistics*, 193–212.
- BALDACCINI, N.E., GIUNCHI, D., & MONGINI, E. 1999. A long term study on initial orientation in sand martins (*Riparia riparia*). *Behaviour*, **136**(10), 1311–1323.
- BALDACCINI, N.E., GIUNCHI, D., MONGINI, E., & RAGIONIERI, L. 2001. Release experiments with wild rock doves (*Columba l. livia* Gm.). *Behaviour*, **138**(8), 923–936.
- BARRON, D.G., BRAWN, J.D., & WEATHERHEAD, P.J. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in ecology and evolution*, **1**(2), 180–187.
- BASCHELET, E. 1981. *Circular statistics in biology*. London: Academic Press.
- BEASON, R., DUSSOURD, N., & DEUTSCHLANDER, M. 1995. Behavioural evidence for the use of magnetic material in magnetoreception by a migratory bird. *Journal of experimental biology*, **198**(1), 141–146.
- BEASON, R.C., WILTSCHKO, R., & WILTSCHKO, W. 1997. Pigeon homing: effects of magnetic pulses on initial orientation. *The auk*, **114**(3), 405–415.
- BECKER, J., & VAN RADEN, H. 1986. Meteorologische Gesichtspunkte zur olfaktorischen Navigationshypothese. *Journal of ornithology*, **127**(1), 1–8.
- BENVENUTI, S., & FIASCHI, V. 1983. Pigeon homing: combined effect of olfactory deprivation and visual impairment. *Comparative biochemistry and physiology part a: Physiology*, **76**(4), 719–723.
- BERNDT, R., & WINKEL, W. 1979. Verfrachtungs-Experimente zur Frage der Geburtsortsprägung beim Trauerschnäpper (*Ficedula hypoleuca*). *Journal of ornithology*, **120**(1), 41–53.
- BINGMAN, V.P., HOUGH, G.E., KAHN, M.C., & SIEGEL, J.J. 2003. The homing pigeon hippocampus and space: In search of adaptive specialization. *Brain, behavior and evolution*, **62**(2), 117–127.

## Bibliography

- BIRO, D., GUILFORD, T., DELL'OMO, G., & LIPP, H.P. 2002. How the viewing of familiar landscapes prior to release allows pigeons to home faster: evidence from GPS tracking. *Journal of experimental biology*, **205**(24), 3833–3844.
- BIRO, D., MEADE, J., & GUILFORD, T. 2004. Familiar route loyalty implies visual pilotage in the homing pigeon. *Proceedings of the national academy of sciences of the united states of america*, **101**(50), 17440–17443.
- BIRO, D., FREEMAN, R., MEADE, J., ROBERTS, S., & GUILFORD, T. 2007. Pigeons combine compass and landmark guidance in familiar route navigation. *Proceedings of the national academy of sciences*, **104**(18), 7471–7476.
- BÉLISLE, M., DESROCHERS, A., & FORTIN, M.J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology*, **82**(7), 1893–1904.
- BOWLIN, M.S., HENNINGSSON, P., MUIJRES, F.T., VLEUGELS, R.H.E., LIECHTI, F., & HEDENSTRÖM, A. 2010. The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods in ecology and evolution*.
- BRAITHWAITE, VA. 1993. When does previewing the landscape affect pigeon homing? *Ethology*, **95**(2), 141–151.
- BRAITHWAITE, VA., & GUILFORD, T. 1995. A loft with a view: exposure to a natural landscape during development may encourage adult pigeons to use visual landmarks during homing. *Animal behaviour*, **49**(1), 252–254.
- BRAMANTI, M., DALL'ANTONIA, L., & PAPI, F. 1988. A new technique to monitor the flight paths of birds. *Journal of experimental biology*, **134**(1), 467–472.
- BURT, T., HOLLAND, R., & GUILFORD, T. 1997. Further evidence for visual landmark involvement in the pigeon's familiar area map. *Animal behaviour*, **53**(6), 1203–1209.
- CASTILLO, VM, & HOOVER, W.G. 1998. Entropy production and Lyapunov instability at the onset of turbulent convection. *Physical review e*, **58**(6), 7350–7354.
- CHELAZZI, G., & PARDI, L. 1972. Experiments on the homing behaviour of caged pigeons. *Monitore zoologico italiano*, **6**, 63–73.
- CRISTOL, D.A., REYNOLDS, E.B., LECLERC, J.E., DONNER, A.H., FARABAUGH, C.S., & ZIEGENFUS, C.W.S. 2003. Migratory dark-eyed juncos, *Junco hyemalis*, have better spatial memory and denser hippocampal neurons than nonmigratory conspecifics. *Animal behaviour*, **66**(2), 317–328.
- DENNIS, T.E., RAYNER, M.J., & WALKER, M.M. 2007. Evidence that pigeons orient to geomagnetic intensity during homing. *Proceedings of the royal society b: Biological sciences*, **274**(1614), 1153–1158.



