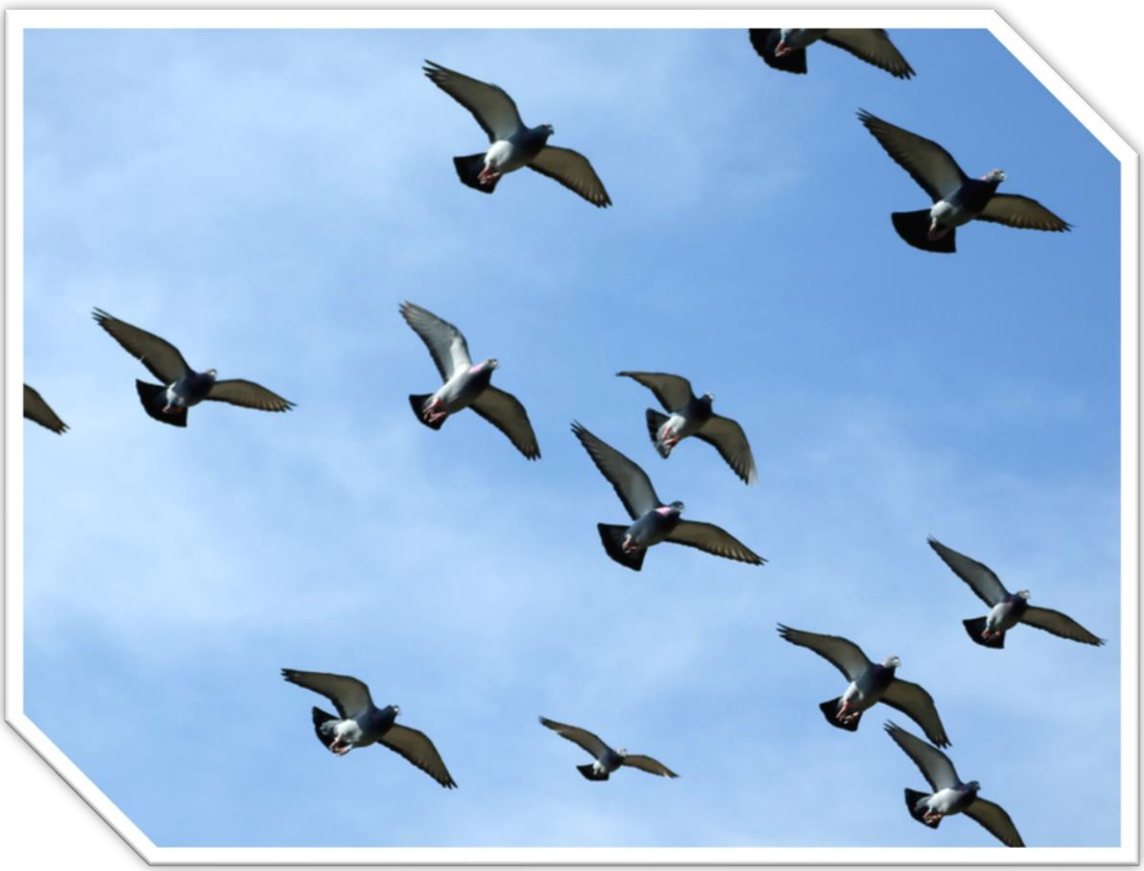
Wageningen University and Research

MSc. Thesis report

Development of flight efficiency in juvenile homing pigeons *(Columba livia domestica)*

Evelien Witte, 24 April 2019



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Development of flight efficiency in juvenile homing pigeons *(Columba livia domestica)*

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Kampen, 24 April 2019

Source front picture: Zoom.nl. 'Duiven in volle vlucht'.

Preface & Acknowledgements

You are about to read the research report about the development of flight efficiency in juvenile homing pigeons as they gained more experience. This report was made in order to complete the master thesis within the study program Forest & Nature Conservation at Wageningen University. The topic of this study was formed due to a mutual interest of the Wageningen University and the Nederlandse Postduivenhouders Organisatie (NPO). With this report it has been tried to contribute in reducing the knowledge gap on the flight behaviour of juvenile pigeons, and hopefully thereby reduce the losses of juveniles in racing flights.

Before this thesis I had never done any analyses on GPS data. Therefore, the data analysis of this thesis has been difficult at some moments. Fortunately I had two supervisors, Fred de Boer and Kevin Matson, who gave me useful tips and ideas so I could proceed when I did not know what to do. This thesis gave me the opportunity to learn a lot more about GPS analysis and the analysis of a dataset in general. A few months ago I would not have been able to do these analysis. Therefore I would like to thank my supervisors for their effort in give me helpful feedback and guidance throughout this process. During this thesis project I learned to work with R. I would like to thank Henjo de Knegt for his time in teaching me the very basics of R, so I could continue doing the rest of the calculations in R myself.

Furthermore I would like to thank the NPO and WOWD for enabling this study and providing the GPS rings. Special thanks to Jaap van Doormaal. Without him there would have been no data to work with and thus no thesis report. Besides the practical part he and Leo v/d Waart discussed with me about the possible explanations for some of the flight behaviours and gave me useful feedback on the report. This gave me inspiration for further discussion and future research ideas.

I hope you enjoy reading this report. Hopefully this report contributes to decrease the number of juveniles getting lost during racing flights.

Evelien Witte

24-04-2019

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Summary

Title: Development of flight efficiency in juvenile homing pigeons *(Columba livia domestica)*.

Abstract

Background: Many studies have been done on the navigation skills of adult homing pigeons. Knowledge about the flight development of juvenile pigeons is lacking. From a sports perspective knowledge about the development of flights and flight efficiency of juvenile homing pigeons is just as important as for adults because during races, especially juvenile pigeons are being lost. In order to take a first step in reducing this knowledge gap, this study focussed on the flight development of juvenile homing pigeons.

Aim: To test the hypothesis that flight speed and flight efficiency of juvenile homing pigeons improves when they get more experienced.

Organisms: Homing pigeons *(Columba livia domestica)*

Place of research: Various locations in The Netherlands and Belgium.

Methodology: A total of 6 racing flights were recorded by means of GPS rings of flights starting from the Netherlands or Belgium. Furthermore, weather data was collected and variables such as body mass and moult status were measured.

Principal findings: During racing flights these juvenile pigeons had a higher speed at the start of a race than at the end of a race. They gradually reduced their flight speed over time on every race. Also, the flight speed did not increase when birds participated in more flights, i.e. with increasing racing experience and age. The juvenile pigeons of this study had the highest flight speeds when experiencing tail- or cross-winds. When wind speed increased the overall flight speeds increased as well. Considering the development of flight efficiency, the juvenile pigeons did not show an improvement when they gained more experience. In contrast to flight speed, weather variables did not influence the flight efficiency during flights. However, a lot of variation in flight efficiency was recorded between races, as well as between individuals, i.e. if a bird had a low flight efficiency in one race, it may have performed better in another race. Furthermore the GPS tracks showed that juveniles start the race by flying in the right direction but get 'lost' when they are almost home. In order to fill the knowledge gap and reduce the losses of juveniles further research is necessary. Other studies show that there are more variables which influence the flight of a pigeon than just experience and age. For example flock size and composition are of importance as well.

Conclusion: Juvenile homing pigeons do not improve their flight speed and flight efficiency when gaining more experience.

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1 Introduction

Probably the most well known skill of a homing pigeon *(Columba livia domestica)*, as its name suggests, is its abilty of finding its way home over long distances. However, there are more species which are able to fly long distances to a certain location. Migratory birds are able to fly around the world to reach their breeding or wintering sites. However, pigeons are known to return to their homes every time, even if they are released from an unfamiliar location. This ability enables experimental or manipulative studies on flight behaviour and to repeat these measurement within a short range of time (Wallraff, 2005; Wiltschko & Wiltschko, 2017). The navigational skill of homing pigeons has been a topic which is widely studied for many years (Mehlhorn & Rehkaemper, 2016). These domesticated homing pigeons are especially convenient since they are used to be handled by humans. Due to their experience for being handled, their stress levels are minimised. Since the responses of relaxed animals are much more reliable than of stressed animals, a relaxed animal is preferred (Wallraff, 2005).

In order to win a race, two factors are of importance. Firstly, navigation skills. With well developed navigation skills a pigeon is able to find the shortest route possible towards its home and may therefore arrive earlier than another contesting pigeon. Nowadays there are a lot of detailed studies on flight behaviour of birds like pigeons because the GPS devices have improved a lot over the years. Research with these devices revealed which route pigeons choose. Now we know that pigeons do not always fly along the bee-line, which is the direct and shortest route possible. It also became clear that the flock size and flock composition is affecting the homing behaviour of pigeons. Pigeons flying in a group showed better homing behaviour than individual birds (Meade et al., 2005; Mehlhorn & Rehkaemper, 2016). Secondly, flight speed might be just as important as navigation in order to win a race. After all, when a bird flies an inefficient route, which is much longer in distance, this bird can still win the race if its flight speed exceeds the flight speed of other contesting birds. The flight speed and manoeuvrability of avian flight is highly dependent on feather quality. For example, moulting of the primary feathers has a tremendous influence on the flight performance of a bird (Swaddle, et al., 1996).

Considering these two factors, it can be said that in order to win a race it is beneficial when a pigeon has both well-developed navigational skills and high flight speeds. Nevertheless, flight speed and the chosen flight route may not only be affected by the qualities and skills of a bird, but by external conditions such as weather conditions as well. For example, the speed of avian flights is known to be increasing when experiencing tail-winds, and to be decreasing with cross-winds (Safi et al., 2013).

Even though many studies have been performed on homing pigeons and their flight, most of these studies focussed on adult pigeons. Knowledge on the development of flight speed and navigation skills in juvenile homing pigeons is lacking or old and perhaps outdated. It is remarkable that there are not that many studies on juvenile homing pigeons. Matthews already mentioned this in 1951 and still most studies are focussed on adults (Matthews, 1951). Juvenile homing pigeons are a major concern to the owners because relatively more juvenile homing pigeons do not arrive back at the loft after a race, especially the first races. It is still not completely clear what happens to these birds when they do not arrive at the loft. For example, they may have been lost, had a fatal accident or caught by a bird of prey. In 2008 these losses even led to parliamentary questions in The Netherlands (Nederlandse Postduivenhouders Organisatie, 2014; Partij voor de Dieren, n.d.). A first step in order to know more about the flight development of juvenile homing pigeons is by looking at their flight behaviour. Therefore this study focusses on gaining insight in the development of flight speed and flight efficiency in juvenile pigeons. It is hypothesised that juvenile homing pigeons improve their flight speed and flight efficiency when they gain more experience (Meade et al., 2005).

