Who is the fastest racing pigeon of all?

A preliminary study on the influence of the physical condition of racing pigeons on their flight performance in a varying environment.

Lizanne Jeninga
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Wageningen University & Research
Resource ecology group

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In the context of my master thesis, part of the study Forest and Nature Conservation.

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Preface and acknowledgements

Various studies have addressed the navigational abilities of pigeons during their flight and how they form habitual routes. However, in contrast, few is known about the factors influencing the flight performance of a pigeon during a race; for instance, is the habitual route influenceable? This research report is the result of a study that is performed in context of a master thesis at the Wageningen University and Research in cooperation with the Dutch Racing Pigeon Fanciers Organisation (NPO) and deals with the effects of the physiological traits of pigeons on the flight performance and how this is related to the environmental circumstances they encounter along the route to home.

The field study and this research report are established by the help of a lot of people. I want to thank everyone who has contributed. Special thanks to Fred de Boer and Kevin Matson, who supervised me on behalf of the Resource Ecology Group of the Wageningen University and Research. They gave me very helpful feedback on concept versions of my research proposal and research report. I also want to give special thanks to Jan van Wanrooij of Interpalomas Lofts b.v., who helped me with the data collection. He drove many kilometres for me to release the pigeons and has learned me a lot on pigeon holding and racing. Moreover thanks to Interpalomas Lofts b.v., and in special Dr. De Weerd, for providing the pigeons and facilities for this study. Additionally, I would like to thank the NPO and its scientific board, WOWD, in providing the needed GPS rings and the pleasant corporation, and in special Jaap van Doormaal for revising the concept version of my research report on behalf of the WOWD. Other people I want to mention are Yanjie Xu and Jasper Eijkelboom, both PhD students at the Resource Ecology Group; they helped me with the data analyses in ArcGis, Excel and ''R''. Lastly, I want to thank Jeroen Maas, as he has given me feedback on my research proposal and report, which was very helpful.

I hope that this study can contribute to the understanding of the pigeon's flight performance and will be helpful for the further improvement of pigeon racing.

Lizanne Jeninga
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Summary

Background: The flight performance of pigeons in pigeon racing is determined by their flight speed and route efficiency. Although pigeons have been well studied in relation to their navigational abilities, much less is known about other factors that can influence the orientation and flight speed during a flight. For instance, questions are remaining on the influence of landscape and weather conditions along the track on the flight performance and whether this interacts with the body condition of the pigeons. More knowledge on this topic can contribute to a better understanding of the variation in flight performance and can contribute to the improvement of racing strategies in pigeon racing.

Aim: To determine the contribution of pre-flight physical condition to the flight performances of pigeons under different environmental conditions, and at different trajectories.

Organisms: homing pigeons (*Columba livia domestica*)

Place of research: Benelux (from multiple release sites in Belgium to the loft site in Breda, Netherlands).

Methodology: In this GPS tracking study, the flight paths of individual pigeons at three different trajectories were tracked and data on the pigeons' body condition were gathered, including measuring weight and size, scoring the appearance of the physical condition, and noting the moulting status (number of old primary feathers remaining). Landscape features and climatic conditions along the flight trajectories were also quantified. Eventually, several movement step characteristics, including the flight speed, turning angle, deviation from the bee-line (shortest track to home), and flight height, under different body-, landscape- and weather conditions were compared.

Principal findings: I found an influence of wind and temperature on both flight speed and orientation along the track. For instance, high wind speeds cause pigeons to fly home less directly and more slowly. Moreover, higher temperatures seem to improve homing, as under this condition higher speeds, lower turning angles and higher flight heights were observed. In contrast, landscape characteristics and body condition indices did not clearly influence flight performance, although small effects of the moulting status and conditions score on arrival time were found.

Conclusion: This study is one of the few studies which tries to elucidate the flight performance of pigeons, in terms of their flight speed and orientation, along their way home, and the factors influencing it. The study results confirm the importance of wind in the flight performance, but leaves ambiguity on the influence of landscape and the physical condition of pigeons. Although, the study results were not all convincing, the present work is valuable as preliminary study on the use of GPS tracker rings in unravelling the flight performance of pigeons along the track.

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1. Introduction

In nature, various animal movement patterns are observed. These patterns are the result of complex interactions between multiple internal drivers and external stimuli (Jonsen, Myers, & Flemming, 2003; Nathan et al., 2008; Schick et al., 2008). When trying to understand movement patterns in nature and the underlying decisions, four fundamental questions can be addressed: 1) why move, 2) how to move, 3) when to move, and 4) where to move (Nathan et al., 2008). Lots of studies have examined the ''how'' of the movement in avian navigation by looking at the flight of homing pigeons, *Columba livia domestica* (further called ''pigeons''; Wiltschko & Wiltschko, 2017). Pigeons are known for their remarkable navigational skills by which they are able to reach home from far away and unfamiliar sites. Studies on the navigational abilities of pigeons have provided insight in the environmental cues that pigeons use when navigating (reviewed in: Wiltschko & Wiltschko, 2015). As described by Kramer (1957) in his "Map-and-Compass' model, a pigeon first maps its position relative to the goal and determines the direction to head home, after which it determines the setting of a course with the help of an integrated compass system. Pigeons can use various compasses for this, including the magnetic-, sun- and star compass. Besides, they can use environmental factors, like gravity, odours and landscape features, to head home (Wiltschko & Wiltschko, 2015). Due to their navigational skills, homing pigeons have been used by humans for centuries, in the earlier days for mail delivery, and now for sport races. These races are about reaching home the fastest, and so the pigeon's performance, and the factors that are influencing it, are of importance.

Two components determine flight performance, thereby homing time, and hence are of interest: 1) the flight speed, as a faster pigeon will arrive earlier at the loft than its conspecifics, and 2) the route efficiency, since a more efficient route is equal to a shorter travelling distance. Although pigeons have the tendency to fly in flocks (Gould, 2006; Mehlhorn & Rehkaemper, 2016), they also can form individual preferred routes to which they are loyal to (Biro, Meade, & Guilford, 2004, 2005, Meade, Biro, & Guilford, 2005, 2006). The development of these habitual routes is suggested to be related to a higher energetic or cognitive cost of flying in an unfamiliar area (Meade et al., 2005; Taylor, Portugal, & Biro, 2017). The habitual routes vary greatly among individuals and are rarely the most direct way home (Biro et al., 2004; Guilford & Biro, 2014; Meade et al., 2005). Comparing the actual flight track to the shortest path back home reveals the pigeon's route efficiency (e.g. Biro et al., 2004; Mehlhorn & Rehkaemper, 2016; Schiffner & Wiltschko, 2014). The observed route efficiencies in earlier pigeon studies ranges between 0.66 – 0.91 (Maximum = 1 = 100% efficiency, review in: Guilford et al., 2014). Also flight speed varies among individuals and flights. During a flight, a the pigeon's speed is around 50-80 km/h (Dell'Ariccia, Dell'Omo, Wolfer, & Lipp, 2008; Gagliardo, Ioalè, Savini, Lipp, & Dell'Omo, 2007; Gessaman & Nagy, 1988; Schiffner & Wiltschko, 2009; Tyson, 2013). Though, the flight speed over the total track is often lower, due to the circling time at the release and arrival sites, and possible stops along the way (Scullion, 2016).

Flight performance can be improved by the experience that individuals gain through repetitive flights on a single trajectory. Often, birds that are trained in this way have a better orientation towards home (Wiltschko & Wiltschko, 2015). This learning process is reflected by an increase in route efficiency, which is often observed up to the 3-6th flight. From there on the route efficiency is becoming steady, indicating that the habitual route is formed. (Biro et al., 2004; Flack, Pettit, Freeman, Guilford, & Biro, 2012; Guilford & Biro, 2014; Meade et al., 2005; Mehlhorn & Rehkaemper, 2016). Besides training, also social factors can influence the performance of pigeons in a flight, for instance flock forming. Pigeons flying in small flocks leave the release site faster (Dell'Ariccia et al., 2008; Schiffner & Wiltschko, 2009), have improved directionality in the flight back home (Dell'Ariccia et al., 2008; Mehlhorn & Rehkaemper, 2016), fly faster and have fewer stops (Dell'Ariccia et al., 2008), which is probably due to group cohesion. Moreover, the pre-flight motivation can influence flight performance, as found by Mehlhorn & Rehkaemper (2016). They found that female pigeons with an existing or upcoming clutch were more efficient in the flight then without, which is likely related to the motivational factor provided by the investment in the clutch. Furthermore, a longer waiting time at the release site can result in higher flight speeds during homing, probably due to an increase in determination to reach home (Dell'Ariccia, Costantini, Dell'Omo, & Lipp, 2009). Although training and social factors, like group cohesion, breeding status and waiting time, provide an explanation for the variation in flight performance, it cannot explain all variation observed. According to the framework of Nathan et al. (2008), movement paths are influenced by an individual's internal state, the motion capacity, the navigation capacity, external factors, and the interactions among those factors. Furthermore, the selected speed of movement is based on an interaction between the maximum possible speed, the ecological context of the movement (e.g., an animal's need to find food or a partner) and the biotic environment (e.g., predation pressure or landscape composition, Wilson, Husak, Halsey, & Clemente, 2015). So, it is highly likely that also other factors are involved in the flight performance. Although pigeons have been well studied in relation to their navigational abilities, much less is known about how, for example, internal factors, like the pigeon's body condition, and environmental factors, like the weather conditions and landscape composition, influence the flight performance.