- EBINGER, P. 1995. Domestication and Plasticity of Brain Organization in Mallards (*Anas platyrhynchos*). *Brain, behavior and evolution*, **45**(5), 286–300.
- ECKMANN, J.P., & RUELLE, D. 1985. Ergodic theory of chaos and strange attractors. *Reviews of modern physics*, **57**(3), 617–656.
- FIASCHI, V., FARINA, A., & IOALE, P. 1974. Homing experiments on swifts (*Apus apus* L.) deprived of olfactory perception. *Monitore zoologico italiano*, **8**, 235–244.
- FLEISSNER, G., HOLTkamp-RÖTZLER, E., HANZLIK, M., WINKLHOFER, M., FLEISSNER, G., PETERSEN, N., & WILTSCHKO, W. 2003. Ultrastructural analysis of a putative magnetoreceptor in the beak of homing pigeons. *The journal of comparative neurology*, **458**(4), 350–360.
- FLEISSNER, G., STAHL, B., THALAU, P., FALKENBERG, G., & FLEISSNER, G. 2007. A novel concept of Fe-mineral-based magnetoreception: histological and physicochemical data from the upper beak of homing pigeons. *Naturwissenschaften*, **94**(8), 631–642.
- FRASER, A.M., & SWINNEY, H.L. 1986. Independent coordinates for strange attractors from mutual information. *Physical review a*, **33**(2), 1134–1140.
- FÜLLER, E., KOWALSKI, U., & WILTSCHKO, R. 1983. Orientation of homing pigeons: compass orientation vs piloting by familiar landmarks. *Journal of comparative physiology a: Neuroethology, sensory, neural, and behavioral physiology*, **153**(1), 55–58.
- GAGLIARDO, A., ODETTI, F., & IOALÈ, P. 2001. Relevance of visual cues for orientation at familiar sites by homing pigeons: an experiment in a circular arena. *Proceedings of the royal society of london. series b: Biological sciences*, **268**(1480), 2065–2070.
- GAGLIARDO, A., ODETTI, F., & IOALÈ, P. 2005. Factors reducing the expected deflection in initial orientation in clock-shifted homing pigeons. *Journal of experimental biology*, **208**(3), 469–478.
- GAGLIARDO, A., SAVINI, M., DE SANTIS, A., DELL'OMO, G., & IOALÈ, P. 2009. Reorientation in clock-shifted homing pigeons subjected to a magnetic disturbance: a study with GPS data loggers. *Behavioral ecology and sociobiology*, **64**(2), 289–296.
- GESSAMAN, J.A., & NAGY, K.A. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor*, **90**(3), 662–668.
- GRASSBERGER, P., & PROCACCIA, I. 1983a. Characterization of strange attractors. *Physical review letters*, **50**(5), 346–349.
- GRASSBERGER, P., & PROCACCIA, I. 1983b. Measuring the strangeness of strange attractors. *Physica d: Nonlinear phenomena*, **9**(1-2), 189–208.