2 Methods

2.1 Data Collection

2.1.1 Study species

A total of 24 juvenile homing pigeons was used in this study. All birds wore an unique aluminium ring for identification and a plastic ring with a RFID chip to register their arrival at the loft after a race. During this study no distinction was made between males and females when assigning them to treatment group. Initially 20 juvenile pigeons were used, of which 10 equipped with a GPS ring and 10 control birds. The remaining 4 birds were considered as surplus birds. The assignment of birds to a treatment group was done based on their unique identity number on the aluminium ring. Birds with odd identity numbers were equipped with a GPS ring. This can be considered as random sampling since these identity numbers were given to these pigeons without any further reasoning. Birds with even identity numbers were assigned to the control group. During the races not all birds made it back to the loft. Therefore, some of the surplus birds were later included in the study of which some were equipped with a GPS ring. These surplus birds did participate in the previous races as well.

2.1.2 Study area

Home base of this study was the loft of the pigeons which was situated in Noordhorn (53°15’46.1”N 6°23’28.1”E), a small town in the Netherlands. During this study, pigeons participated in official races which started from different locations in the Netherlands and Belgium: from here they flew back to the loft. Furthermore, the pigeons were released at the loft itself and given the opportunity to fly around freely. These flights are called ‘training flights’ and occurred several times a week at the start of this study.

2.1.3 Housing conditions

In the loft birds were exposed to a natural day-night rhythm and natural light. The windows and the entry/exit of the loft both faced toward the south. Inside the loft the pigeons lived in a mixed group of males and females. The number of resting places exceeded the number of pigeons present so birds did not have to compete for a resting place. Furthermore the pigeons were fed at regular hours; water was available ad libitum.

2.1.4 GPS rings

During a race it is important to the owner that a bird returns as fast as possible and is home earlier than other contesting pigeons. In order to do so, it is important that the homing pigeon chooses an efficient flight route to avoid wasting energy. GPS rings were used in order to record the flight routes of pigeons. The rings from the company Skyleader weighed 4g, which is about 1% of a pigeons body weight. Each ring includes a rechargeable battery. The duration of the battery depends on the frequency of recordings. Batteries last longer when rings are set to record positions less frequently. For this study the rings were set on 12h duration with 180 seconds between positions. However, it was not always the case that there were exactly 180 seconds between measuring points. This could have several causes, such as difficulties connecting to satellites or a software bug. However, since the elapsed time between two measuring points was recorded as well proper calculations could still be done. After each flight the data was collected from the GPS rings by connecting the ring to a computer. These data were then saved in the cloud of Skyleader and can be reopened at any time and at any computer. The raw data of each flight was collected by downloading the ‘data.js’ files from the Skyleader cloud web page. These files contain information such as time, latitude, longitude, height and accuracy of each way point.

2.1.5 Flights

To gain insight into how the orientation, navigation and efficiency of young birds develop, the waypoints (longitude and latitude) along flight routes were recorded. Firstly, some test flights were performed to let the birds get familiar to their new rings. These flights were used to check if the GPS rings were working properly and to test if any adjustments should be made to the fitting on the birds leg. Once birds did not show different behaviour due to the GPS rings, the data collection for this study started.

During the first week the birds were set free to fly around the loft as much as possible. In addition to the flights around the loft, the pigeons participated in racing flights. In total there were 6 race flights, each starting at different locations in The Netherlands or Belgium. The exact date of each race is shown in table 1.

2.1.6 Weather

The flight performance is not only dependent on traits of the bird itself but as earlier studies have shown weather conditions play a role as well (Jeninga, 2018; Safi et al., 2013). Therefore the weather data was included in the analyses too. These data were retrieved from the Koninklijk Nederlands Meteorologisch Instituut (KNMI) web page (KNMI, 2018). The weather station which was closest to the release site of a race was used (table 1).

Table 1: Overview of race locations and weather stations

Date	Start location racing flight	Distance to loft (km)	Total number of contesting pigeons	Weather station	Distance from weather station to start location racing flight (km)
01-09-2018	Deventer	115	10248	Heino	21
08-09-2018	Gennep	177	9595	Volkel	24
22-09-2018	Tongeren	281	6695	Maastricht	18
29-09-2018	Gorinchem	184	1859	Herwijnen	12
06-10-2018	Boxtel	196	1508	Eindhoven	23
13-10-2018	Roosendaal	237	1345	Woensdrecht	20

The KNMI measures variables such as wind direction, wind speed, temperature, duration of sunshine, amount of rain, air pressure, horizontal sight, moist etc. These variables were measured every hour on every day when the birds flew in races or training. A more explicit list of variables can be found in the appendix II. Since birds only flew a few hours per day and not during the night, only weather data between 7.00 a.m. and 7.00 p.m. was used in these analyses.

As mentioned before the GPS rings had measuring points every 180 seconds during the flights. In order to compare the weather data with the GPS data daily averages for weather data were calculated. By doing so each weather variable now had one average value for each day. For some variables the sum was calculated instead of an average value for the day. These variables contained 'duration of sunshine', 'duration precipitation', 'sum hourly precipitation' and occurrence of 'rain'. Furthermore the data of the KNMI contained information about snow, ice and thunder. Since all of these variables were measured as zero for each day, these were removed from the data.

2.1.7 Moult status

The pigeons of this study had started moulting their primary feathers before the data collection and continued throughout the data collection. To be able to check if this might affect the performance of the pigeons, the moult status of each bird was noted during a month. This notation was done according to a method which is often used in research including migratory birds. With this method all primary feathers received an individual score, 0 – 5, for the length of the new grown feather (table 2). This method did not only provide information on how many primary feathers were renewed but also an estimation on the length of the new grown feather. For example, a feather with a score 3 (50% grown) was shorter than a feather which scored a 5 (100% grown) (figure 1). When the newly grown primary feathers had low scores, this means that the gap is bigger than when scores are higher (Piersma & Ramenofsky, 1998). Moult status was included in the analysis of flight efficiency and development of speed as well.

Table 2: Moult scores and description

Moult score	Description
0	old primary feather, not moulted this season
-	no new grown feather visible, gap
1	start of new feather visible
2	25% of full feather length grown
3	50% of full feather length grown
4	75% of full feather length grown
5	100%, complete feather length

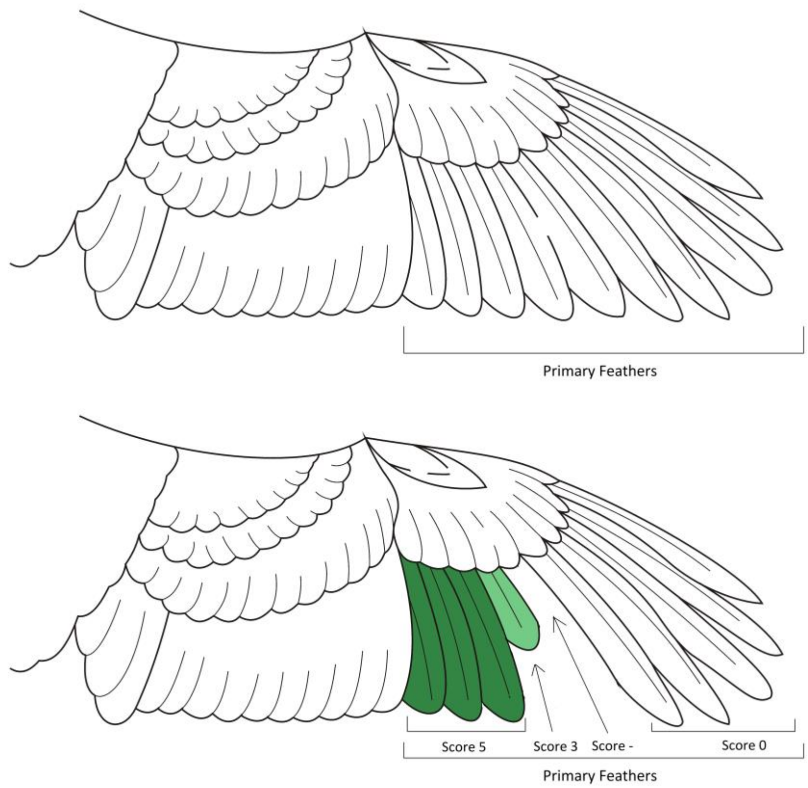

Figure 1: The top figure shows a wing with a complete set of primary feathers. The bottom figure shows a bird which is moulting. The green feathers indicate new grown feathers and the score indicates how far the new feather has grown (Gottrop, 2006).

2.1.8 Juveniles versus Adults

In a previous MSc thesis report of Jeninga in 2018, the flight patterns of adult homing pigeons were studied. To see if there are differences between flight patterns and speed during flights between juveniles and adults the results of Jeninga will be compared to the results of this study. However, even though these studies seem to be similar at first sight, their results cannot be compared that easily. Some of the methods used in the research of Jeninga are very different from this study on juveniles.

Jeninga also equipped a group of pigeons with similar GPS rings and released them several times in order to analyse their flights. However, during these flights the pigeons were released in pairs. These pairs were based on moult status, sex and weight of the pigeons. The type of flights used in the study of Jeninga was different as well, most flights were rather short (mostly 75 km from the loft), and these flights were not official racing flights. The juveniles of this study were all released in racing flights, which means that they were released in big flocks of thousands of birds and flew much longer distances.

The flights of Jeninga were conducted in September and October as well as this study with juveniles, but only one year earlier. Furthermore, Jeninga used similar analysing methods as was used for analysing the data of juveniles (Jeninga, 2018).

2.2 Methods of data analysis

Due to different user accounts and software difficulties it was not possible to plot the flight tracks of bird 18-061 within the same map as the other birds. Therefore two figures per race were made in which the flight tracks are shown. Nevertheless, the GPS ring recorded the flight tracks without any problems and these tracks can thus be compared to the tracks of the other birds. For the last sixth race, Roosendaal, there is only one map because bird 18-061 did not participate in this flight.

2.2.1 Preparing the raw data

The data files from the Skyleader cloud were processed in R. Before any calculation was done the accuracy of way points was checked. This accuracy was called the horizontal dilution of precision (hdop). Way points and corresponding data with hdop values higher than 10 were excluded from calculations because the accuracy of these way points was considered to be not trustworthy (Fischer et al., 2018; Hulbert & French, 2001). The longitude and latitude data was then converted into x- and y-coordinates of the Amersfoort mapping system to calculate distances in km.

2.2.2 Calculations

The software of the GPS ring did provide information on flight direction and flight speed. However it was not clear how this was calculated. It might have been through the Doppler-shift, which is a measure for the movement of the GPS ring compared to the movement of the satellites. This method is known to be unreliable and therefore flight speed and flight direction were calculated afterwards by using R (Safi et al., 2013). Calculations on flight speed were done for every line segment, which is the line between two measuring points. In order to calculate speed, first the distance of each line segment was calculated. Since the two measuring points each have their own x- and y-coordinates, then the values for 'dx' and 'dy' can easily be calculated. By using these in the Pythagoras' theorem the length of the line segment can be calculated, i.e. the distance between two measuring points. Thereafter, speed was calculated by introducing the time between the two measuring points. Analyses on flight speeds were done on the differences within and between individuals as well as between and within the races.