Body condition is a broad term and used in different ways, but it often relates to the energetic status and health of an individual and includes, for instance, measures of morphology (Schulte-Hostedde, Zinner, Millar, & Hickling, 2005; Stevenson & Woods, 2006). A bird's morphology is related to its aerodynamics and affects thereby its flight performance. The wing size, structure, and its movements are considered to be of major importance, as well as the body mass and its relation with wing loading. Differences in these characteristics can affect the energy expenditure and thereby can cause changes in route choices and flight speeds (Pennycuick, 1968; Tyson, 2013). This was, for instance, found in several migration studies, showing that individuals with a lower body weight (lower fuel load) dropped out earlier from the migrating flock or changed their flight direction at barriers, to replenish energy storages (Alerstam, 1978; Deutschlander & Muheim, 2009; Sandberg, 1994; Sandberg & Moore, 1996; Yosef, Markovets, Mitchell, & Tryjanowski, 2006). Besides, manoeuvrability can be negatively affected by a higher weight (Dietz, Piersma, Hedenström, & Brugge, 2007). Furthermore, also external morphological changes, such as reduced feather quality, have been related to changes in flight behaviour (Barbosa, Merino, Lope, & Møller, 2009; Rätti, Dufva, & Alatalo, 1993). For instance, moult can affect flight performance by reducing flight speed, stability and manoeuvrability and demanding energy (Hedenström & Sunada, 1999; John P. Swaddle & Witter, 1997; John P. Swaddle, Witter, Cuthill, Budden, & McCowen, 1996; Williams & Swaddle, 2003). In contrast, not much is known about the effects of the pigeon's physical condition on its flight performance. However, some studies address aspects, for instance, showing that dehydration can restrict the duration and length of a pigeon's flight (Biesel & Nachtigall, 1987; Gessaman & Nagy, 1988; Gessaman, Workman, & Fuller, 1991). In addition, Mercieca, Jilly, & Gáspárdy (2017) studied the effect of body weight and wing length on the flight speed of racing pigeons, but did not found any effects. From practice, we know that moult negatively affects the pigeon's flight performance, however the way flight performance is affected and the effect size with the different moulting stages, is unreported.

The effect of the landscape on the flight of pigeons has been studied in the light of their navigation. For instance, it was found that ecological barriers, like extended seas or mountains can cause pigeons to deviate from the most direct route to home (Bonadonna, Dall'Antonia, Ioalè, & Benvenuti, 1997; Wagner, 1972; R. Wiltschko & Wiltschko, 2015). Moreover, the landscape can be important for the visual-based route learning and following (Armstrong et al., 2008; Biro, Freeman, Meade, Roberts, & Guilford, 2007; Lau et al., 2006). Linear features, like roads and railways, can, for example, be used for homing, if they are positioned in the home direction (Dell'ariccia, Dell'omo, & Lipp, 2009; Guilford, Roberts, Biro, & Rezek, 2004; Lipp et al., 2004). However, the extent to which this is done seems to be region dependent (Guilford & Biro, 2014; Schiffner & Wiltschko, 2014), Herewith, the amount of edges in the landscape is suggested to be importance as it can influence the route choice and flight characteristics. Edge containing features can used by pigeons for navigation (Armstrong et al., 2008; Lau et al., 2006). However, more edges in a landscape is not necessarily improving orientation, as too much complexity in a landscape, like it is observed in cities, can lead to less route learning (Armstrong et al., 2008; Mann et al., 2008).

Differences in homing routes of birds, as well as the flight speed and altitude, are also related to the weather conditions. For instance, the way birds react to wind conditions can significantly affect their flight duration and energy expenditure and therefore their flight performance (Alerstam, 1979a, 1979b; Richardson, 1978). Depending on their abilities, birds have strategies to compensate direct or indirectly for non-optimal wind conditions, including changing their heading or air speed (Thomas Alerstam, 2011; McLaren, Shamoun-Baranes, Dokter, Klaassen, & Bouten, 2014; Richardson, 1990; Tucker & Schmidt-Koenig, 1971). Moreover, they can take advantage of more favourable wind conditions, like tailwinds, which can reduce the required time and energy per unit distance of flight (Alerstam, 1979b; Butler, Williams, Warnock, & Bishop, 1997; Pennycuick, 1989 in (Liechti, 2006); Richardson, 1990). This was also observed in the pigeons' flight; pigeons were homing faster and more successfully under tail wind conditions (Li, Courchamp, & Blumstein, 2016; Tamboryn, 1992 in (Winkel et al., 2008)). Furthermore, it was observed that pigeons were able to fully compensate for crosswinds by changing their heading (Michener & Walcott, 1967). Birds can also change their vertical heading, thereby changing in altitude. Many factors can ensure that a bird change its flight altitude. However wind is considered to be most influential on this decision (Kemp, Shamoun-Baranes, Dokter, van Loon, & Bouten, 2013). Choosing a certain flight altitude can provide the bird with the most optimal wind conditions (Bruderer, Underhill, & Liechti, 2008; Liechti, 2006). For instance higher wind speeds, as generally wind speed increases with altitude (Liechti, 2006; Tyson, 2013). Therefore, it is often found that birds fly lower with headwinds and higher with tailwinds, as this is most optimal in terms of wind speed and direction (Dornfeldt, 1991; Taylor et al., 2017). Besides, also precipitation, cloudiness and foggy conditions can affect the flight performance, as it reduces the flight capability and navigation and thereby can increase the number of stops or route deviation (Dornfeldt, 1991; Schietecat, 1991, Tambouryn, 1992 in (Winkel et al., 2008)). In addition, higher air temperature is increasing water loss during the flight and thereby restricts flight distances and duration (Biesel & Nachtigall, 1987; Gessaman & Nagy, 1988). However, during races, temperature seems rarely be of influence on the flight performance, as long as it is within a normal temperature range (between 5°C and 30°C, Dornfeldt, 1991; Li et al., 2016; Schietecat, 1991 and Tambouryn, 1992 in (Winkel et al., 2008)).

Past studies on the homing performance of pigeons were often limited to the observations of the vanishing bearings at the release site and arrival times at the loft, or observations from airplane or experimental settings, like wind tunnels. The invention of the GPS loggers and the future improvement of the size of these devices, has made it possible to track the pigeons' movement and collect data on flight characteristics along their way home. This offers the potential to further unravel the factors influencing the flight performance and thereby to improve our understanding on the variation in observed flight performances of pigeons and other migrating birds. Moreover, more knowledge on the influence of body condition in relation to the pigeon's environment, can contribute to better racing strategies and to reduced losses in pigeon racing. Therefore, *the aim of this study was to determine the contribution of pre-flight physical condition to the flight performances of pigeons under different environmental conditions*. In this study, flight performance was defined as flight speed and orientation. Also the flight height was included in this study as this can be related to the flight speed and orientation. For instance, the flight height can determine the wind conditions encountered and thereby can influence flight speed, as discussed above. To study the flight performance of pigeons, flight paths of individual pigeons in several flights over different trajectories were tracked using GPS tracking rings. In addition, data on the pigeons' physical condition were gathered indirectly by measuring the body weight and structural size (wing length and tarsus length), scoring the physical appearance and recording the moulting status. Landscape features and climatic conditions along the flight trajectories were also quantified. Eventually, the flight speed and orientation, and flight height under different body-, landscape- and weather conditions were compared. Additionally, the effects of wearing a GPS ring were explored.

It was expected to observe differences in flight performance between the flights; when released from an unfamiliar area, the pigeons can develop a fixed route and thereby increase their route efficiency over time (e.g. Guilford & Biro, 2014; Meade et al., 2005). Within the flights, we might observe improved homing towards the loft, as the familiarity with the area increases. For instance, Michener & Walcott (1967) reported that pigeons, which were released from unfamiliar sites, were straitening their flight once they came within a few kilometres of the loft. In contrast, a more stable flight speed over the flight was reported by Tyson (2013). So distance to the loft might have an effect on the orientation and not on flight speed. All parameters of the physical condition of the pigeons were expected to influence the flight performance along the track. Since weight/size ratio is often related to the energy load (Labocha & Hayes, 2012), I expected an optimum weight/size ratio, which allows a maximum flight speed (Klaassen, 1996). Weight/size ratio might also affect the orientation during the flight directly by manoeuvrability (Dietz et al., 2007) or indirectly through the movement decisions (e.g. Alerstam, 1978; Sandberg, 1994). Condition score is an external examination of the pigeons' condition. It was expected that when a pigeon is scored low, this was reflected in its performance, by either a lower speed or a worse orientation. Moult was expected to affect the flight performance of the pigeons negatively, due to reduced feather quality and increased energy expenditure (e.g. Hedenström & Sunada, 1999). Most severe effects of moult were expected in the middle stage of the moult (from 5-8 primary feather), reducing the flight speed and orientation, as this is observed in Harris's hawks (*Parabuteo unicinctus*, Tucker, 1991), and also found in the work of Hedenström & Sunada (1999) and Swaddle & Witter (1997). Landscape composition was expected to affect the flight performance along the track mainly through the occurrence of urban area, as it was also found in the route learning (Armstrong et al., 2008). The complexity of the urban area might cause less orientation or lower flight speeds, as it is assumed that there is less possibility to follow the linear landscape features. It was expected that especially the wind conditions have a large effect on the flight performance of pigeons (Mercieca, Jilly, & Gáspárdy, 2017; Winkel et al., 2008). Based on earlier studies, I expected with quite some certainty the following trends: higher flight speeds and flight heights in tailwind compared to headwind and a possible change in heading in crosswinds due to compensation (Li et al., 2016; Michener & Walcott, 1967; Taylor et al., 2017). In contrast, it was expected that the temperature had no effect on flight performance, as the temperature range in my flights is likely within the range of what is considered to be normal (Schietecat, 1991 and Tambouryn, 1992 in (Winkel et al., 2008)).