## Bibliography

- GRAUE, L.C. 1963. The effect of phase shifts in the day-night cycle on pigeon homing at distances of less than one mile. *Ohio j. sci*, **63**, 214–217.
- GRIFFIN, D.R. 1940. Homing experiments with Leach's petrels. *The auk*, **57**(1), 61–74.
- GRIFFIN, D.R. 1943. Homing experiments with herring gulls and common terns. *Bird-banding*, **14**(1), 7–33.
- GRIFFIN, D.R. 1952a. Airplane observations of homing pigeons. *Bulletin of the museum of comparative zoology*, **107**, 411–440.
- GRIFFIN, D.R. 1952b. Bird Navigation. *Biological reviews*, **27**(4), 359–390.
- GRIFFIN, D.R., & HOCK, R.J. 1949. Airplane observations of homing birds. *Ecology*, **30**(2), 176–198.
- GRÜTER, M., WILTSCHKO, R., & WILTSCHKO, W. 1982. *Distribution of Release Site Biases Around Frankfurt a.M., Germany*. Springer. Pages 222–231.
- GUILFORD, T., ROBERTS, S., BIRO, D., & REZEK, I. 2004. Positional entropy during pigeon homing II: navigational interpretation of Bayesian latent state models. *Journal of theoretical biology*, **227**(1), 25–38.
- HAGSTRUM, J.T. 2001. Infrasound and the avian navigational map. *The journal of navigation*, **54**(3), 377–391.
- HAKE, M., KJELLÉN, N., & ALERSTAM, T. 2001. Satellite tracking of Swedish Ospreys *Pandion haliaetus*: autumn migration routes and orientation. *Journal of avian biology*, **32**(1), 47–56.
- HAKE, M., KJELLÉN, N., & ALERSTAM, T. 2003. Age-dependent migration strategy in honey buzzards *Pernis apivorus* tracked by satellite. *Oikos*, **103**(2), 385–396.
- HANZLIK, M., HEUNEMANN, C., HOLTkamp-RÖTZLER, E., WINKLHOFFER, M., PETERSEN, N., & FLEISSNER, G. 2000. Superparamagnetic magnetite in the upper beak tissue of homing pigeons. *Biometals*, **13**(4), 325–331.
- HATCH, J.J. 1971. Homing Experiments with Arctic Terns Released over Land and Sea. *Bird-banding*, 47–54.
- HEINROTH, K., & HEINROTH, O. 1941. Das Heimfinde-Vermögen der Brieftauben. *Journal of ornithology*, **89**(2), 213–256.
- HITCHCOCK, H.B. 1952. Airplane observations of homing pigeons. *Proceedings of the american philosophical society*, **96**(3), 270–289.
- HOFMANN-WELLENHOF, B., LICHTENEGGER, H., & COLLINS, J. 1992. *Global positioning System. Theory and Practice*. Springer.

- IOALÈ, P., ODETTI, F., & GAGLIARDO, A. 2006. Do bearing magnets affect the extent of deflection in clock-shifted homing pigeons? *Behavioral ecology and sociobiology*, **60**(4), 516–521.
- KANTZ, H., & SCHREIBER, T. 1997. *Nonlinear time series analysis*. Cambridge University Press.
- KAPLAN, D., & GLASS, L. 1995. *Understanding nonlinear dynamics*. Springer.
- KEETON, W.T. 1971. Magnets interfere with pigeon homing. *Proceedings of the national academy of sciences of the united states of america*, **68**(1), 102.
- KEETON, W.T. 1973. Release-site bias as a possible guide to the map component in pigeon homing. *Journal of comparative physiology a: Neuroethology, sensory, neural, and behavioral physiology*, **86**(1), 1–16.
- KEETON, W.T., & GOBERT, A. 1970. Orientation by untrained pigeons requires the sun. *Proceedings of the national academy of sciences*, **65**(4), 853–856.
- KEETON, W.T., LARKIN, T.S., & WINDSOR, D.M. 1974. Normal fluctuations in the earth's magnetic field influence pigeon orientation. *Journal of comparative physiology a: Neuroethology, sensory, neural, and behavioral physiology*, **95**(2), 95–103.
- KEISER, J.T., ZIEGENFUS, C.W.S., & CRISTOL, D.A. 2005. Homing success of migrant versus nonmigrant dark-eyed juncos (*Junco hyemalis*). *The auk*, **122**(2), 608–617.
- KIEPENHEUER, J. 1993. The ambiguity of initial orientation of homing pigeons. *In: Proceedings of the royal institute of navigation conference, oxford, uk*.
- KOWALSKI, U. 1994. Das Richtungsverhalten verfrachteter Brieftauben (*Columba livia*) im Orientierungskäfig. *Journal of ornithology*, **135**(1), 17–35.
- KOWALSKI, U., & WILTSCHKO, R. 1987. Pigeon homing: familiarity with the release site reduces the release site bias. *Journal of experimental biology*, **133**(1), 457–462.
- KOWALSKI, U., WILTSCHKO, R., & FÜLLER, E. 1988. Normal fluctuations of the geomagnetic field may affect initial orientation in pigeons. *Journal of comparative physiology a: Neuroethology, sensory, neural, and behavioral physiology*, **163**(5), 593–600.
- KRAMER, G. 1957. Experiments in bird orientation and their interpretation. *Ibis*, **99**(2), 196–227.
- KRAMER, G. 1959. Recent experiments on bird orientation. *Ibis*, **101**(3-4), 399–416.
- LAI, Y.C., OSORIO, I., HARRISON, M.A.F., & FREI, M.G. 2002. Correlation-dimension and autocorrelation fluctuations in epileptic seizure dynamics. *Physical review e*, **65**(3), 031921.
- LARKIN, T.S., & KEETON, W.T. 1976. Bar magnets mask the effect of normal magnetic disturbances on pigeon orientation. *Journal of comparative physiology a: Neuroethology, sensory, neural, and behavioral physiology*, **110**(3), 227–231.