One way to arrive home quickly is to fly the shortest route possible. The shortest route would be the route which is found when drawing a straight line from point A to point B. This line is also known as the bee-line. When the distance of the bee-line is divided by the flight distance of the pigeon an efficiency index is given, formula 1.

$$flight\ efficiency = \frac{distance\ beeline}{flight\ distance} \tag{1}$$

This index is an indication of the flight efficiency of the pigeon. A flight efficiency of 1 means that the pigeon has flown exactly on the bee-line, e.g. the shortest route possible. Since the direction and length of a beeline changed every time a bird changed its flight direction (figure 2), the flight efficiencies were calculated for each line segment a bird has flown. These flight efficiencies for each line segment were used to see how flight efficiency developed throughout the races. Thereafter an average was calculated for flight efficiency per bird per race. GLMM was used to analyse differences in flight efficiency between races and to test whether flight efficiency improved over time, over the number of races. Here, flight efficiency index was the dependent variable.

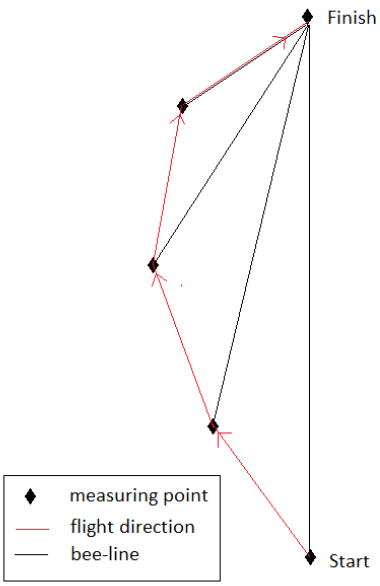

Figure 2: Schematic flight route of a pigeon (red line) and the bee-lines at every measuring point (black lines). With every change in flight direction the bee-line changes as well.

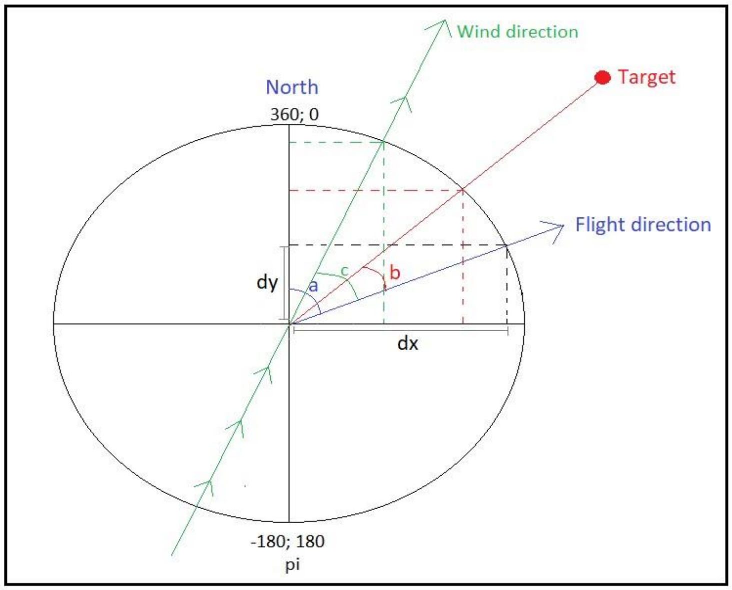

Figure 3: A schematic visualization of wind and flight direction. Here 'target' is the direction towards the loft, or bee-line of each line segment.

Calculating the flight efficiency index is one way of analysing the development of flight patterns among different races. Another, and more detailed, way of analysing the development of flight patterns is by calculating the angles of the flight directions along the race. For example when a bird flies from measuring point 1 to point 2, a straight line can be drawn between these points (line segment), the direction of this line segment is called the 'flight direction' (figure 3). For each line segment the angle compared to north can be calculated. A bird might deviate from the bee-line while flying and, as already indicated by the flight efficiency index as well, the more deviation from the bee-line the less efficient flight. Therefore the angles between the flight direction and the bee-line, called 'heading2beeline' ('b' in figure 3), were calculated for each line segment. For the purpose of this study it did not matter if the bird flies on the left or right side of the bee-line. It is important to know how much the bird deviated from this line. Therefore all angles were made absolute, which means that an angle of -45° and 45° were similar. For wind direction compared to flight direction, similar calculations were done for each line segment, called 'winddirection2heading' ('c' in figure 3). Since birds did not fly the entire race in the same direction, the angles between the wind direction and flight route differed along a race. All these 'winddirection2heading' angles were then categorised in three classes. First class was head-wind, second class was cross-wind and third class was tail-wind. Not only did the wind direction compared to the flight route differ throughout the race but thereby also the wind direction to bee-line angles. Therefore these were calculated as well for each line segment and were called 'winddirection2beeline'. These angles were then made categorical by using the same three classes as 'winddirection2heading'.

2.2.3 Removing measurement errors.

Before starting the analysis, mistakes and measurement errors were removed from the data in order to be sure that results are reliable. First speeds higher than 35 m/sec were removed, these higher speeds were very unlikely for homing pigeons (Pennycuick, 1968; Von Hünerbein, et al., 2001). Furthermore many measuring points had a speed <0,1 m/sec. Before removing these data from the analysis it had to be studied what happened at these measuring points. Therefore it was checked at what heights these birds flew when they had such a low speed. In most cases the birds had a height of 0,0 m. (figure 4). This suggest that birds were sitting somewhere. This behaviour could be explained by birds taking breaks during the race for drinking or resting (Portugal et al., 2017).

Birds that arrived at the loft more than 24 hours after the start of the race were excluded from this calculation as well. It is unknown what did happen to these birds, they might have been wandering around or perhaps entered another loft and stayed there for a few days. These scenarios cannot be checked and can neither be included as flying speed since it is unclear if they flew or not. Then there are still a few measuring points left in which a certain height was measured but without speed. This could have been caused by pigeons sitting on rooftops, church towers etc. Another explanaition is that birds may have flown in rounds in which the distance between two measuring points was exactly 0,0 m. and therefore a speed of 0,0 m/sec was calculated.

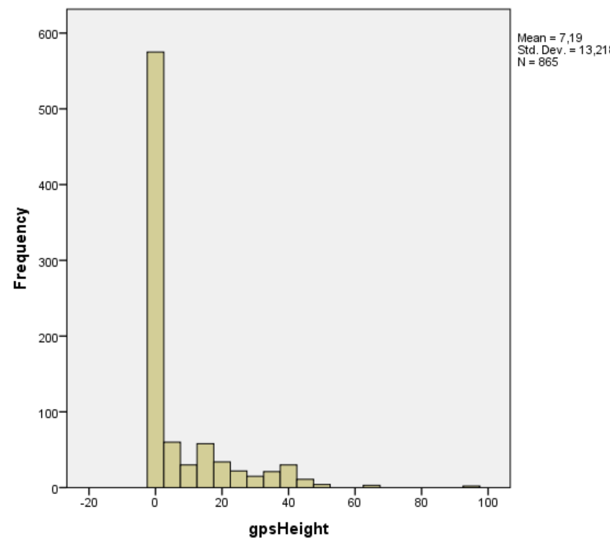

Figure 4: Frequency of measured gpsHeight (m) while speed was <1,0 m/sec.

2.2.4 Models

Throughout the races there were unequal sample sizes. This was caused by the fact that some birds did not arrive back at the loft or were taken out of the races for other reasons. This means that for example in the first race there was a total of 23 birds, of which 9 had a GPS ring and 14 control birds, but in other races the numbers were different (table 3). In order to be able to do some statistics on flight speed and flight efficiency a General linear Mixed Model was used. This model was able to work with unequal sample sizes along the races by means of selecting the 'scaled identity' option. The aim of this model was to understand how flight speed and flight efficiency were affected by the weather conditions, moult, start location and finally the distance and time in a race. In order to do so, it is important to understand that weather conditions were averaged throughout the day and therefore made continuous. This means that weather variables and start locations would explain the same variation, they are confounding factors. When including both, the model did not run. Therefore two models were made for flight speed and two models were made for flight efficiency. One model included the weather variables and the other model included the start locations. In all models 'bird' was included as a random factor. Backward selection was used to create the final models.

Table 3: Division of GPS and control birds within each racing flight

Number of birds participating			
Flight number	Control	GPS	Total
1	14	9	23
2	10	6	16
3	7	6	13
4	7	6	13
5	6	4	10
6	5	5	10

2.2.5 Effects GPS ring

Even though the GPS rings weighed only 4 gram and pigeons did some test flights to get used to wearing a GPS ring it could have been that wearing a GPS ring did influence the flight performance. A t-test was done in order to check if wearing a GPS ring was of any influence on flight speed. To calculate the average speed of control birds the arrival times which were measured at the loft were used. Together with the official distance of each flight, which was provided by the club, the average flight speed of these control birds was calculated. This will always be an estimation since it is not known how many kilometres these control birds have flown exactly.

2.2.6 Juveniles versus Adults

The data of the study on adults from Jeninga was compared with the data of this study on juvenile pigeons. Since 'hdop' values higher than 10 were excluded from the juvenile data, because it is not reliable, this was done as well for the adult data (Fischer et al., 2018; Hulbert & French, 2001). Furthermore the adult data was checked on abnormalities in terms of unrealistic high speeds similar as was done for juvenile data. Then the compared dataset was analysed by means of a Mann-Whitney U test in which speed was the dependent variable and the groups were defined as the different flights.
Furthermore a Generalized Linear Model was made to test whether or not there was an interaction between flight number and age (adult or juvenile).

2.2.7 Drop-outs

Drop-outs are birds which did not participate in the next racing flight. This had several reasons. Firstly, there were some cases in which birds did not arrive back at the loft after a flight. Secondly, during this study some birds were considered not fit enough to participate any further due to small injuries or behavioural cues such as being less active or eating less. The health of the pigeons always had priority. When a bird did not seem fit enough for racing flights, this bird was taken out of this study in order to improve its health.

3 Results

All races were recorded by means of GPS rings. These recordings were plotted in a map provided by Google (Appendix I). The flight tracks show that at the start of most races the birds were heading in the right direction. However when the birds reached the provinces Groningen and Friesland they often started to fly in the wrong direction. Especially in the first race, Deventer, some birds flew a very large distance compared to the bee-line (straight black line). One bird flew all the way to Ganderkesee which is close to Bremen (Germany). This bird returned on its own to the loft a few days later. By then the battery of the GPS ring was empty and therefore the ring did not record the complete flight. In the maps with the plotted flight tracks it is shown that juvenile pigeons did not cross large water areas such as seas or big lakes except one bird. During the last race bird 18-067 did fly across the IJselmeer between Andijk and Stavoren which is a distance of approximately 17 km.