In summary, I have tested the following hypotheses:
1. Flight performance improves over flights from unfamiliar areas and release sites.
2. Closer the loft the orientation will improve.
3. There is an optimum body condition at which the speed and orientation is at its maximum (quadratic function).
4. The higher the condition score, the better the flight performance of the pigeon.
5. There is a specific moulting stage at which speed and orientation are at its minimum.
6. Flying over urban areas reduces the flight speed and orientation of the pigeons.
7. Wind effects on flight performance are conform the following well-known predictions: higher flight speeds and flight heights in tailwind compared to headwind and a possible change in heading in crosswinds due to compensation.
9. Temperature within the normal range is not affecting flight performance.

2. Materials and methods

This study consisted of two types of experimental flights: dummy flights, and GPS flights. Dummy flights were executed first, to ensure that wearing GPS loggers did not negatively affect the pigeons' performance. Thereafter, GPS flights were executed to track the flight of the pigeons by use of GPS tracker rings. The protocols followed in the experimental flights and the analyses of the collected data are described in this chapter.

2.1 Animals and housing

Figure 2.1. Situation loft.

This study was carried out with homing pigeons (*Columba livia* f. *domestica)*, which were hatched and hand reared at the breeding centre of Interpalomas Lofts of Belgica de Weerd, Breda, The Netherlands[1] . The pigeons were in the age class of 1-6 years old and had different racing experiences (Appendix 1 & 2). During this study, the pigeons were housed in closed lofts where they lived in mixed groups (consisting of females and males, Figure 2.1), which is similar to their original housing. In the period of the dummy flights, the pigeons were divided over two lofts, in the period of the GPS flights all participating pigeons were housed in one loft (Appendix 1 & 2). In the lofts, natural daylight was available. Moreover, fresh water, grit and Vitemineral® were available *ad libitum*. The pigeons were fed twice a day with a food mixture for pigeons (30 gram of mixture per pigeon per day of which 50% was flying mixture and 50% purifying mixture[2]). During the study, the pigeons got one treatment of ''B.S. (Betere spijsvertering[3])'' (Belgica de Weerd) for two days, which is a preventive and curative measure against the following parasitic infections: Trichomoniasis, Coccidiosis and Hexamitiasis.

2.2. Experimental flights

The dummy flights (Section 2.2.1) have been performed from August until September 2017 and the GPS flights (Section 2.2.2) from September until October 2017. On a release day, the pigeons were transported by car to the release site, housed in transport baskets with individual stalls. As the racing pigeons are raised by humans and used to be handled, it was assumed that handling stress at the flight preparations and releases was minimal. All releases took place on sunny or moderately cloudy days without extreme wind conditions, except for the last GPS flight (flight 1, trajectory 3, Sub-

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[1] Except for three pigeons which were originally from Belgium.

[2] Mixture of Beyers. Flying mixture is consisting of: Popcorn 23%, small cribs mais 15%, white dari 10%, white wheat 8%, cardy 7%, extra red sorghum 6%, toasted soybeans 5%, peeled oats 5%, brown rice 4%, small green peas 3,5%, maple peas 3%, small yellow peas 3%, vetch 2%, Dun peas 1,5%, lentils 1%, Katjang idjoe 1%, hempseed 1%, buckwheat 1%, and purifying mixture is consisting of: small cribs mais 31%, extra white dari 20%, cardy 20%, paddy rice 20%, Katjang idjoe 2%, white wheat 1,9%, peeled oat 1,6%, extra red sorghum 1,6%, barley1%, rapeseed 0,3%, linseed 0,3%, buckwheat 0,3%.

[3] The active component of BS is sulphachloropyrazine-natrium-monohydrate, which has anticoccidial efficacy.

section 2.2.2.2), which was held on a day with less optimal weather conditions: a reduced vision due to a high air humidity (Appendix 3).

2.2.1. Dummy flights

2.2.1.1 Flight preparations

Before the dummy flights started, one dummy and one non-dummy group were composed, in which an equal representation of males and females was ensured (Appendix 1). The composition of both groups was kept the same in every flight. Individuals of the dummy group got to wear a dummy ring. This ring is similar to the actual GPS ring (Paragraph 2.3) in appearance, size and weight (Figure 2.2 and 2.3). The dummy ring was attached to the left leg of the pigeon, a week before the first release, and the pigeons continued to wear the ring until the last flight, to ensure habituation.

Figure 2.2. Pigeon with dummy ring (left) and pigeons without a ring (right).

Figure 2.3. Dummy ring in close-up.

2.2.1.2 Test flight and loft observations

Before the actual dummy flights, a short test was performed to test the automatic recognition system in the lofts and to have a first check on the performance of the pigeons. This was a group release: dummy wearing and non-dummy wearing individuals were released together at a release site in Brecht, Belgium (23 km South-West from the lofts, Appendix 4). This site and region was familiar for the pigeons through earlier training flights. No strong abnormalities (e.g. extreme delays, excessive sitting behaviour or improper walking) were observed in this test flight (Appendix 5). However, in the lofts, we did observe some reactive behaviour of the pigeons on the dummy rings, including pecking towards the ring and pulling up the leg with the dummy ring. To determine the frequency of this behaviour and the development of the behaviour over time, several behavioural observations were performed (Box 1). Nonetheless, as no strong abnormalities, like extreme delays, were observed in the test flight, we decided to proceed to the actual dummy flights.

Box 1. Behavioural observations

Behavioural observations were executed to determine the frequency of occurrence of ring-related behaviour, like pecking towards the ring, and the development of the behaviour over time.

Method: The behavioural observations were executed in October in the loft (loft situation described in paragraph 2.1). In total, 21 pigeons were observed, of which 7 pigeons without a ring, 7 pigeons with a dummy ring and 7 pigeons with a dummy ring with rubber lining (Figure underneath). The rubber lining was suggested as a measure to limit the movement of the ring on the leg and thereby the discomfort for the pigeon, and was included to test its effectiveness as mitigating measure. During an observation, a pigeons' behavioural state (for example sitting), as well as the events (for example pecking towards the ring) were recorded for three minutes per pigeon. By means of an ethogram and protocol (Appendix 7), the type of behaviours displayed and the duration were noted. The observations were repeated three times, on day 1, day 4 and day 8. Each repetition consisted of 2 or 3 observational rounds, which all took place from 13:00 till 17:00.

Results and discussion: As expected, more ring-related behaviour was shown by the individuals wearing a ring. However, these differences could not be statistically proven. This might be due to the small sample size. Also, no differences were observed between days or between the ‘’’Dummy ring’’ and ‘’Dummy ring with rubber lining’’ groups. These groups might not be that different in our setting, as the rubber lining was not exactly fitted on the leg of the pigeon and movement of the ring was still possible. So, whether this could be a good mitigating measure still needs some additional study.

Conclusion: Wearing a GPS ring might cause some discomfort to the pigeon, as some reactions on wearing of the rings are observed. However, no differences in behaviour could be statistically proven. This, together with the absence of abnormalities in the test flight, suggests that the rings are not causing major abnormalities in the pigeons' behaviour and that GPS flights can be performed without serious welfare consequences for the pigeons. However, the behaviour of the pigeons, wearing a ring, need to be continually monitored and compared to pigeons without a ring to be able to intervene when negative changes in the behaviour occur.

2.2.1.3 Execution dummy flights

Three repetitive dummy flights were performed from a release site located in Sint Job-in-'t-Goor, Belgium (30 km South-West of the lofts, Appendix 6). This release site and region was to a certain extent familiar to the pigeons through earlier training flights. In the dummy flights, individual releases would be preferred, since we are interested in individual flight performances and flight performance can advantageously be influenced by grouping (e.g. Dell'Ariccia et al., 2008; Mehlhorn & Rehkaemper, 2016). Nonetheless, to assure that both dummy wearing and non-dummy wearing individuals fly as much as possible under similar social and environmental conditions[4], pigeons were released pair-wise: one pigeon with a dummy ring and one without were released together. The release interval was five minutes. In case it took more time before a pair disappeared from sight, the interval was extended with several minutes, to prevent flock forming and thereby group flights. To limit the differences between the individuals in a pair, the pigeons were matched before the first flight. Thereafter, the pairs were kept the same in every flight (Appendix 1). Matching was done based on the three following criteria, using data of the pigeons' body condition, which was collected before the dummy flights took place (Section 2.2.1.4):

- Firstly, individuals of the same sex were matched
- Secondly, individuals with the least difference in moulting status (number of old primary feathers remaining) were matched
- Lastly, when multiple individuals were in the same stage of moult, matching was done based on the least difference in weight.