## Bibliography

- LEDNOR, A.J., & WALCOTT, C. 1984. The orientation of pigeons at gravity anomalies. *Journal of experimental biology*, **111**(1), 259–265.
- LEDNOR, A.J., & WALCOTT, C. 1988. Orientation of homing pigeons at magnetic anomalies. *Behavioral ecology and sociobiology*, **22**(1), 3–8.
- LÖHRL, H. 1959. Zur Frage des Zeitpunkt einer Prägung auf die Heimatregion beim Halsbandschnäpper (*Ficedula albicollis*). *Journal of ornithology*, **100**(2), 132–140.
- LIPP, H.P., VYSSOTSKI, A.L., WOLFER, D.P., RENAUDINEAU, S., SAVINI, M., TRÖSTER, G., & DELL'OMO, G. 2004. Pigeon homing along highways and exits. *Current biology*, **14**(14), 1239–1249.
- LORENZ, E.N. 1963. Deterministic Nonperiodic Flow. *Journal of the atmospheric sciences*, **20**(2), 130–141.
- MANN, R., FREEMAN, R., OSBORNE, M., GARNETT, R., ARMSTRONG, C., MEADE, J., BIRO, D., GUILFORD, T., & ROBERTS, S. 2010. Objectively identifying landmark use and predicting flight trajectories of the homing pigeon using Gaussian processes. *Journal of the royal society interface*.
- MAZZOTTO, M., NACCI, L., & GAGLIARDO, A. 1999. Homeward orientation of pigeons confined in a circular arena. *Behavioural processes*, **46**(3), 217–225.
- MEADE, J., BIRO, D., & GUILFORD, T. 2005. Homing pigeons develop local route stereotypy. *Proceedings of the royal society b: Biological sciences*, **272**(1558), 17–23.
- MEHLHORN, J., & REHKÄMPER, G. 2009. Neurobiology of the homing pigeon – a review. *Naturwissenschaften*, **96**(9), 1011–1025.
- MICHENER, M.C., & WALCOTT, C. 1967. Homing of Single Pigeons – Analysis of Tracks. *Journal of experimental biology*, **47**(1), 99.
- MIYATA, M., BURIOKA, N., SAKO, T., SUYAMA, H., FUKUOKA, Y., TOMITA, K., HIGAMI, S., & SHIMIZU, E. 2004. A short daytime test using correlation dimension for respiratory movement in OSAHS. *European respiratory journal*, **23**(6), 885–890.
- NASTASE, A.J. 1982. Orientation and homing ability of the Barn Swallow. *Journal of field ornithology*, **53**(1), 15–21.
- NEHMZOW, U. 2006. *Scientific methods in mobile robotics: quantitative analysis of agent behaviour*. Springer.
- PAPANA, A., & KUGIUMTZIS, D. 2008. Evaluation of mutual information estimators on nonlinear dynamic systems. *Complex phenomena in nonlinear systems*, **11**(2), 225–232.
- PAPI, F., & WALLRAFF, H.G. 1982. *Avian navigation*. Springer.