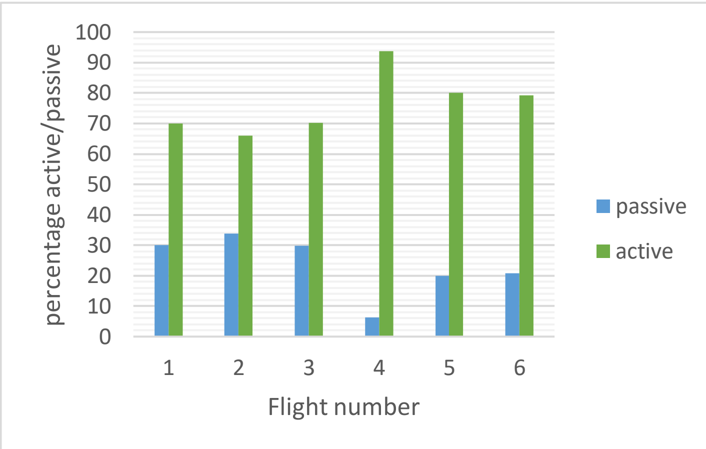

Figure 3: Percentage of birds being active (speed >1,0 m/s) and passive (speed <1,0 m/s) during each racing flight.

As mentioned in paragraph 2.2.3, Removing measurement errors, there were many measurements at which the flight speed was lower than 1,0 m/s, passive behaviour. It was expected that birds would show more passive behaviour in the first races since flying long distances was new to them. This seems to be the case, however it is not very obvious (figure 4). Here a correction was done for the length of the races, therefore the amount of passive and active behaviour is shown in percentages. As expected the percentage of passive behaviour increased throughout races (figure 5). This could be due to birds getting tired. In the graph there is a shifting point between active and passive behaviour between measuring points 100 – 110. The distances of the races were not all of equal length. Only a few races had measuring points counting until 200 or more. Therefore it was calculated in terms of percentages where measuring points 100 -110 were within these races. The shifting point at measuring point 100-110 were mainly at the end of a race. Thus showing an increase in passive behaviour was as expected.

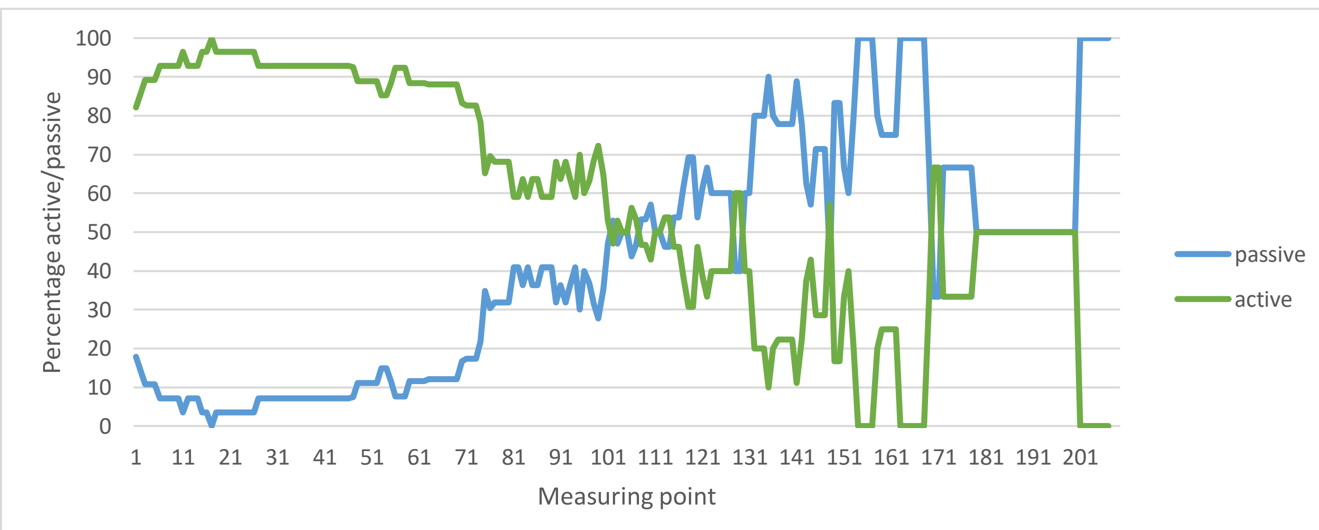

Figure 4: Percentage of active (speed >1,0 m/s) and passive (speed <1,0 m/s) behaviour throughout the racing flights.

3.1 Speed development

A the start of this study it was expected that juvenile pigeons were able to improve their calculated flight speed when they participated in more flights. First, speed throughout a race was plotted to gain insight in how speed within a race changes. The juvenile pigeons of this study started their flights with a high speed and slowed down throughout the race, that is with increasing measuring points (figure 5).

In figure 6 the mean speed throughout the races was plotted. The first race did not decrease in speed as much as later races (figure 6). A posthoc test showed that race 3 had the highest mean speed, and race 1 had the lowest (*ANOVA*; $F_{5,2449}$ = 47,153, P<0,001; figure 7). The other races did not differ from each other in mean speed.

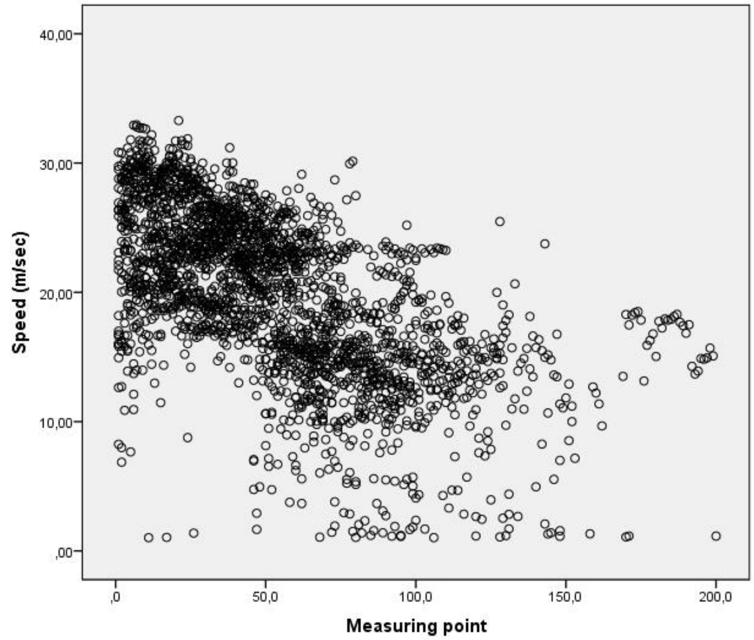

Figure 5: Scatter dot of change in flight speed with increasing measuring points. Each dot represents one measurement of one bird.

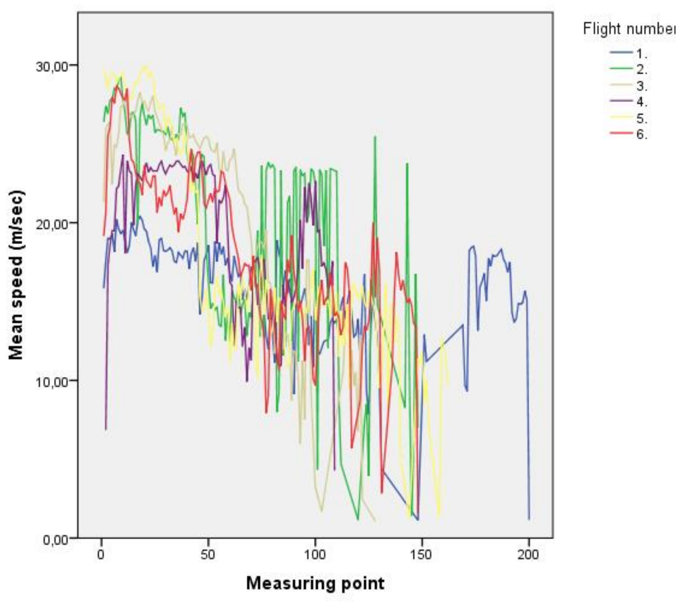

Figure 6: Line graph of the raw data on speed throughout a race, that is with increasing measuring points. Each line represents the mean speed of all birds during a race.

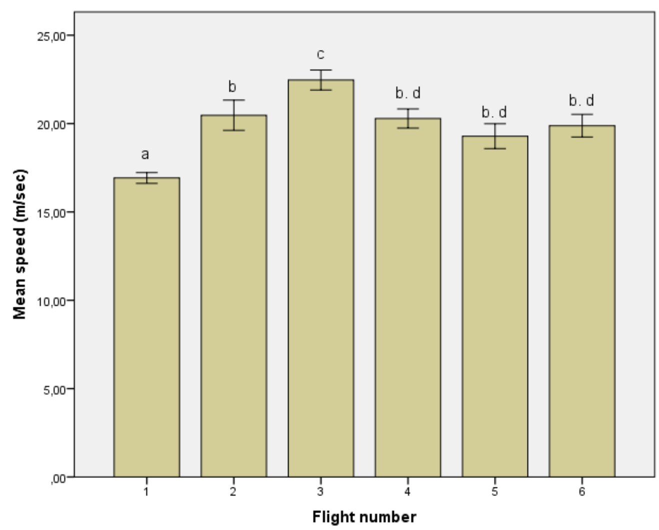

Figure 7: Mean speed of juvenile pigeons during the 6 racing flights. Different letters indicate significantly different mean speeds during these flights.

During this study the measured wind speeds were not very high, they varied from 1,33 to 4,17 m/sec which is equal to 1 – 3 Beaufort. The wind direction differed throughout the races but mainly orientated between south and west (table 4). These wind directions were categorised and compared to the flight direction of each line segment of the flights. These comparisons of wind direction to flight direction were then included as relative wind direction in the General Linear Mixed Model.

Table 4: Wind direction and wind speed during each race.

Flight number	**Location**	**wind direction**		**Average wind speed (m/sec)**	**Beaufort**
1	Deventer	318°	NW	1.33	1
2	Gennep	228°	SW	4.17	3
3	Tongeren	221°	SW	3.92	3
4	Gorinchem	160°	SSE	1.50	1
5	Boxtel	268°	W	2.67	2
6	Roosendaal	165°	SSE	3.08	3

3.1.1 Effects of weather on flight speed

For more understanding on what exactly influenced these differences in mean flight speed between the races, a General Linear Mixed Model (GLMM) was made. This type of model was chosen because it is able to take into account the different sample sizes and random effects among races. For the analysis on speed, two of these models were made; one including weather data and another including location. This was done because weather data was continuous throughout the day and thereby confounded with location. When including both, location and weather data, the model did not work. This aspect is explained more thoroughly in chapter 'Methods'.

Table 5: Overview of variables which had an effect on speed (m/sec) when weather data was included in the GLMM.