2.2.1.4 Measurements

After the first recordings of weight and moulting status to match the pairs before the first dummy flight, weight and moulting status were continued to be recorded before the other dummy flights to monitor the body condition of the pigeons (Appendix 1). The pigeons were weighted after the feeding in the morning by use of a digital scale. For moulting status, the number of old primary feathers was noted. The flight measurements included the release time of every pair and the individual time of entering the loft. The latter was registered by means of an electronic recognition system at the entrance of the loft. From these flight measurements the duration of the flight was calculated.

2.2.2. GPS flights

As no significant negative effects on flight performance or behaviour was found in the dummy flights and behavioural observations (Section 3.1.1, Box 1 and Appendix 7), GPS flights were subsequently executed.

2.2.2.1 Flight preparations

As with the dummy flights, it is also preferred to work with individual releases in the GPS flights. However, as time progresses, moult also progresses, which might influence the pigeons' performance with a GPS ring. Moreover, as some behavioural abnormalities were observed in the lofts (Sub-section 2.2.1.2), it has been decided to include an control group without a GPS ring in the GPS flights. Therefore, before the GPS flights started, one GPS and one non-GPS group were composed, using data on the body condition of the pigeons, as measured before the last dummy flight (Appendix 1). This was done in such a way that an equal amount of females and males were presented in both groups and moult and body weight were balanced *(GPS group - mean weight: 459 ±33 gr, median moulting status: 3 old primary feathers; Non-GPS group- mean weight: 462, ±17 gr, median moulting status: 3 old primary feathers;* Appendix 2). All pigeons that were used in the GPS flights also participated in the dummy flights, in which they were part of the dummy group. The

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[4] As wind conditions and waiting time can change over time and might influence performance (T. Alerstam, 1990; Thomas Alerstam, 1979b; Dell'Ariccia et al., 2009; McLaren, Shamoun-Baranes, Camphuysen, & Bouten, 2016).

individuals allocated to the GPS group kept their dummy rings after the dummy flights to maintain habituation.

2.2.2.2 Execution GPS flights

Five GPS flights were performed: one long flight (118 km from the loft), three repeated flights at an intermediate distance from the loft (75 km) and one short flight (30 km from the loft) (South-West of the lofts, Appendix 8). The first two release sites were unfamiliar for the pigeons. The last release site and the surroundings, instead, was familiar to the pigeons through earlier training flights. The GPS flights had a similar release procedure as the dummy flights; the pigeons were released pair-wise: one pigeon with GPS ring and one without. The release interval was five minutes, and the interval was extended with several minutes when the pair took more time to disappear from sight to prevent flock forming and thereby group flights. The release pairs were matched before the first GPS flight, also in a similar manner as in the dummy flights (Section 2.2.1.3), using data on the body condition of the pigeons, collected before the first GPS flight (Section 2.2.2.4; Appendix 2). To be able to record the pigeon's track along the GPS flights, the dummy rings were replaced by GPS rings (Sub-section 2.2.2.3) before every flight. As the GPS rings need charging and setting, the rings were also switched back after the flights.

2.2.2.3 GPS tracker rings

In the GPS flights, GPS tracker rings (further called ''GPS rings'', Figure 2.4 and 2.5) were used to follow the pigeons' movement from the release site back to the lofts. Tests on the lifespan of the battery, before and after the GPS flights, revealed that the GPS rings recorded positions roughly every 3 minutes of 577±112 (SD) minutes in total (Box 2). Recorded data included coordinates of the position (decimal degrees), height (meters above sea level) and speed (meters/second). The level of accuracy of these recordings by the GPS rings was determined by executing multiple tests, which are described in Box 2.

Figure 2.4. Pigeon with a GPS ring on its left leg.

Size: 20x20x14mm
Weight: 4 grams (including battery, on average 0.8% of the body weight)
Battery type: Rechargeable Lithium battery 3.7V 45mAh
Satellite system: GPS and GLONASS Dual - core system

Figure 2.5. GPS ring in close-up and ring

2.2.2.4 Measurements

Besides weight and moulting status, which were recorded to match the release pairs before the first GPS flight, also a general external condition score was given to the pigeons (scale 1-10). All three parameters were continued to be recorded before the other GPS flights to monitor the body condition of the pigeons and for later track analyses (Appendix 2). Body mass was recorded, after feeding in the morning, by use of a digital scale. Moulting status was recorded by noting the number of old primary feathers (Appendix 9). The external condition score was appointed to every pigeon by a pigeon expert[5] and was based on appearance of the feathers, the throat, eyes and fullness of the body (scale 1-10). Meanwhile, wing length and tarsus length (an indication of skeletal size) were

Box 2. Accuracy test GPS tracker rings

The level of accuracy of the location recordings and height and speed measurements of the GPS rings was determined by executing multiple tests. When possible, the tests were executed before and after the flights, so that the stability of measurements over time could be determined.

Methods: The accuracy of ***location*** recording was tested in three ways: by comparing the recordings of our GPS rings to a RDW registered location, the recordings of an exact GPS device (RTK GNNS, Topcon Hiper V), and to the recordings of a regular GPS device (Garmin 60CSx and Garmin eTrex Legend HCx). This last test was performed for a minimum of twelve hours. In that way, not only the accuracy of location recording over a longer time span was tested, but also the maximum life span of the battery was determined. The accuracy of ***height*** recording was tested in two ways: by comparing the recordings of our GPS rings to the height measurements of a regular GPS device (Garmin 60CSx and Garmin eTrex Legend HCx) on the outside area of an apartment building, and to the recordings of a GPS logger during a flight of a glider (Sample frequency: 1Hz). Due to problems with the GPS logger of the glider, this last accuracy measurement was only completed before the flights. The accuracy of ***speed*** recording was tested by comparing the recordings of our GPS rings to the speed indicated by a GPS navigation device (Garmin). These speed recordings were only made after the flights.

Results/discussion: Lifespan of the battery was less than the manufacturer indicated (12 hours), on average 10 hours before the flight and on average 8,5 hours after the flight. Although some GPS rings were showing a decrease in recording time, no significant differences in the lifespan of the battery were found between the before and after flight measurements. This is in contrast to the accuracy of the recordings in some of the tests. In the fixed location test, the accuracy of the recordings before the flights was significantly lower compared to those after the flights. This was not expected, but can be due to several factors, including blockage of the signal by buildings, the atmospheric conditions and the quality of the materials. Also in the RDW registered location test, a less accurate before measurement was observed, but only for the longitude. No clear cause for this could be found. The height recordings did not differ in time. The accuracy of location recording of our GPS rings was, besides the first fixed location recordings, in line with some other studies (Dessault et al., 2001, Rose et al., 2005), although some found higher accuracies (Bouten et al., 2013, Scullion, 2016, Steiner et al., 2000). This can be due to the compromise that often have to be made between weight and the amount and quality of data that can be recorded by the device (Bouten et al., 2013). The height recordings of our GPS rings were less accurate than the location recordings and also more variable. However, this is not unusual for GPS devices (Scullion, 2016).

Conclusion: When comparing the accuracy of the measurements by our GPS rings to what is commonly observed, the deviation is range with what can be expected, and so the accuracy of our GPS rings can be considered as good for the type device. However, some extreme values were observed, likely due to an error in signal receiving. In flight, pigeons will be mostly in open area, and so less blocking of the signal is expected. However, the possibility of errors by bad signal receiving needs to be taken into account when analysing the tracking data.

A more extensive explanation on the accuracy tests is included in Appendix 10.

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[5] Pigeon expert: Jan van Wanrooij of Belgica de Weerd.

measured once, before the start of the GPS flights by use of a ruler and a calliper, respectively. These were used to calculate weight/size ratios, which is weight divided by size. The flight measurements included, besides the flight track recordings by the GPS rings, the release time of every pair and the individual time of entering the loft. The latter was registered by means of an electronic recognition system at the entrance of the loft. From these flight measurements the duration of the flight was calculated.

Additionally, for each of the recorded tracks in the GPS flights, the landscape composition was determined. Landscape composition data were obtained from a worldwide land cover dataset (Climate Change Initiative, 2015). Furthermore, information on the climatic conditions during the flights was obtained from weather stations, located on or near the trajectories, including Gilze-Rijen, Woensdrecht, Antwerp, Zemst, Molenkouter, Oppuurs and Vlaamsgewest. The collected climatic data included the temperature (°C), wind direction (partly in degrees or converted into degrees) and wind strength (0.1 m/s and km/h). Data were obtained from ''Koninklijk Nederlands Meteorologisch Instituut'' (KNMI, n.d.) and ''Weather Underground'' (WU, n.d.). The environmental data were used for further track analyses (Sub-section 2.4.2.2).