- PAPI, F., FIORE, L., FIASCHI, V., & BENVENUTI, S. 1971. The influence of olfactory nerve section on the homing capacity of carrier pigeons. *Monit. zool. ital.*, **5**, 265–267.
- PFUHL, G., TJELMELAND, H., & BIEGLER, R. 2010. Precision and Reliability in Animal Navigation. *Bulletin of mathematical biology*, 1–27.
- RAMSEY, J.B., & YUAN, H.J. 1990. The statistical properties of dimension calculations using small data sets. *Nonlinearity*, **3**(1), 155–176.
- REHKÄMPER, G., FRAHM, HD, & CNOTKA, J. 2007. Mosaic evolution and adaptive brain component alteration under domestication seen on the background of evolutionary theory. *Brain, behavior and evolution*, **71**(2), 115–126.
- ROSENSTEIN, M.T., COLLINS, J.J., & DE LUCA, C.J. 1993. A practical method for calculating largest Lyapunov exponents from small data sets. *Physica d: Nonlinear phenomena*, **65**(1-2), 117–134.
- RÜPPELL, W. 1935. Heimfindeversuche mit Staren 1934. *Journal of ornithology*, **83**(3), 462–524.
- RÜPPELL, W. 1936. Heimfindeversuche mit Staren und Schwalben 1935. *Journal of ornithology*, **84**(2), 180–198.
- RÜPPELL, W. 1937. Heimfindeversuche mit Staren, Rauchschnalben, Wendehälsen, Rotrückenvürgern und Habichten (1936). *Journal of ornithology*, **85**(1), 120–135.
- RUELLE, D. 1990. Deterministic chaos: the science and the fiction. *Proceedings of the royal society a*, **427**, 241–248.
- RÜPPELL, W., & SCHIFFERLI, A. 1939. Versuche über Winter-Ortstreue an *Larus ridibundus* und *Fulica atra*. *Journal of ornithology*, **87**(2), 224–239.
- SAINT PAUL, U. 1982. Do Geese Use Path Integration for Walking Home. *Avian navigation, springer*, 297–307.
- SANO, M., & SAWADA, Y. 1985. Measurement of the Lyapunov spectrum from a chaotic time series. *Physical review letters*, **55**(10), 1082–1085.
- SARGENT, T.D. 1962. A study of homing in the bank swallow (*Riparia riparia*). *The auk*, **79**(2), 234–246.
- SAUER, F. 1957. Orientation by the stars of night-migrating warblers. *Zeitschrift für tierpsychologie*, **14**, 29–70.
- SCHIFFNER, I., & WILTSCHKO, R. 2009. Point of decision: when do pigeons decide to head home? *Naturwissenschaften*, **96**(2), 251–258.
- SCHIFFNER, I., SIEGMUND, B., & WILTSCHKO, R. 2006. Approaching Home: When do Pigeons recognise their homeloft? *In: 26th european telemetry conference*.



## Bibliography

- SCHMIDT-KÖNIG, K. 1958. Der Einfluss experimentell veränderter Zeitschätzung auf das Heimfindvermögen bei Brieftauben. *Naturwissenschaften*, **45**(2), 47–47.
- SCHMIDT-KÖNIG, K. 1963. On the role of the loft, the distance and site of release in pigeon homing (the "cross-loft experiment"). *The biological bulletin*, **125**(1), 154–164.
- SCHMIDT-KÖNIG, K., & SCHLICHTE, H.J. 1972. Homing in pigeons with impaired vision. *Proceedings of the national academy of sciences*, **69**(9), 2446–2447.
- SCHMIDT-KÖNIG, K., & WALCOTT, C. 1978. Tracks of pigeons homing with frosted lenses. *Animal behaviour*, **26**(2), 480–486.
- SKILES, D.D. 1985. The geomagnetic field: its nature, history, and biological relevance. *in magnetite biomineralization and magnetoreception in organisms: A new biomagnetism, plenum press*, 43–102.
- SKINNER, J.E. 1994. Low-dimensional chaos in biological systems. *Nature biotechnology*, **12**(6), 596–600.
- SMALL, M. 2005. *Applied nonlinear time series analysis: applications in physics, physiology and finance*. World Scientific Pub Co Inc.
- SMALL, M., & TSE, CK. 2004. Optimal embedding parameters: a modelling paradigm. *Physica d: Nonlinear phenomena*, **194**(3-4), 283–296.
- SOUTHERN, W.E. 1959. Homing of purple martins. *The wilson bulletin*, **71**(3), 254–261.
- STAHL, B., FLEISSNER, G., FLEISSNER, G., & FALKENBERG, G. 2006. Cross-species unveiling of a putative avian magnetoreceptor. *Hasylab annual report*, 1269–1270.
- STEFANOVSKA, A., STRLE, S., & KROELJ, P. 1997. On the overestimation of the correlation dimension. *Physics letters a*, **235**(1), 24–30.
- STEINER, I., BURGI, C., WERFFELI, S., DELL'OMO, G., VALENTI, P., TRÖSTER, G., WOLFER, D.P., & LIPP, H.P. 2000. A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiology and behavior*, **71**(5), 589.
- TAKENS, F. 1980. Detecting strange attractors in turbulence. *Lecture notes in mathematics (dynamical systems and turbulence, warwick 1980)*, 366–381.
- THEILER, J. 1986. Spurious dimension from correlation algorithms applied to limited time-series data. *Physical review a*, **34**(3), 2427–2432.
- THEILER, J., & LOOKMAN, T. 1993. Statistical error in a chord estimator of correlation dimension: the "rule of five". *International journal of bifurcation and chaos*, **3**, 765–771.
- TIAN, L., XIAO, B., LIN, W., ZHANG, S., ZHU, R., & PAN, Y. 2007. Testing for the presence of magnetite in the upper-beak skin of homing pigeons. *Biomaterials*, **20**(2), 197–203.