Type III Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	7.027	405.616	.000
windcategory2heading	2	2445.602	10.639	.000
Measuring point	1	1978.987	92.686	.000
Cumulative distance	1	2240.819	34.839	.000
Average wind speed/hour	1	2036.198	23.218	.000
windcategory2heading * Average wind speed/hour	2	2446.074	61.539	.000

Dependent Variable: Speed (m/sec)

Table 6: Effects of variables in GLMM on speed (m/sec) including weather data.

Estimates of Fixed Effects[a]

Parameter	df	t	Sig.	95% Confidence Interval Lower Bound	95% Confidence Interval Upper Bound
Intercept	9.247	17.650	.000	18.030094	23.306717
[windcategory2heading=1]	2438.099	1.871	.061	-.064946	2.780325
[windcategory2heading=2]	2445.796	4.551	.000	1.526804	3.839059
[windcategory2heading=3] [b]					
Measuring point	1978.987	-9.627	.000	-.066785	-.044181
Cumulative distance	2240.819	-5.902	.000	-1.553286E-05	-7.785555E-06
Average wind speed/hour	2318.888	13.167	.000	.165257	.223094
[windcategory2heading=1] * Average wind speed/hour	2446.844	-9.670	.000	-.302481	-.200490
[windcategory2heading=2] * Average wind speed/hour	2442.818	-9.106	.000	-.216340	-.139674
[windcategory2heading=3] * Average wind speed/hour [b]					

Dependent Variable: Speed (m/sec)

b. This parameter is set to zero because it is redundant.

The GLMM which included weather variables showed that as expected measuring point (*GLMM*; $F_{1,\ 1978,987}$ = 92,686, *P*<0,001) and cumulative distance (*GLMM*; $F_{1,\ 2240,819}$ = 34,839, *P*<0,001) had negative effects on speed. Furthermore, wind direction is of importance for flight speed (*GLMM*; $F_{2,\ 2445,602}$ = 10,639, *P*<0,001), here crosswind had the strongest positive effect on speed. Wind speed itself had a positive influence on speed as well (*GLMM*; $F_{1,\ 2036,198}$ = 23,218, *P*<0,001) (Table 5 & 6). An interaction was found between wind speed and wind direction (*GLMM*; $F_{2,2446,074}$ = 61,539, *P*<0,001).

3.1.2 Effects of start location on flight speed

The second GLMM model included the start locations instead of weather variables. As measuring points increased in this model the flight speed lowered, there was a negative effect *(GLMM;* $F_{1,\ 1758,071}$ *= 46,791, P<0,001:* Appendix III). This is similar to the previous model (table 5 & 6). However, in contrast to the previous results, here cumulative distance had a positive effect on speed *(GLMM;* $F_{1,\ 2016,735}$ *= 14,713, P<0,001:* Appendix III). Two interactions were found: firstly between start location and measuring point *(GLMM;* $F_{5,\ 1900,788}$ *= 23,192, P<0,001)* and secondly between start location and cumulative distance *(GLMM;* $F_{5,\ 2175,670}$ *= 34,637, P<0,001:* Appendix III). Furthermore start location itself affected flight speed *(GLMM;* $F_{5,\ 1072,807}$ *= 98,448, P<0,001:* Appendix III). In contrast to previous results in which Tongeren was tested as the race with the highest mean speed, here Boxtel had the highest speed (Appendix III).

When considering flight speed throughout a race it was hypothesised that this would decrease as the race progressed. Furthermore it was expected that birds had a lower calculated flight speed in the first race than in the later races. In SPSS a table with predicted values for mean speed at measuring points 0, 50, 100, 150 and 200 was made. As expected the flight speed decreased throughout the races. However the expectation of birds having a higher speed in the later races is not necessarily true. The predicted values show the interaction for measuring point and speed. This interaction can be recognized by the lines which cross each other in the graph (figure 8). In order to check for individual development a bar graph was made in which each cluster of bars represented a bird, and each bar within this cluster represented a race. Here only a subset of birds was measured since individual development can only be measured if a bird flew several races. No obvious pattern was visible, it seems to be that the first flight is slightly slower for every bird than later races (figure 9). This is in line with earlier results but contradicting with the expectation. The expectation was that birds would increase their speed when participating in more flights. They only improved until the third race, after that the flight speed seems to decrease.

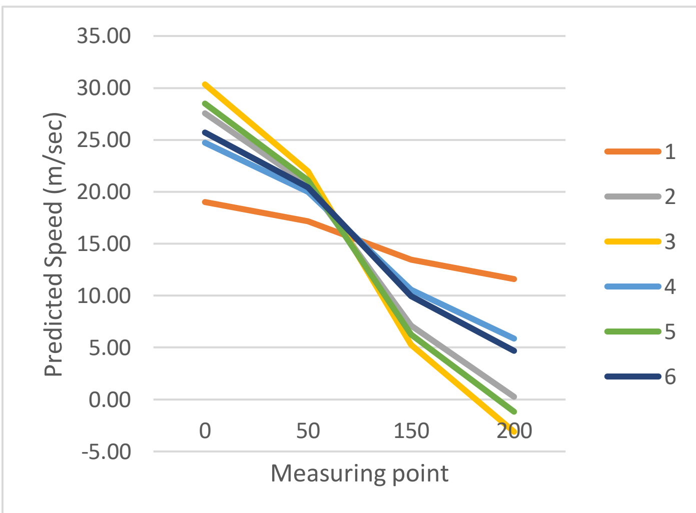

Figure 8: Predicted values calculated by SPSS for change in speed (m/sec) over measuring points (1 to 200). The interaction of start location and measuring point on speed is visible.

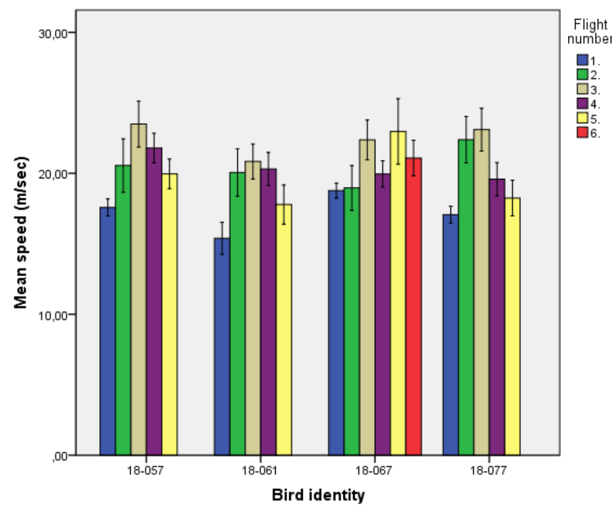

Figure 9: Individual differences in speed (±95% CI) over the different races.

3.1.3 GPS effect

A difference was found in flight speed between birds wearing a GPS ring and control birds *(T-test; $t_{52,470}$=2,630, P=0,011)*. The mean of average flight speed was higher in GPS birds (M=16,3947, SD=3,71286) than in control birds (M=13,1786, SD=5,34290).

3.2 Flight efficiency

Besides improvement of flight speed it was also expected that juvenile pigeons got better at choosing their flight route. It was expected that they would be flying closer to the bee-line when they gained more experience. To test if this was the case several tests on flight efficiency were done. First a general overview of the data was made to get a rough estimate on what

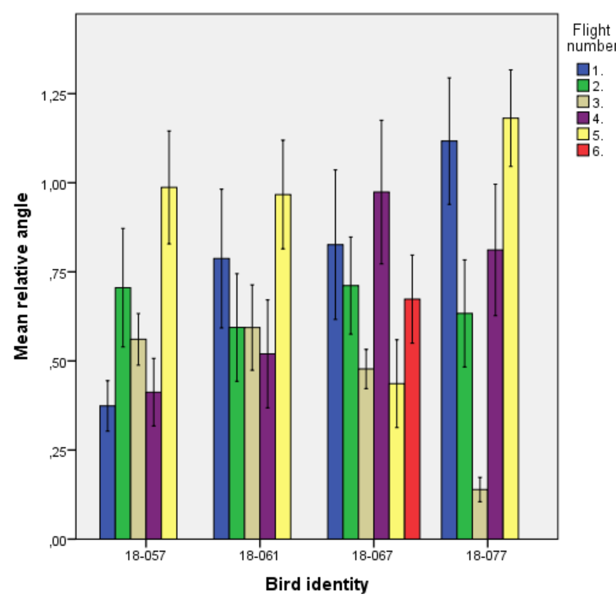

Figure 10: Mean relative angle (±95% CI) plotted for each individual during the different races

could be expected (figure 10). Here the mean of relative angles, the angles between flight direction and bee-line, were plotted for each bird in each race. The lower the mean relative angle the closer the bird flew to the bee-line. In this graph it can be seen that there is a lot of variation both between and within individuals. For example, bird 18-077, had the highest mean relative angle of all birds in the first race, but during the third race was the lowest and then in the fifth race it was relatively high again. A General Linear Model was used to test whether there was a difference in the mean relative angles between flights. Bird 18-057 increased its relative angles when participated in more races (*GLM*; $F_{4,412}$ = 13,175, P<0,001). This was not seen in other birds. The other birds did not show such a large difference between first and last race. Nevertheless bird 18-077 showed a very low mean relative angle during race 3, the Tongeren race (*GLM;* $F_{4,484}$ = 27,145, P<0,001).

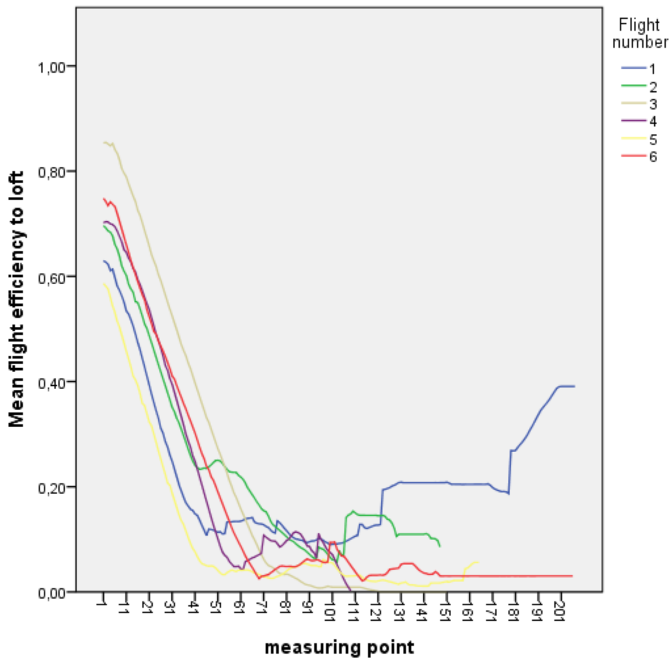

Figure 11: Flight efficiency throughout the races decreases when with increasing measuring points i.e. flight duration.

The maps of the GPS tracks showed that birds flew in more or less the correct direction during the first part of the race. Somehow when they were close to their loft these juveniles started to fly in wrong directions as if they were lost. Their calculated flight efficiencies throughout the races decreased (figure 11), which was in accordance with these GPS tracks. Since birds which are wandering around do not follow the bee-line and thus have lower flight efficiencies.