2.4. Data analyses

All data of the dummy flights and GPS flights were statistically analysed by using IBM SPSS Statistics 24. In all tests, an effect was considered to be significant with a p-value of ≤ 0.05.

2.4.1. Dummy flight data

The effects of the dummy rings on the pigeon's flight performance were studied by comparing the flight performance of the dummy wearing and the non-dummy wearing individuals. For this purpose, the arrival times (in minutes after release) of the individuals arriving home on the release day were compared by means of a Generalized Linear Mixed Model (GzLMM) repeated measures analysis with Gamma probability distribution and log link function, as the data were not normally distributed (Appendix 11). Also, flight number and distance to the loft were included in the model to determine their influence. Moreover, physical condition (weight and moulting status) was included in the GzLMM to test for possible additional effects. Sequential Sidak was applied afterwards whenever a significant effect of a categorical variable was observed. In case the condition variables were significant their interaction with treatment group (dummy/non-dummy) was tested. In addition, the arrival groups were compared, including ''on time'' arrivals, ''extremely delayed'' arrivals and lost pigeons. Extreme delayed was defined was defined as an arrival later than 1-2/3 of the time at which the first quarter of all pigeons of that flight arrived. This is based on the assumption that flight arrivals of a race follow a Gaussian curve (in fact, the arrivals of a race are skewed distributed). As the number of extremely delayed birds or lost birds was low compared to that of the ''on time'' arrivals, statistical analysis of the data on arrival group was not performed, only descriptive statistics were done.

2.4.2. GPS flight data

2.4.2.1 Homing performance GPS and non-GPS group

In the GPS flights, a control group was included to determine if the GPS rings were not affecting the pigeons' performance. The arrival times on the release day were compared by means of a GzLMM repeated measures analysis, in a similar manner as with the dummy flight data, because of non-normal distributed data (Section 2.4.1, Appendix 12). However, in contrast, in this analysis, weight/size ratios, moulting status and condition scores were included as physical condition variables. Both weight/size ratios were included as squared factors to test the optimum hypothesis (chapter 1). Additionally, Sequential Sidak was applied whenever a significant effect was found of a categorical variable, and whenever a condition variable was significant, its interaction with treatment group (GPS/non-GPS) was tested. Also for the GPS flights, the arrival groups were compared and descriptive statistics were applied.

2.4.2.2 Track analyses

Overall track efficiency: The recorded flight tracks of the pigeons are deviating from the shortest track back home, which is called the bee-line and is defined by a straight line between release site and loft. By establishing the bee-lines for the different flight trajectories, an efficiency index was calculated for every complete flight track. The efficiency index is the distance from release site to the loft according to the bee-line divided by the distance from the release site to the loft according to the route followed by the pigeon (as used by e.g. Biro et al., 2004; Mehlhorn & Rehkaemper, 2016; Schiffner & Wiltschko, 2014). The release site and surroundings (buffer: 2000m radius), and lofts and surroundings (buffer: 300m radius) were excluded from the calculation, as the pigeons were not in a direct flight in that phase of the route (buffers were based on visual inspection of my data and other studies, including: Dell'Ariccia, Costantini, Dell'Omo, & Lipp, 2009; Schiffner & Wiltschko, 2009; R. Wiltschko, Schiffner, & Siegmund, 2007). Due to the low number of completed tracks, the efficiency index results were analysed with descriptive statistics.

Movement steps: In order to further study the orientation during the flight and the flight speed along the track, the individual tracks were unravelled into movement steps. Movement steps are defined as the straight linear segments between successive GPS fixes (Turchin, 1998; Figure 2.6). The track in between the fixes was studied by looking at the following characteristics: the turning angles (change in movement direction relative to last movement direction), the deviation of the fix from the bee-line (shortest track back home), the flight speed and flight height (Figure 2.6). Flight height was obtained from the recordings of the GPS rings. The flight speed was calculated by dividing the distance of displacement between the fixes by the time interval between the fixes (which in most cases was 3 minutes). The turning angle and deviation from the bee-line are both measures of orientation. Larger turning angles reflect more tortuous routes, and less steep turning angles reflect a straighter and more direct route to the goal. In addition, the smaller the deviation from the bee-line, the higher the efficiency of the route. The turning angles were determined by first calculating the angle of the line segments relative to the north line (0 degrees) by use of a python code in the field calculator in ArcGis (v. 10.5.1). Thereafter, several calculations were done to determine the difference in angle between two successive line segments and to obtain the absolute turning angles (Appendix 13). The deviation from the moving bee-line was calculated in R statistics (v.3.4.1) with the use of angle addition formulas (Appendix 14). After determining the movement step characteristics, this data were used in the data analyses (described underneath).

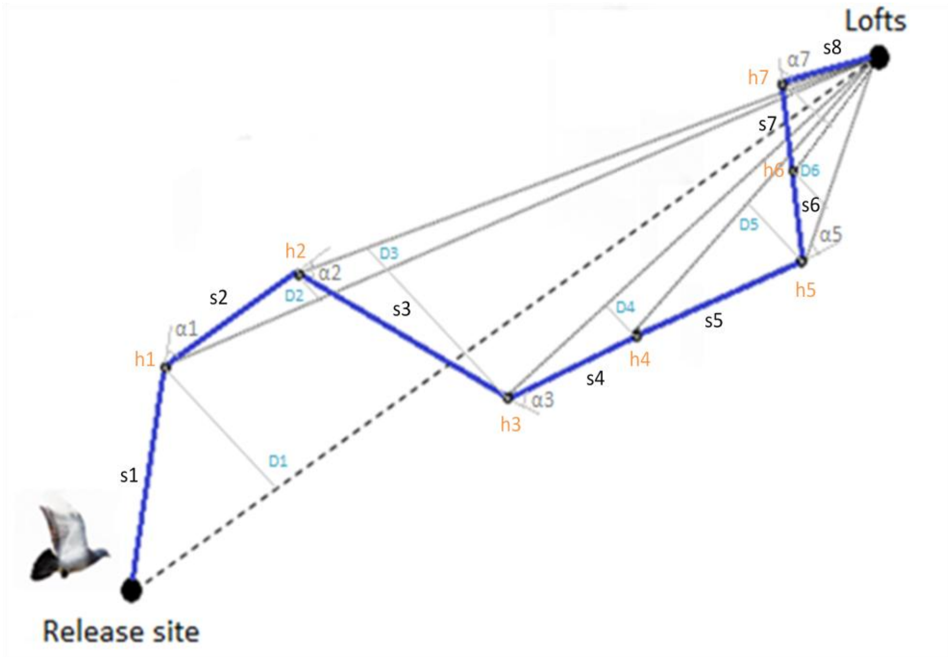

Figure 2.6. Fictional flight path, showing the different GPS fixes (black dots) and the division into steps (s1, and so on). Every step has its own characteristics, including the speed at which the step is taken, the angle between the previous step and the new step (α1 and so on), the deviation of the beginning of the step from the moving bee-line (D1 and so on), and the flight height at the fix (h1 and so on).

Landscape composition and climatic conditions: The data on climatic conditions had to be interpolated before it could be used in the track analyses. In this interpolation, the distance from the points to the weather stations was determined and from there on a weighting factor per station was set. Furthermore a weighted average of the weather parameters was calculated per fix. The wind direction data were further transformed into the relative wind direction, which is the wind direction relative to the movement direction of the pigeon (0 degrees = tailwind, 180 degrees = headwind). To be able to link the landscape composition data to the tracks, buffers (1km radius, set by looking at the maximum deviation in location recording in the accuracy tests) were set around the line segments of the steps. Thereafter the landscape composition data were linked to the buffers with use of the 'Isectpolyrst' function in Geospatial Modelling Environment (GME 0.7.4 - Beyer). By making use of buffers, I accounted for possible deviations due the inaccuracy of the GPS rings and unexpected movements of the pigeons in between the fixes. After determining the percentage of buffer cover for each landscape type (Appendix 15), the dominant landscape type of each buffer was determined. This was defined as the landscape type which had a cover of 75% or higher. When none of the landscape types were covering the buffer for 75% or more, the buffer was described as ''mixed landscape types''. After the transformations, the landscape and climatic data were used in the statistical analysis (described underneath).

Statistical analyses track characteristics and performance: In order to analyse the contribution of the orientation indices and flight speed in the overall flight performance of the pigeons, and to analyse the influence of pre-flight physical condition, landscape composition and weather conditions on the flight performance, GzLMM's were executed (for each category separately). All analyses had a Gamma probability distribution and log link function, with a unique pigeon ID per flight as random factor and no further repeated measures design, due to model complications. In the condition model, both weight/size ratios were included as squared factors to test the optimum hypothesis (chapter 1). In all models (physical condition, landscape and weather), the flight characteristics were included to test for effects of the distance to the loft and flight number. Sequential Sidak was applied whenever a significant effect of a categorical variable was observed. Also additional GzLMM's were run when variables of more than one category (pre-flight condition, landscape composition or weather conditions) were found significant to check for a combined effect of those variables on the dependent variable. Not all fixes were included in the analyses. Similar as with the calculation of the efficiency index, all fixes in the surroundings of the release site (buffer of 2000m radius) and loft (buffer of 300m radius) were excluded from the track analyses to have left the period that the pigeon was in direct flight (based on visual inspection of my data and other studies, including: Dell'ariccia et al., 2009; Gagliardo, Ioalè, Filannino, & Wikelski, 2011; Schiffner & Wiltschko, 2009; R. Wiltschko et al., 2007) . Thereafter, in the track analyses, stops were excluded from the data, for the same reason. Stops were defined as moments at which flight speed, recorded by the GPS ring, was below 3 m/s (based on visual inspection of my data and the methodology of Gagliardo, Ioalè, Filannino, & Wikelski, 2011, Appendix 16). Lastly, the fixes were excluded at which the data were not trustable enough, for example if unrealistic parameter values were recorded (excluded fixes are listed in Appendix 17).