- VON HÜNERBEIN, K., HAMANN, H.J., RÜTER, E., & WILTSCHKO, W. 2000. A GPS-based system for recording the flight paths of birds. *Naturwissenschaften*, **87**(6), 278–279.
- VON SCHWEPPENBURG, G. H. 1933. Zur Theorie der Leitlinie. *Ardea*, **22**, 83–92.
- WAGNER, G. 1970. Verfolgung von Brieftauben im Helikopter. *Revue suisse de zoologie*, **77**, 39–60.
- WALCOTT, C. 1978. *Anomalies in the earth's magnetic field increase the scatter of pigeons' vanishing bearings*. Springer. Pages 143–151.
- WALCOTT, C. 1996. Pigeon homing: observations, experiments and confusions. *The journal of experimental biology*, **199**(1), 21–27.
- WALCOTT, C., & GREEN, R.P. 1974. Orientation of homing pigeons altered by a change in the direction of an applied magnetic field. *Science*, **184**(133), 180–182.
- WALDVOGEL, J.A. 1987. Olfactory navigation in homing pigeons: are the current models atmospherically realistic? *The auk*, **104**(3), 369–379.
- WALLRAFF, G., *et al.* 2003. Zur olfaktorischen Navigation der Vögel. *Journal für ornithologie*, **144**(1), 1–32.
- WALLRAFF, H.G. 1966. Über die Anfangsorientierung von Brieftauben unter geschlossener Wolkenendecke. *Journal of ornithology*, **107**(3), 326–336.
- WALLRAFF, H.G. 1974. *Das navigationssystem der Vögel*. Oldenburg.
- WALLRAFF, H.G. 1989a. Simulated navigation based on assumed gradients of atmospheric trace gases (models on pigeon homing, part 2). *Journal of theoretical biology*, **138**(4), 511–528.
- WALLRAFF, H.G. 1989b. Simulated navigation based on unreliable sources of information (models on pigeon homing. Part 1). *Journal of theoretical biology*, **137**(1), 1–19.
- WALLRAFF, H.G. 1994. Initial orientation of homing pigeons as affected by the surrounding landscape. *Ethology ecology & evolution*, **6**(1), 23–36.
- WALLRAFF, H.G. 2000. Simulated navigation based on observed gradients of atmospheric trace gases (models on pigeon homing, part 3). *Journal of theoretical biology*, **205**(1), 133–145.
- WALLRAFF, H.G., KIEPENHEUER, J., NEUMANN, M.F., & STRENG, A. 1995. Homing experiments with starlings deprived of the sense of smell. *Condor*, **97**(1), 20–26.
- WATSON, J.B., & LASHLEY, K.S. 1915. An historical and experimental study of homing. *Department of marine biology of the carnegie institution of washington*, **7**, 1–82.
- WHITNEY, H. 1936. Differentiable manifolds. *Annals of mathematics*, **37**(3), 645–680.
- WIKSWO, J.P., BARACH, J.P., & FREEMAN, J.A. 1980. Magnetic field of a nerve impulse: first measurements. *Science*, **208**(4439), 53–55.