3.2.1 Effect of weather and start location on flight efficiency

Similar to flight speed, it was expected that weather conditions affected flight efficiency as well. Especially certain wind speed and wind directions were expected to affect flight efficiency. It was thought that cross-winds for example would cause birds to have a lower flight efficiency. Therefore Generalized Linear Mixed Models were made. For flight efficiency two models were made as well, due to the same reasons as for flight speed, namely the weather data being continuous throughout the day and thereby confounding start location. One model included the weather variables and the other model included start location.

Surprisingly, none of the weather variables had an effect on flight efficiency and also no interactions were found. For the model including the start location also no variables were left after backward selection in the GLMM of flight efficiency. Overall there were no variables or interactions that affected flight efficiency.

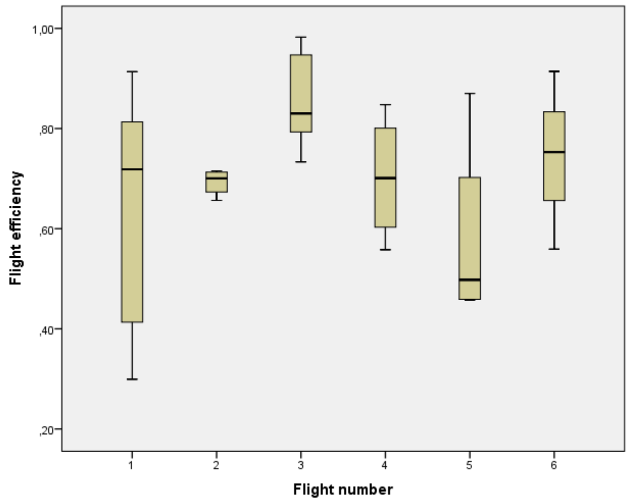

Figure 12: Boxplot of flight efficiencies during each flight.

When plotting the differences in flight efficiency between races it seems that flight 3 had the highest flight efficiency: however, no difference was found *(Kruskal Wallis; N=28, P=0,194)* (figure 12).

In order to see how much faster these juvenile GPS birds could have been when they would have flown along the bee-line some calculations were made. These calculations were based on the earlier calculated average speed and the official distances given by the pigeon club. Only the birds which homed within 24 hours were included, since birds that spend more time might have entered the wrong loft and rested before they continued homing. Even if these juvenile pigeons had followed exactly the bee-line from start to finish, they would not have won the race (Appendix IV).

3.3 Juveniles versus adult

It was expected that adults would have a higher speed throughout flights than juveniles since they have more experience and possibly more muscle strength. However, when plotting the mean speeds per flight its seems to be that juveniles flew faster (figure 13). For juveniles, flight number 1 was the first racing flight of their life, for adults this was just the first flight which was measured. However, the flight data of adult pigeons was measured during flights one year ago. Since the data was not gathered from the same flights many variables may have been different and may have affected the measurements. Although the flight speeds cannot be compared, the patterns in which speed develops throughout flights could be compared. Both juveniles and adult show similar patterns of flight speed throughout a race. Both adults and juveniles, decreased their flight speed with increasing measuring points, i.e. with time flying (figure 14).

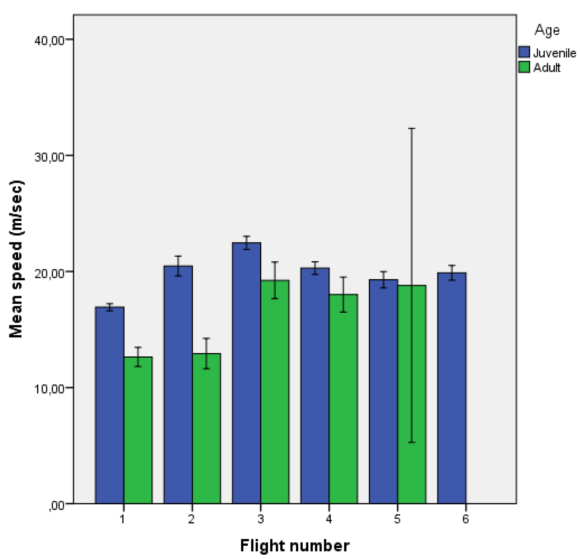

Figure 13: Mean speed during the different flights, separated for juveniles and adults

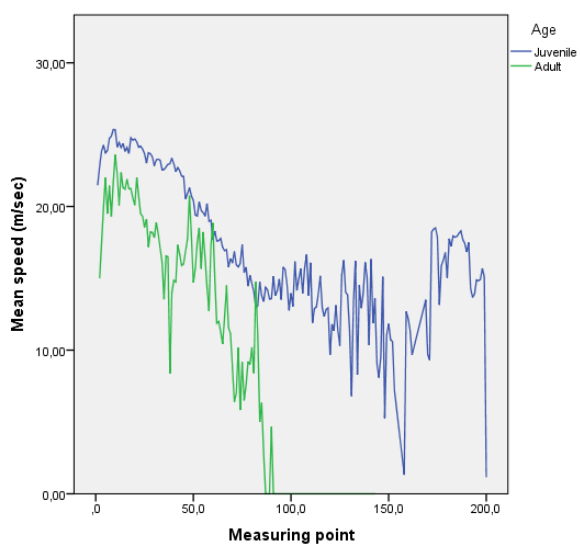

Figure 14: Line graph showing the decreasing mean speed of juveniles and adults over increasing measuring points.

3.4 Drop-outs

A test on correlation resulted that there was no correlation between wearing a GPS ring and dropping out of this study *(Fisher's; N=82; P=0,083)*. However, the sample sizes in this study were rather small (table 7).

Table 7: Cross table on the number of birds wearing a GPS ring and drop outs.

GPS_(yes_no) * Drop out Crosstabulation

Count

		Drop out		Total
		0	1	
GPS_(yes_no)	0	40	6	46
	1	26	10	36
Total		66	16	82

4 Discussion

Even though the first race had the lowest mean flight speed, overall there was no obvious improvement of flight speed when juvenile birds gained more experience or participated in more flights.. Besides that, the juvenile pigeons did not show a clear improvement of flight efficiency between flights and within individuals. There was a lot of variation measured in flight speed and flight efficiency, both between and within individuals.
Earlier studies have shown that weather conditions affect flight speed of birds during a flight. Birds have higher flight speeds when they experience tail-winds, furthermore flight speed decreases when cross-wind becomes stronger (Safi et al., 2013). Similar results were found during this study with juvenile pigeons. Here flight speed was affected by windspeed and wind direction. Flight speed of juvenile pigeons was lower with head-winds than with tail- or cross-wind. Furthermore an interaction was found between wind direction and wind speed on the flight speed of juveniles. While flying with head-wind the wind speed had a negative effect on the flight speed. Thus when wind became stronger these juveniles slowed down their flight speed whereas flight speed increased when birds experienced tail-wind and the wind became stronger.
In every race the flight speed of juvenile pigeons decreased throughout a race. At the beginning of the race birds had a higher flight speed than at the end of the race. This was the case for all races. This decreasing flight speed over time was not found in literature. However, most literature studies on flights behaviour of pigeons have flights with rather short distances and do not contain racing flights (Biro, et al., 2006; Meade et al., 2005; Pettit, et al., 2015). The decreasing flight speed might suggest that these birds were getting tired in the course of the race. Adults in the study of Jeninga did show a similar pattern of decreasing speed throughout flights (Jeninga, 2018). Another explanation for the decrease in flight speed could be that at the first part of the race pigeons flew in a big flock and later on separated into smaller groups as they got closer to their loft. It is known that pigeons in a flock have a higher flight speed than individuals (Dell'Ariccia, et al., 2008).

In contrast to earlier studies, the juvenile pigeons wearing a GPS ring had a higher flight speed than birds without GPS ring. Earlier studies with pigeons wearing a harness or transmitter with a bit heavier weight had a contrary results, they flew slower than pigeons without additional gear (Irvine, et al., 2007). However, attaching a harness with loops around the legs might be a different experience to the bird than an extra ring since these birds were already used to wearing rings. At the same time it must be said that the research of Irvine et al. is already a few years old and transmitters and GPS devices have gotten smaller. Nevertheless the method of attachment and weight must be taken into consideration when attaching devices to a bird. In this study with juvenile birds, it did not seem of influence on the flight speed, although the sample size of this study was rather small. In order to study this any further, a larger sample size is recommended.

During a race the main goal is not to be the fastest pigeon per se, but to be home faster than other contesting pigeons. This can be achieved by flying the most optimal route as well. The flight efficiency is a way of measuring how well a pigeon has chosen the optimal route and has a higher value when pigeons fly in groups (Mehlhorn & Rehkaemper, 2016). This is due to a hierarchy and leadership within a group, decisions on route direction are commonly made by a more bold pigeon (Portugal 2017). However, it was not tested whether flight efficiency would be different when flying in different group compositions such as alone, in couples or large groups. Testing how group composition affects the flight efficiency was not within the scope of this study, but might have interesting results for juvenile pigeons. During the racing flights of this study, juveniles flew in large groups with other contesting pigeons. There was no possibility to adjust the group compositions during these races.

Within this study it was shown that at the start of the race the juvenile pigeons flew mostly in the correct direction with a bit of deviation from the bee-line. When they reached the provincial border of Groningen and Friesland they often started to fly in the wrong directions and flying in rounds (Appendix I). One explanation for this may be that the large flock separated into smaller subgroups in order to go home. The juvenile pigeons may then have followed the wrong subgroup and thus the wrong direction. In the races 1 – 3 only pigeons from the northern part of Groningen participated in the races. This does not explain why one bird flew towards the eastern side of Friesland. In race 4 – 6 the spread of lofts was wider as participants came from the whole north-east area of the Netherlands (every place above the line between Swifterband and Zwartemeer). In race 6 there were some participants from Noord-Holland. This might explain why bird 18-067 was the only bird which flew in the area of Noord-Holland and later on crossed the IJselmeer.

Several studies show that training of unexperienced or juvenile pigeons does help them to home faster than untrained pigeons (Wiltschko & Wiltschko, 1981). These juvenile pigeons were not trained beforehand and therefore may not have recognized the surrounding areas. They had to fly around until they were very close to their own loft before recognizing it. There were even some birds which passed the loft very close and still continued flying further before arriving at the loft. Similar as within this study, in the study of Portugal et al. (2017) pigeons did not follow the bee-line while homing. Schiffner et al. explained this behaviour by birds being curious or willing to expand their navigational map rather than being lost. Portugal argues that the explanation of Schiffner et al. is not correct. Rejecting this explanation was based on the fact that in the study of Portugal et al. birds were not actively exploring the surrounding but were sitting a lot (Portugal et al., 2017; Schiffner et al., 2011). In this study there were a lot of measurements with a speed <0.1 m/s and a height of 0.0 meters as well, which indicated sitting or resting behaviour. Therefore the explanation of expanding their navigational map seems to be incorrect here as well. It rather agrees with the expectation of birds getting tired as the race continuous and taking breaks. Furthermore the study of Portugal et al. showed that pigeons choose less efficient routes when they fly from unfamiliar sites than from familiar sites. Consequently these inefficient routes costs more energy. They found similar results for personality traits: bold birds flew a more efficient route than birds which were more shy (Portugal et al., 2017). Furthermore it is known that pigeons choose flight routes they know from previous flights (Meade et al., 2005). This might cause a lower flight efficiency than flying an unfamiliar shorter route.