3. Results

3.1. Dummy flights

3.1.1 Arrival time

The performance of the pigeons with and without dummy rings was compared by using the arrival times (minutes after release). First, the arrival times of the individuals arriving on the release day were compared (Figure 3.1). No significant difference in arrival time was found between the pigeons with and without dummy ring (Table 3.1). In contrast, the arrival times of the three dummy flights were significantly different from each other; later arrival times were found in the first dummy flight compared to the third dummy flight (Table 3.1, Figure 3.1). No interaction effect was found between treatment group (dummy/non-dummy) and flight number (Table 3.1), and thus there were neither differences between the pigeons with a dummy ring and without in each of the flights nor differences between the flights for the dummy and non-dummy group. Moreover, no significant effects of the conditional parameters on the arrival times were detected (Table 3.1).

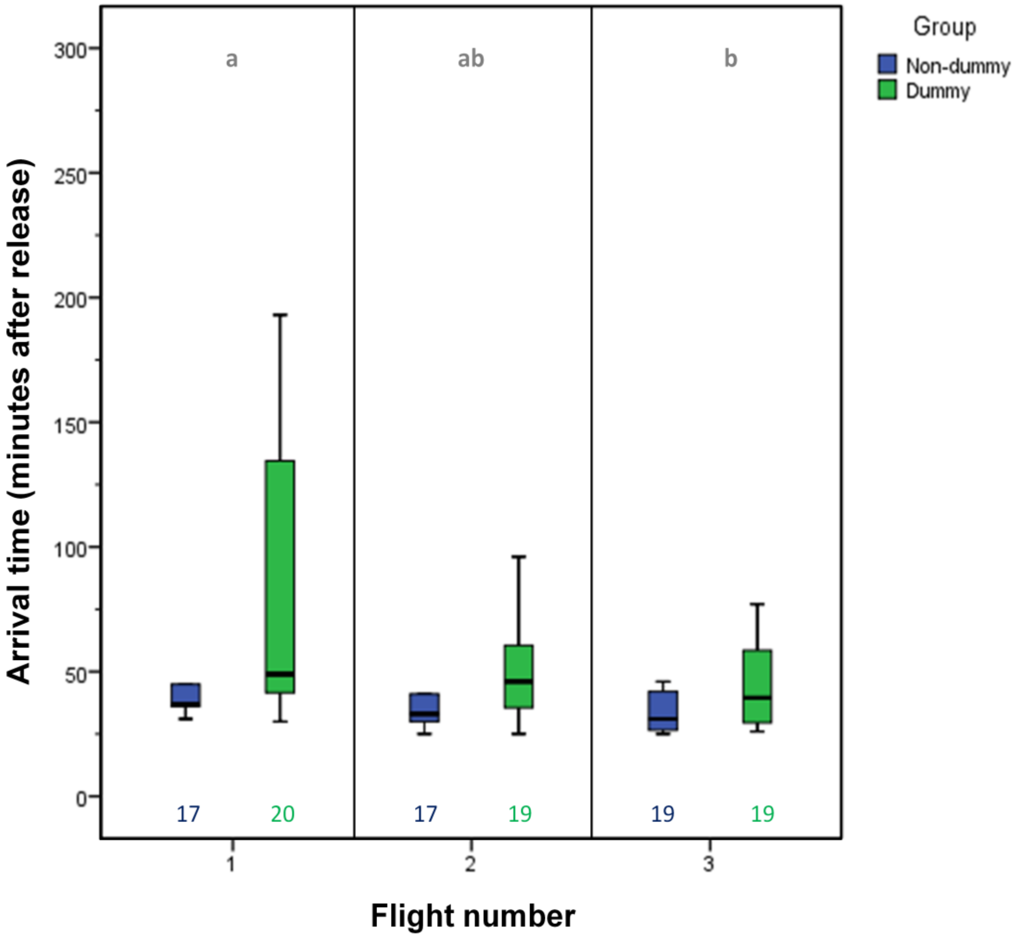

Figure 3.1. Boxplot of the arrival times, in minutes after release, of the dummy wearing (green bars) and non-dummy wearing pigeons (blue bars), in the three dummy flights. Sample sizes are indicated in green (Dummy) and blue (No dummy) (bottom of graph). Significant differences are indicated with alphabetic letters (top of graph).

Table 3.1. Model outputs of the GzLMM analysis of the arrival times in the dummy flights and of the additional pair-wise comparisons (Sequential Sidak) for flight number. The model results include the coefficients, F-values, degrees of freedom (d.f.) and p-values, and for flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Group **(reference = dummy)**		3.573	1	100	0.062
Group = No dummy	-0.299				
Flight number **(reference = 3)**		8.850	2	100	<0.001
1	0.472				
2	0.162				
Moulting status **(reference = 6)**		1.490	5	100	0.200
1	-0.026				
2	0.240				
3	0.115				
4	-0.004				
5	0.368				
Group * flight number		1.510	2	98	0.226[a]
Weight		1.092	1	97	0.299[a]

[a] These variables were excluded from the model one by one (weight first, group*flight second), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight numbers	**Marginal mean**	**SE**
1	63.237	8.802
2	48.567	5.778
3	41.129	4.075

Comparisons flight numbers	**p**
1-2	0.051
2-3	0.089
1-3	0.004

3.1.2 Arrival group

In addition to the comparison of the arrival times on the release day, the performance of the individuals from the dummy and non-dummy group were compared by looking at the number of ‘on time’ and ‘extreme delayed’ arrivals and lost pigeons in each flight. The time limit for which a pigeon was considered to be ‘’extremely delayed’’ was calculated per flight (Section 2.5.1). In flight 1, a pigeon was considered extremely delayed from 99 minutes after release; in flight 2, 88 minutes after release; and in flight 3, 77 minutes. When comparing the occurrence of extreme delays and losses between the dummy and non-dummy group over all flights, no clear patterns could be seen (Figure 3.2), besides the later arrival of several pigeons with dummy ring in the first flight, as this was also visible in Figure 3.1.

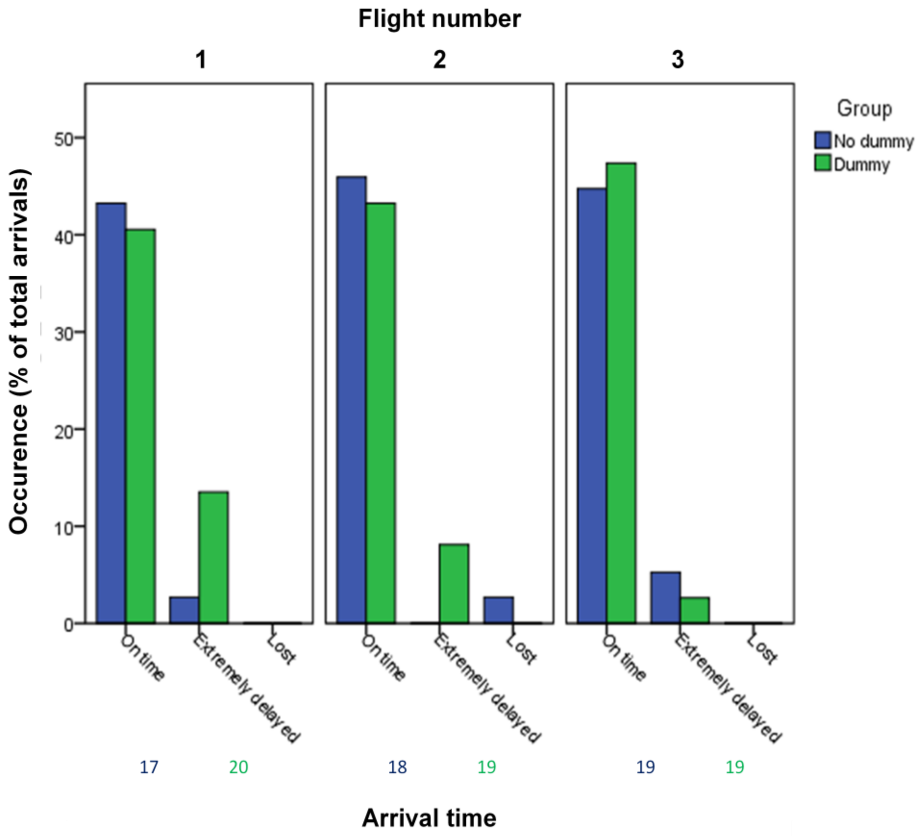

Figure 3.2 Occurrence (given in % of the arrivals of the dummy and non-dummy wearing pigeons together per flight) of individuals arriving 'on time', 'extremely delayed' or were lost in the three dummy flights for the dummy (green bars) and non-dummy group (blue bars). Sample sizes are indicated in green (dummy) and blue (non-dummy) at the bottom of the graph.