## Bibliography

- WILLIAMS, M.N., & WILD, J.M. 2001. Trigeminally innervated iron-containing structures in the beak of homing pigeons, and other birds. *Brain research*, **889**(1-2), 243–246.
- WILTSCHKO, R. 1992. Das Verhalten verfrachteter Vögel. *Vogelwarte*, **36**(4), 249–310.
- WILTSCHKO, R., & NEHMZOW, U. 2005. Simulating pigeon navigation. *Animal behaviour*, **69**(4), 813–826.
- WILTSCHKO, R., & WILTSCHKO, W. 1978. Evidence for the use of magnetic outward-journey information in homing pigeons. *Naturwissenschaften*, **65**(2), 112–113.
- WILTSCHKO, R., & WILTSCHKO, W. 1985. Pigeon homing: change in navigational strategy during ontogeny. *Animal behaviour*, **33**(2), 583–590.
- WILTSCHKO, R., & WILTSCHKO, W. 1998. Pigeon homing: effect of various wavelengths of light during displacement. *Naturwissenschaften*, **85**(4), 164–167.
- WILTSCHKO, R., & WILTSCHKO, W. 1999. Das Orientierungssystem der Vögel II. Heimfinden und Navigation. *Journal of ornithology*, **140**(2), 129–164.
- WILTSCHKO, R., & WILTSCHKO, W. 2001. Clock-shift experiments with homing pigeons: a compromise between solar and magnetic information? *Behavioral ecology and sociobiology*, **49**(5), 393–400.
- WILTSCHKO, R., & WILTSCHKO, W. 2003a. Avian navigation: from historical to modern concepts. *Animal behaviour*, **65**(2), 257–272.
- WILTSCHKO, R., & WILTSCHKO, W. 2003b. Orientation behavior of homing pigeons at the Gernsheim anomaly. *Behavioral ecology and sociobiology*, **54**(6), 562–572.
- WILTSCHKO, R., & WILTSCHKO, W. 2009. Avian navigation. *The auk*, **126**(4), 717–743.
- WILTSCHKO, R., KUMPFMÜLLER, R., MUTH, R., & WILTSCHKO, W. 1994a. Pigeon homing: the effect of a clock-shift is often smaller than predicted. *Behavioral ecology and sociobiology*, **35**(1), 63–73.
- WILTSCHKO, R., SIEGMUND, B., & STAPPUT, K. 2005. Navigational strategies of homing pigeons at familiar sites: do landmarks reduce the deflections induced by clock-shifting? *Behavioral ecology and sociobiology*, **59**(2), 303–312.
- WILTSCHKO, R., SCHIFFNER, I., & SIEGMUND, B. 2007. Homing flights of pigeons over familiar terrain. *Animal behaviour*, **74**(5), 1229–1240.
- WILTSCHKO, R., SCHIFFNER, I., & WILTSCHKO, W. 2009a. A strong magnetic anomaly affects pigeon navigation. *Journal of experimental biology*, **212**(18), 2983–2990.
- WILTSCHKO, R., SCHIFFNER, I., FUHRMANN, P., & WILTSCHKO, W. 2010. The Role of the Magnetite-Based Receptors in the Beak in Pigeon Homing. *Current biology*, **20**(17), 1534–1538.