Variables which was not controlled for during this study were the flock size and flock composition during flights. It is known that flock size and composition does affect flights (Biro et al., 2006; Schnell & Hellack, 1979). The level of leadership within the flock of pigeons during a race can be argued since these pigeons have probably never seen each other before. Nevertheless, pigeons from the same club travelled together in a crate towards the release site. During these few hours that they have been together, some sort of hierarchy and leadership could be formed. Despite it being very suggestive, it could be that these pigeons stick together on their flight towards the lofts since they recognize each other.

In this study flight efficiency was considered as flying the shortest route or the route closest to the bee-line. However flight efficiency can also be considered in terms of energy expenditure. The research of Schnell and Hellack (1979) showed that there are three types of strategies. The strategy which applies to homing pigeons would be that they need to find an optimum in distance and flight speed. Within this strategy wind speed and wind direction are important factors to determine the optimum (Schnell & Hellack, 1979). Similar as for flight speed, it was tested whether or not weather conditions had an effect on flight efficiency. Here the flight efficiency of juvenile pigeons was not affected by any of the weather variables, start location, moult or other variables. However, proper measurements of wind speed can be difficult. The local landscape could affect the wind speed and wind direction. Most optimal method for measuring wind conditions would be at a complete open area such as the sea (Safi et al., 2013). However, these pigeons did fly over land mostly within the Netherlands where the land surface is relatively flat. Therefore wind direction would not have changed due to high mountains, steep valleys or other large landscape characteristics. One point of criticism regarding the weather conditions might be that the they were not measured at the height at which these pigeons were flying. If this data would have been available then this would be preferred since wind speed changes over altitudes (Endlich et al., 1969). Furthermore the weather conditions may have been different at the start location than at other location later during the race. In order to analyse the effect of weather conditions on flight behaviour, the weather conditions should preferably be measured at the exact same locations and heights as where the pigeon is at that moment.

In order to improve homing behaviour of juvenile pigeons, it would be recommended to do training flights before letting them participate in a race. For these training flights birds should be brought to different locations on relative short distance to the loft (1 – 10 km) and heading from all possible directions. This method is proven to be effective for juvenile pigeons in improving their homing behaviour compared to untrained juveniles (Wiltschko & Wiltschko, 1981). This would enhance their navigational skills and thereby the flight efficiency. When these two factors are improved then the losses of juvenile pigeons might be reduced. and some of these pigeons may even be able to win a race.

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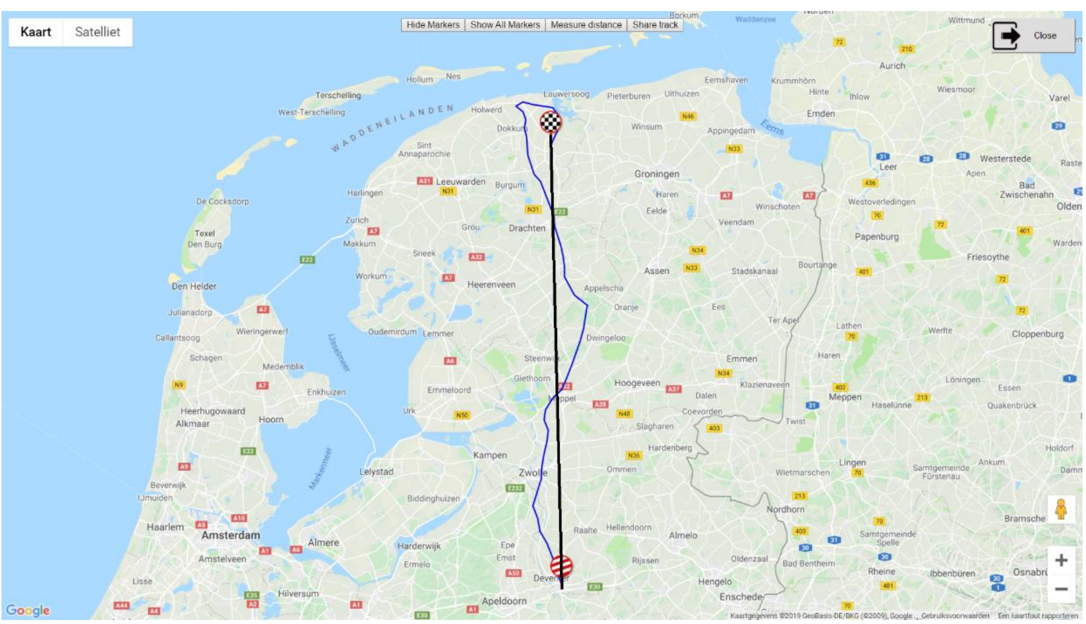
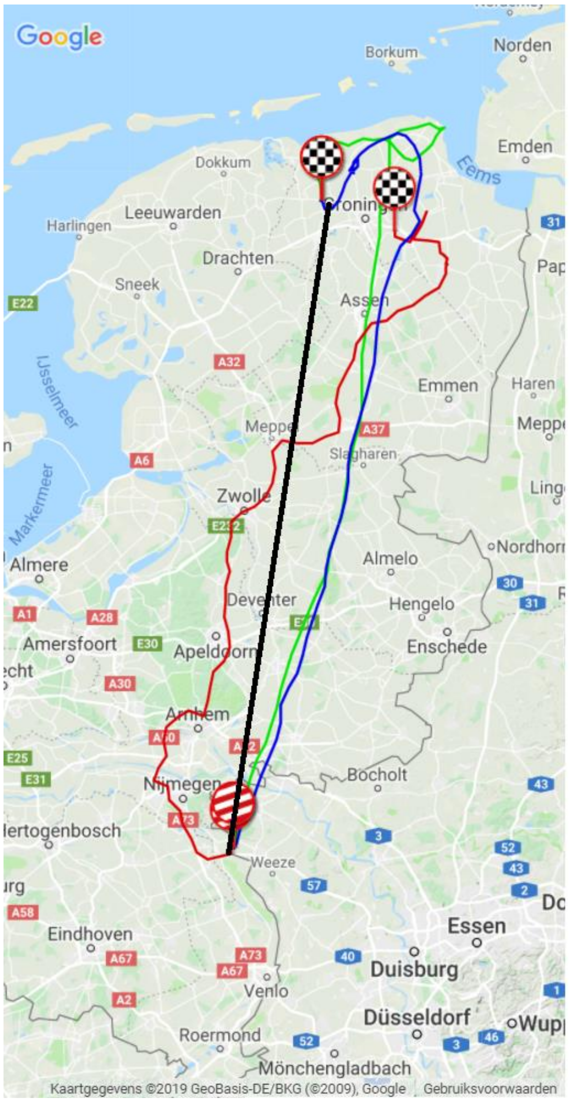
6 Appendices

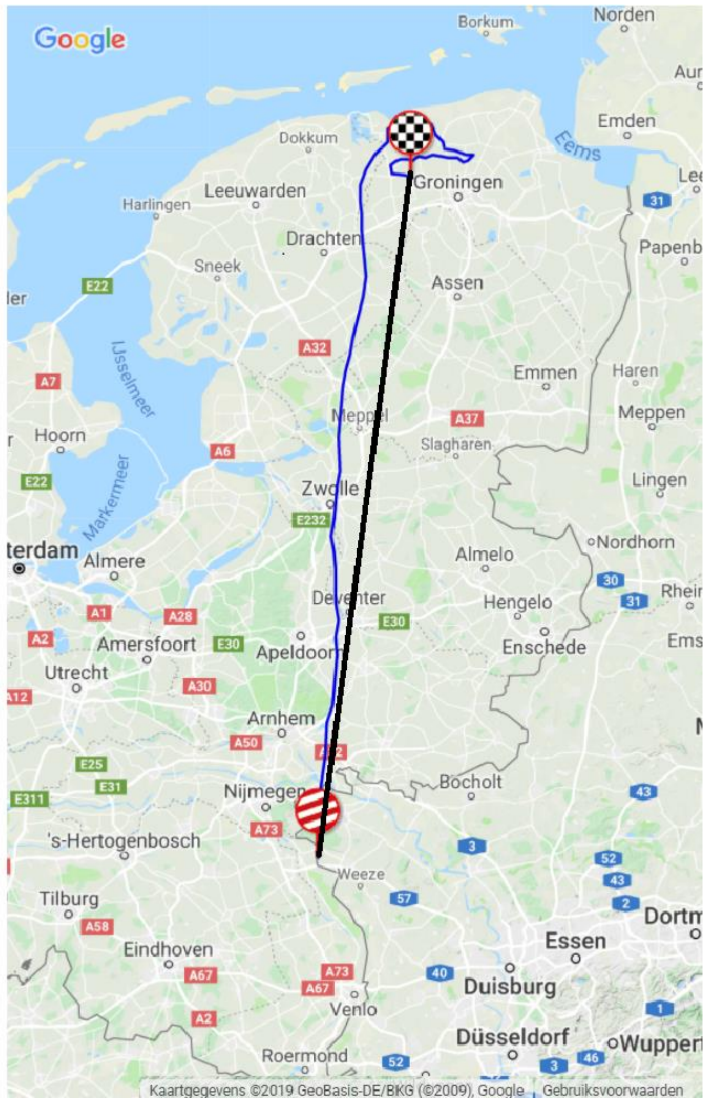
Appendix I – GPS flight tracks

		Bird ID	Colour
Flight number	1	18-077	Blue
Race date	01-09-2018	18-067	Red
Start location	Deventer	18-707	Brown
Race length (km)	115	18-059	Yellow
Black line	Bee-line	18-057	Green
		18-069	Purple
		18-061	Blue (bottom figure)