3.2. GPS flights

3.2.1 Overall flight performance

3.2.1.1 Arrival time

As with the dummy flights, the performance of the pigeons with and without GPS rings was compared by using the arrival times (minutes after release). First, the arrival times on the release day were compared (Figure 3.3). Overall all flights, no significant difference in arrival time was found between the GPS and non-GPS group (Table 3.3). The GPS flights were performed on three different trajectories. Multiple GPS flights were only executed on the second trajectory (Figure 3.3). Comparing the arrival times in these flights did not show any significant differences (Table 3.3). However, an interaction was found between group and flight number; in the first GPS flight individuals with a GPS ring did arrive later compared to the non-GPS wearing individuals (Table 3.3, Figure 3.3). No differences between treatment groups (GPS/non-GPS) were found in the other flights and also no differences in arrival time between the flights of the second trajectory for the GPS and non-GPS group separately. Meanwhile, an effect of moulting status and conditions score on arrival time was found. The arrival time of individuals with one old primary feather was significantly higher compared to individuals with two old primary feathers (Table 3.3, Figure 3.4). Between the other moulting stages no differences were detected, but, instead, the arrival of individuals with a higher condition score was earlier compared to the individuals with a lower score (Table 3.3, Figure 3.5).

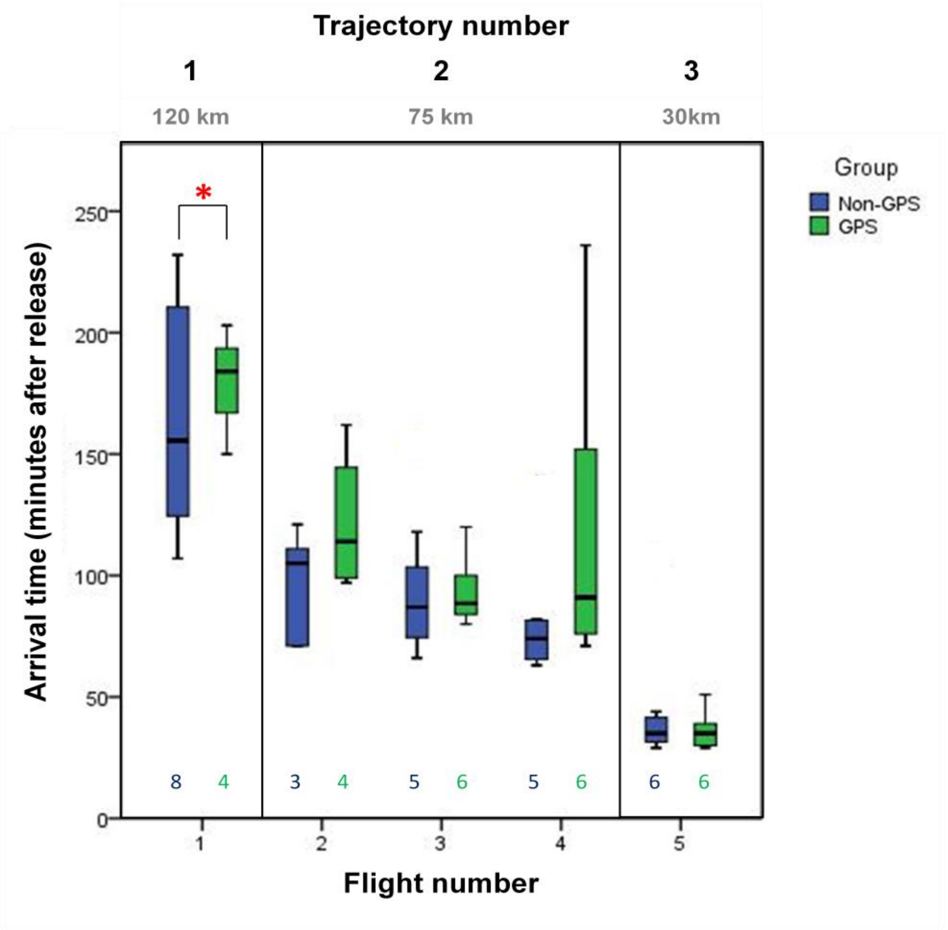

Figure 3.3. Boxplot of the arrival times in minutes after release of the GPS wearing pigeons (green bars)and non-GPS wearing pigeons (blue bars) in the five GPS flights. Sample sizes are indicated in green (GPS) and blue (No GPS) at the bottom of the graph. The significant difference is indicated with a red star.

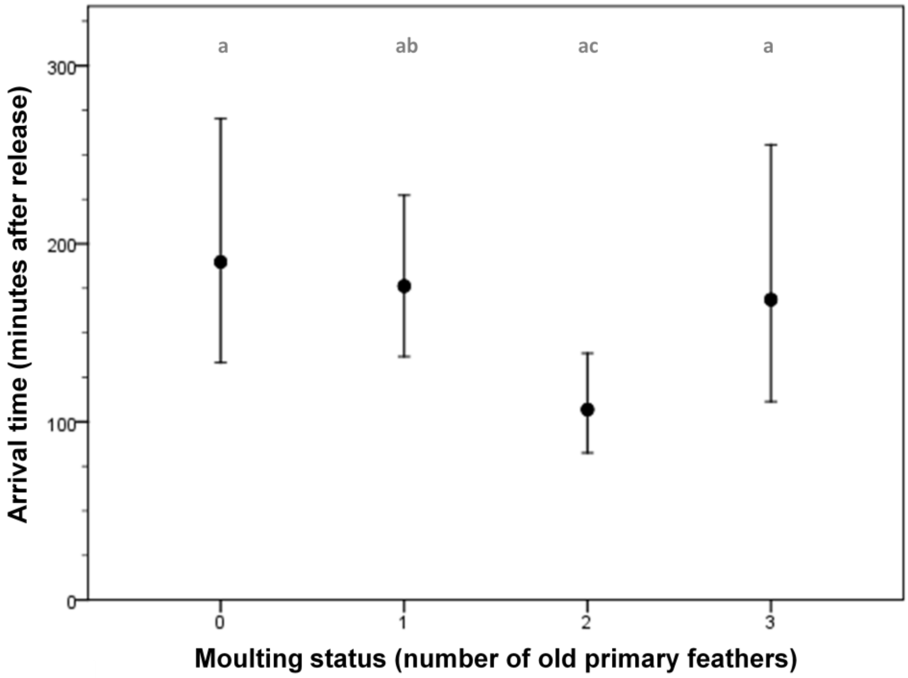

Figure 3.4. The arrival times in minutes after release of all pigeons in the GPS flights separated by their moulting status in number of old primary feathers. Significant differences are indicated with alphabetic letters (top of graph).

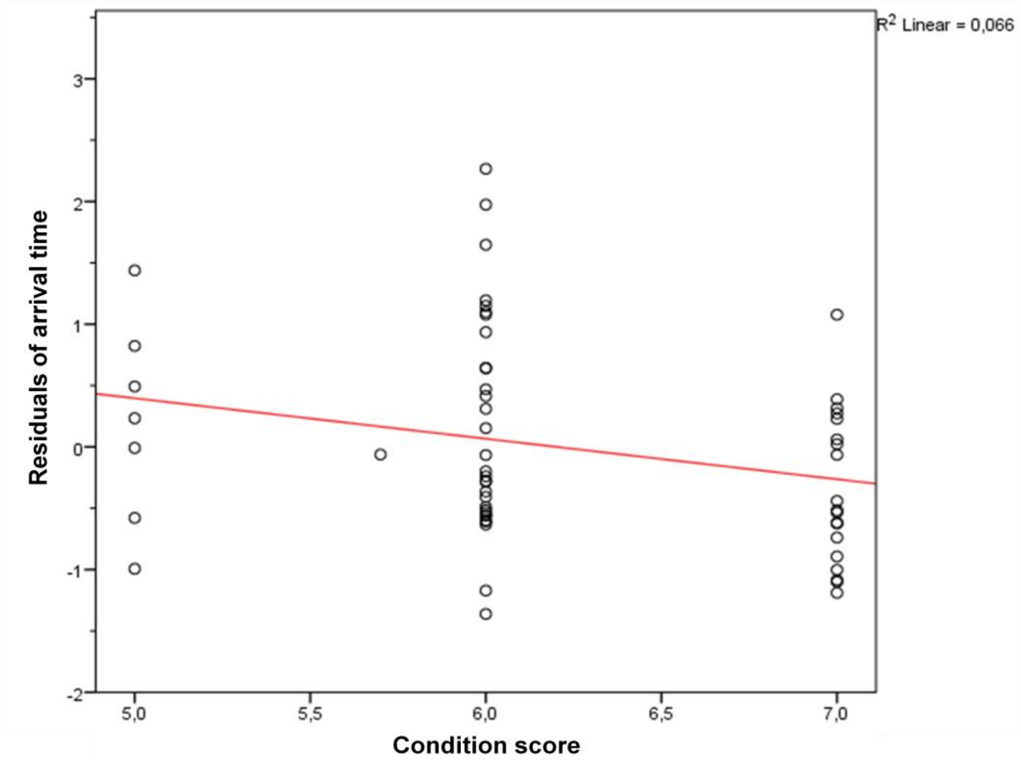

Figure 3.5. Residuals of the individual arrival times in the GPS flights defined by their condition score (Scale = 1-10).