- WILTSCHKO, W. 1968. Über den Einfluss statischer Magnetfelder auf die Zugorientierung der Rotkehlchen (*Erithacus rubecula*). *Zeitschrift für tierpsychologie*, **25**(5), 537–558.
- WILTSCHKO, W., & WILTSCHKO, R. 1981. Disorientation of inexperienced young pigeons after transportation in total darkness. *Nature*, **291**(5814), 433–434.
- WILTSCHKO, W., & WILTSCHKO, R. 1995. Migratory orientation of European robins is affected by the wavelength of light as well as by a magnetic pulse. *Journal of comparative physiology a: Neuroethology, sensory, neural, and behavioral physiology*, **177**(3), 363–369.
- WILTSCHKO, W., WILTSCHKO, R., & WALCOTT, C. 1987. Pigeon homing: different effects of olfactory deprivation in different countries. *Behavioral ecology and sociobiology*, **21**(5), 333–342.
- WILTSCHKO, W., MUNRO, U., FORD, H., & WILTSCHKO, R. 1993. Red light disrupts magnetic orientation of migratory birds. *Nature*, **364**(6437), 525–527.
- WILTSCHKO, W., MUNRO, U., BEASON, RC, FORD, H., & WILTSCHKO, R. 1994b. A magnetic pulse leads to a temporary deflection in the orientation of migratory birds. *Cellular and molecular life sciences*, **50**(7), 697–700.
- WILTSCHKO, W., MUNRO, U., FORD, H., & WILTSCHKO, R. 1998. Effect of a magnetic pulse on the orientation of Silvereyes, *Zosterops l. lateralis*, during spring migration. *Journal of experimental biology*, **201**(23), 3257–3261.
- WILTSCHKO, W., TRAUDT, J., GÜNTÜRKÜN, O., PRIOR, H., & WILTSCHKO, R. 2002. Lateralization of magnetic compass orientation in a migratory bird. *Nature*, **419**(6906), 467–470.
- WILTSCHKO, W., MUNRO, U., FORD, H., & WILTSCHKO, R. 2009b. Avian orientation: the pulse effect is mediated by the magnetite receptors in the upper beak. *Proceedings of the royal society b*, **276**(1665), 2227–2232.
- WINDSOR, D.M. 1975. Regional expression of directional preferences by experienced homing pigeons. *Animal behaviour*, **23**(2), 335–343.
- WINKLHOFER, M., HOLTkamp-RÖTZLER, E., HANZLIK, M., FLEISSNER, G., & PETERSEN, N. 2001. Clusters of superparamagnetic magnetite particles in the upper-beak skin of homing pigeons: evidence of a magnetoreceptor? *European journal of mineralogy*, **13**(4), 659.
- WOLF, A., SWIFT, J.B., SWINNEY, H.L., & VASTANO, J.A. 1985. Determining Lyapunov exponents from a time series. *Physica d: Nonlinear phenomena*, **16**(3), 285–317.
- ZENG, X., EYKHOLT, R., & PIELKE, RA. 1991. Estimating the Lyapunov-exponent spectrum from short time series of low precision. *Physical review letters*, **66**(25), 3229–3232.





# Lebenslauf

## Lebenslauf:

Name: Ingo Schiffner  
geboren am: 01.09.1980 in Aschaffenburg  
Familienstand: ledig  
Staatsangehörigkeit: deutsch

## Schule:

1986-1990 Grundschule Kahl  
1990-2000 Spessart Gymnasium Alzenau

## Studium:

2001-2002 Diplomstudium: Informatik an der Johann Wolfgang Goethe Universität Frankfurt  
2002-2007 Diplomstudium: Biologie an der Johann Wolfgang Goethe Universität Frankfurt  
2007-2010 Promotionsstudium: Biologie an der Johann Wolfgang Goethe Universität Frankfurt

### **Abschlüsse:**

- |      |   |
|------|---|
| 2000 | Abitur  |
| 2007 | Diplom der Biologie an der Johann Wolfgang Goethe Universität Frankfurt |

### **Diplom:**

Thema der Diplomarbeit: "Mathematische Analyse von Taubenflugwegen"

Fächer im Diplom: Neurophysiologie, Tierphysiologie, Pflanzenphysiologie

### **Zivildienst:**

- |           |                          |
|-----------|--------------------------|
| 2000-2001 | BRK-Seniorenheim Alzenau |
|-----------|--------------------------|

### **Ehrenamtliche Tätigkeiten:**

- |           |   |
|-----------|---|
| 1998-2005 | Kassier der Jugendinitiative Alzenau        |
| 2003-2008 | Administration des Kommunales Kinos Alzenau |
| 2007-2008 | Beisitzer der Jugendinitiative Alzenau      |

### **Berufstätigkeit:**

- |           |   |
|-----------|---|
| 2007-2010 | Wissenschaftlicher Mitarbeiter im Arbeitskreis Physiologie und Ökologie des Verhaltens and der Johann Wolfgang Goethe Universität Frankfurt |
|-----------|---|