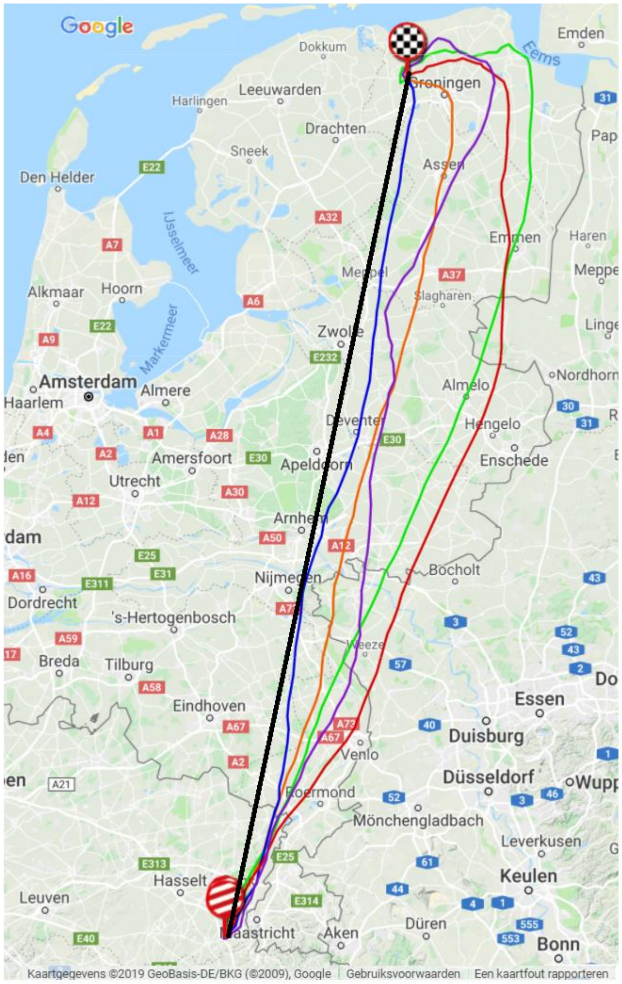


		Bird ID	Colour
Flight number	2	18-077	Blue
Race date	08-09-2018	18-067	Red
Start location	Gennep	18-057	Green
Race length (km)	177	18-061	Blue (right figure)
Black line	Bee-line		

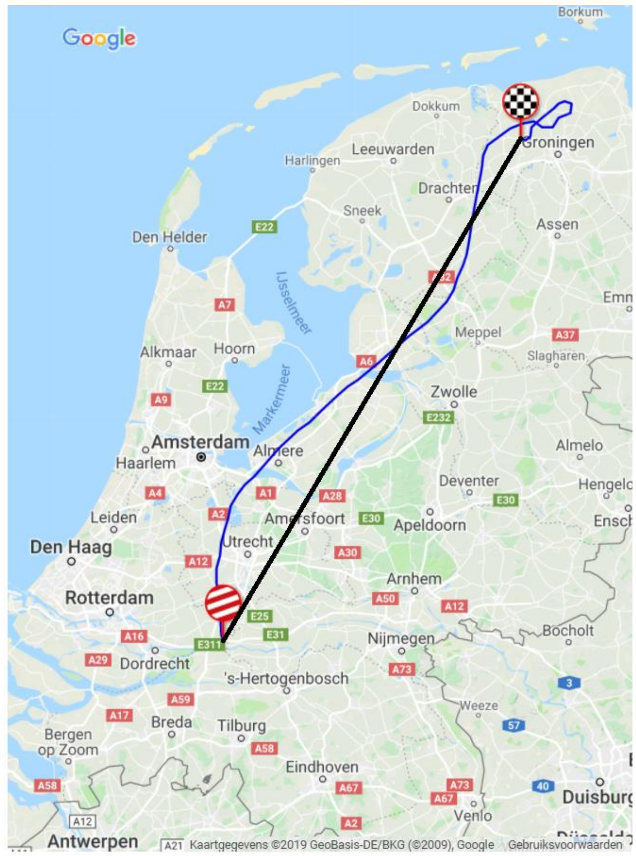




		Bird ID	Colour
Flight number	3	18-077	Blue
Race date	22-09-2018	18-067	Red
Start location	Tongeren	18-057	Green
Race length (km)	281	18-074	Purple
Black line	Bee-line	18-061	Blue (right figure)



		Bird ID	Colour
Flight number	4	18-077	Blue
Race date	29-09-2018	18-067	Red
Start location	Gorinchem	18-057	Green
Race length (km)	184	18-074	Purple
Black line	Bee-line	18-070	Brown
		18-061	Blue (right figure)



		Bird ID	Colour
Flight number	5	18-077	Blue
Race date	06-10-2018	18-067	Red
Start location	Boxtel	18-057	Green
Race length (km)	196	18-061	Blue (right figure)
Black line	Bee-line		

		Bird ID	Colour
Flight number	6	18-067	Red
Race date	13-10-2018	18-064	Brown
Start location	Roosendaal	18-058	Purple
Race length (km)	237		
Black line	Bee-line		

Appendix II - KNMI weather data

Variable	**Description**	**Unit**
STN	Station	278 = Heino 280 = Eelde 340 = Woensdrecht 356 = Herwijnen 370 = Eindhoven 375 = Volkel 380 = Maastricht
YYYYMMDD	Date	YYYY = year, MM = month, DD = day
HH	Time	Hours
DD	Wind direction	Degrees(360=north, 90=east, 180=south, 270=west)
FH	Average wind speed	0.1 m/s
FF	Wind speed	0.1 m/s
FX	Highest wind speed measured	0.1 m/s
T	Temperature	0.1 Celsius
T10N	Minimum temperature	0.1 Celsius
TD	Dew temperature	0.1 Celsius
SQ	Duration of sunshine	0.1 hours
Q	Radiation	J/cm2
DR	Duration of precipitation	0.1 hours
RH	Sum of precipitation per hour	0.1 mm/h
P	Air pressure	0.1 hPa
VV	Horizontal sight	0=<100m, 1=100m, 2=200m, 3=300m etc
N	Overcast	Degree of cover in 1/8, if 9=no sky visible
U	Relative moisture	%
WW	Weathercode	700-99
IX	Weathercode	indicator on measurement
M	Fog	0=absent, 1=present
R	Rain	0=absent, 1=present
S	Snow	0=absent, 1=present
O	Thunder(storm)	0=absent, 1=present
Y	Ice	0=absent, 1=present

Appendix III – Output table GLMM

Overview of variables which affected speed (m/sec) when location was included in the GLMM.

Type III Tests of Fixed Effects[a]

Source	Numerator df	Denominator df	F	Sig.
Intercept	1	6.140	1470.698	.000
windcategory2heading	2	2430.329	96.159	.000
Measuring point	1	1758.071	46.791	.000
Cumulative distance	1	2016.735	14.713	.000
Start location * Measuring point	5	1900.788	23.192	.000
Start location * Cumulative distance	5	2175.670	34.637	.000
Start location	5	1072.807	98.448	.000

a. Dependent Variable: Speed (m/sec).

Effects of variables in GLMM on speed (m/sec) including start location.

Estimates of Fixed Effects[a]

Parameter	Estimate	df	t	Sig.	95% Confidence Interval	
					Lower Bound	Upper Bound
Intercept	29.397180	8.273	39.913	.000	27.708443	31.085918
[windcategory2heading=1]	-3.670952	2418.528	-12.434	.000	-4.249914	-3.091991
[windcategory2heading=2]	-2.496582	2433.158	-11.529	.000	-2.921205	-2.071958
[windcategory2heading=3]	0[b]					
Measuring point	-.322592	1943.045	-11.410	.000	-.378040	-.267143
Cumulative distance	4.973130E-05	1978.130	6.791	.000	3.536844E-05	6.409416E-05
[start location = Boxtel] * Measuring point	.360209	2249.514	10.111	.000	.290344	.430074
[start location = Deventer] * Measuring point	.293294	1872.229	9.790	.000	.234535	.352052
[start location = Gennep] * Measuring point	.260893	2100.187	8.829	.000	.202942	.318844
[start location = Gorinchem] * Measuring point	.233823	2207.634	4.421	.000	.130107	.337540
[start location = Roosendaal] * Measuring point	.307314	1566.194	6.686	.000	.217156	.397471
[start location = Tongeren] * Measuring point	0[b]					
[start location = Boxtel] * Cumulative distance	-.000115	2355.173	-10.961	.000	-.000136	-9.445500E-05

[start location = Deventer] * Cumulative distance	-5.521091E-05	1914.108	-6.373	.000	-7.220171E-05	-3.822011E-05
[start location = Gennep] * Cumulative distance	-9.103433E-05	2233.326	-11.021	.000	-.000107	-7.483599E-05
[start location = Gorinchem] * Cumulative distance	-4.587879E-05	2270.137	-3.001	.003	-7.586322E-05	-1.589436E-05
[start location = Roosendaal] * Cumulative distance	-7.413656E-05	1831.752	-5.346	.000	-.000101	-4.693928E-05
[start location = Tongeren] * Cumulative distance	0[b]					
[start location = Boxtel]	4.213123	2372.970	6.386	.000	2.919421	5.506825
[start location = Deventer]	-7.371822	1304.755	-13.775	.000	-8.421661	-6.321983
[start location = Gennep]	1.608061	2299.387	2.639	.008	.413341	2.802782
[start location = Gorinchem]	-3.869313	2246.767	-6.428	.000	-5.049762	-2.688864
[start location = Roosendaal]	-2.147871	428.274	-3.042	.002	-3.535833	-.759909
[start location = Tongeren]	0[b]					

a. Dependent Variable: Speed (m/sec).

b. This parameter is set to zero because it is redundant.

Appendix IV – Optimal versus winning race duration

Bird ID	Flight number	Average speed (m/s)	Race bee-line distance (m)	Optimal race duration (hh:mm:ss)	Winning race duration (hh:mm:ss)
NL 18 1783707	1	18.65	115382	01:43:00	01:20:38
NL 18 4727057	1	16.93	115382	01:53:00	01:20:38
NL 18 4727061	1	5.00	115382	06:25:00	01:20:38
NL 18 4727067	1	18.28	115382	01:45:00	01:20:38
NL 18 4727077	1	16.93	115382	01:53:00	01:20:38
NL 18 4727057	2	15.37	178393	03:13:00	01:55:22
NL 18 4727061	2	14.87	178393	03:19:00	01:55:22
NL 18 4727067	2	9.38	178393	05:16:00	01:55:22
NL 18 4727077	2	16.74	178393	02:58:00	01:55:22
NL 18 4727057	3	17.11	281423	04:34:00	02:54:38
NL 18 4727061	3	15.20	281423	05:08:00	02:54:38
NL 18 4727067	3	17.28	281423	04:31:00	02:54:38
NL 18 4727077	3	13.00	281423	06:00:00	02:54:38
NL 18 4727070	3	18.89	281423	04:08:00	02:54:38
NL 18 4727074	3	14.76	281423	05:18:00	02:54:38
NL 18 4727057	4	21.10	185000	02:26:00	02:09:32
NL 18 4727061	4	20.02	185000	02:33:00	02:09:32
NL 18 4727067	4	19.04	185000	02:41:00	02:09:32
NL 18 4727077	4	16.90	185000	03:02:00	02:09:32
NL 18 4727057	5	18.72	200000	02:58:00	02:03:36
NL 18 4727061	5	13.22	200000	04:12:00	02:03:36
NL 18 4727067	5	14.88	200000	03:44:00	02:03:36
NL 18 4727064	6	22.42	238000	02:54:00	02:25:09
NL 18 4727067	6	18.75	238000	03:32:00	02:25:09