*Table 3.2. Model outputs of the GzLMM analysis of the arrival times in the GPS flights, and of the additional pair-wise comparisons (Sequential Sidak) for flight number, moulting status and group*flight number interaction. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for flight number, moulting status and group*flight number interaction the estimated marginal means, standard errors and p-values of the pair-wise comparisons.*

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Group **(reference = GPS)**		0.404	1	43	0.528
Group = No GPS	0.092				
Flight number **(reference = 5)**		42.172	4	43	<0.001
1	2.801				
2	2.491				
3	1.003				
4	1.276				
Group * flight number **(reference within group = Flight = X * group = GPS)** **(reference within flight = Flight = 5 * Group = X)**		4.304	4	43	0.005
Flight = 1 * Group = No GPS	-1.290				
Flight = 2 * Group = No GPS	-0.045				
Flight = 3 * Group = No GPS	0.019				
Flight = 4 * Group = No GPS	0.183				
Moulting status **(reference = 3)**		6.287	3	43	0.001
0	0.118				
1	0.044				
2	-0.456				
Condition score	-0.243	6.973	1	43	0.011

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Group * moulting status		1.401	3	36	0.258 [a]
Group*condition score		0.772	1	36	0.386 [a]
Weight/size ratio – wing	-0.098	2.819	1	43	0.100
Weight/size ratio – wing^2		3.065	1	42	0.087 [c]
Weight/size ratio – tarsus		0.009	1	40	0.925 [b]
Weight/size ratio – tarsus^2		0.002	1	40	0.961 [b]

[a] These interactions were taken out of the model, because the variable effect was not significant and caused complications in the model.

[b] These variables were excluded from the model, because the variable effect was not significant and did not improve the model fit (weight/size ratio-tarsus and squared term).

[c] This variable was excluded, because it did not explained the variation in flight speed better than its singular form. The results for the other variables in the table are from the model without these excluded variables.

Flight number	**Mean**	**SE**
2	455.888	193.941
3	106.300	10.591
4	151.596	26.622

Comparisons flight numbers	**p**
2-3	0.249
3-4	0.249
2-4	0.268

Flight number	**Group**	**Mean**	**SE**
1	No GPS	183.153	40.689
	GPS	606.884	141.728
2	No GPS	466.763	292.719
	GPS	445.266	255.091
3	No GPS	112.384	16.294
	GPS	100.545	11.572
4	No GPS	173.973	41.893
	GPS	132.098	29.629
5	No GPS	40.420	4.893
	GPS	36.870	4.465

Comparison No GPS - GPS	
Flight number	**p**
1	0.005
2	0.956
3	0.523
4	0.407
5	0.541

Comparison flight number per group		
	Flight number	**p**
No GPS	2-3	0.652
	3-4	0.600
	2-4	0.693
GPS	2-3	0.554
	3-4	0.554
	2-4	0.554

Moulting status	**Mean**	**SE**
0	189.778	33.281
1	176.221	22.215
2	106.946	13.708
3	168.683	34.766

Comparisons moulting status	**p**
0-1	0.946
0-2	0.073
0-3	0.946
1-2	0.003
1-3	0.946
2-3	0.281

3.2.1.2 Arrival group

In addition to the arrival time, the number of ‘on time’ and ‘extreme delayed’ arrivals and lost pigeons in each GPS flight was compared between GPS and non-GPS group. The time limit from whereon a pigeon was considered to be ‘’extremely delayed’’ was calculated per flight (Section 2.5.1). In flight 1, a pigeon was considered extremely delayed from 413 minutes after release; in flight 2, 289 minutes after release; in flight 3, 220 minutes; in flight 4, 204 minutes; and in flight 5, 83 minutes after release. It was noticed that the flight performance in flight 1 – trajectory 1 and flight 1 – trajectory 2 was less compared to the other flights, as there was a lower frequency of ‘on time’ arrivals and a higher frequency of extremely delayed and lost pigeons (Figure 3.6). In the first GPS flight (trajectory 1), there seems to be a group difference, as non of the pigeons without a ring were extremely delayed in this flight, against 25% extremely delayed arrivals of the GPS wearing individuals (Figure 3.6). This difference was also detected in the analysis of the arrival times of the GPS flights (Sub-section 3.2.1.1). Furthermore, no pattern in group difference can been seen in the arrival groups (Figure 3.6).

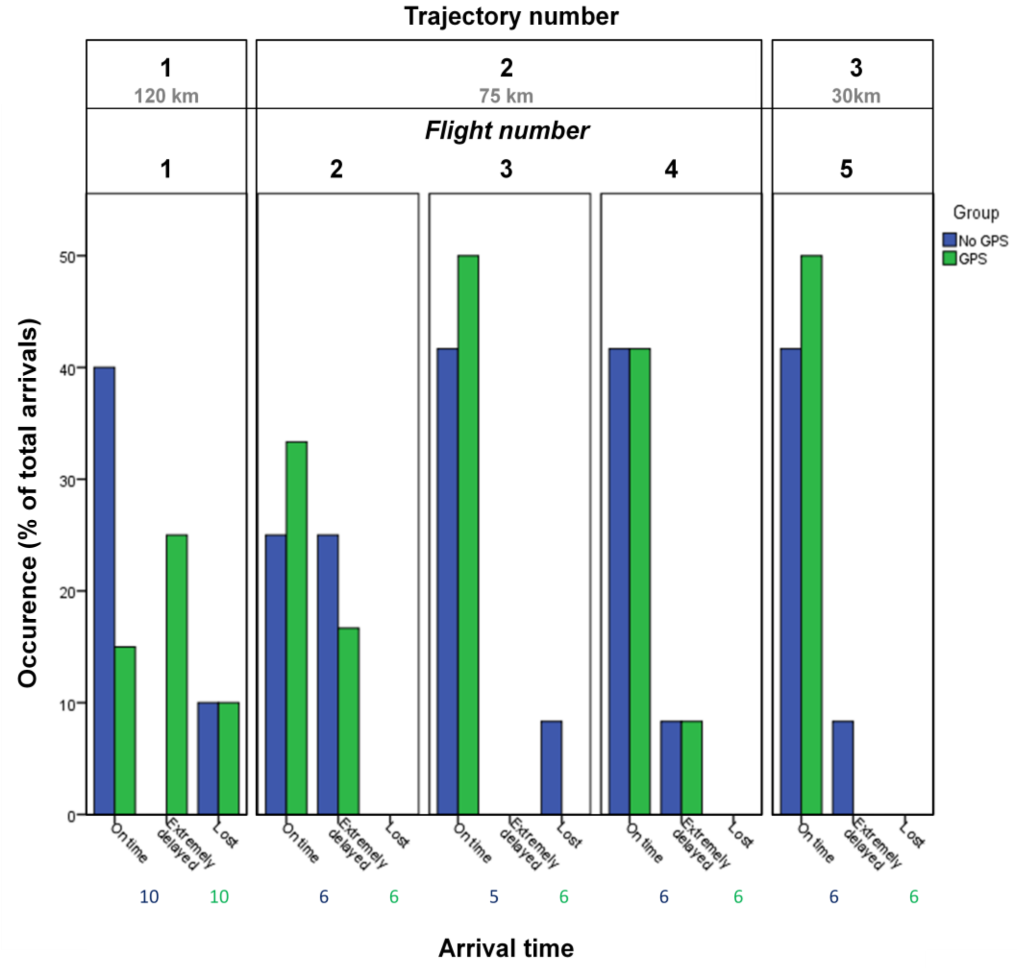

Figure 3.6. Occurrence (given in % of the arrivals of the GPS and non-GPS wearing pigeons together per flight) of individuals arriving ‘on time’ and ‘extremely delayed’, or got lost, in the five GPS flights for the GPS and non-GPS group. Sample sizes are indicated in green (GPS) and blue (No GPS).

3.2.2 Track analyses

3.2.2.1 Efficiency index

To determine the efficiency of the flight tracks of the GPS wearing pigeons in the GPS flights, efficiency indices (EI's) were calculated (Sub-section 2.4.2.2). This could only be done when a complete track was recorded. Complete tracks were not always available due to longer travelling times, exceeding the maximum battery capacity, or to malfunctioning of the GPS rings (sample sizes in Figure 3.7, Appendix 18). The EI's observed ranged from 0.468-0.986. The EI's of the three repetitive flights in trajectory 2 were tested on significant differences. However the model was not functioning well, likely due to the low sample sizes. Therefore no test results were available. However, when comparing the route efficiencies in the trajectories, the highest route efficiency was observed in the third and shortest trajectory (Figure 3.7). In the three flights of trajectory 2, multiple first and second measurements of EI per individual were done. These observations are not showing a clear trend (Figure 3.8).

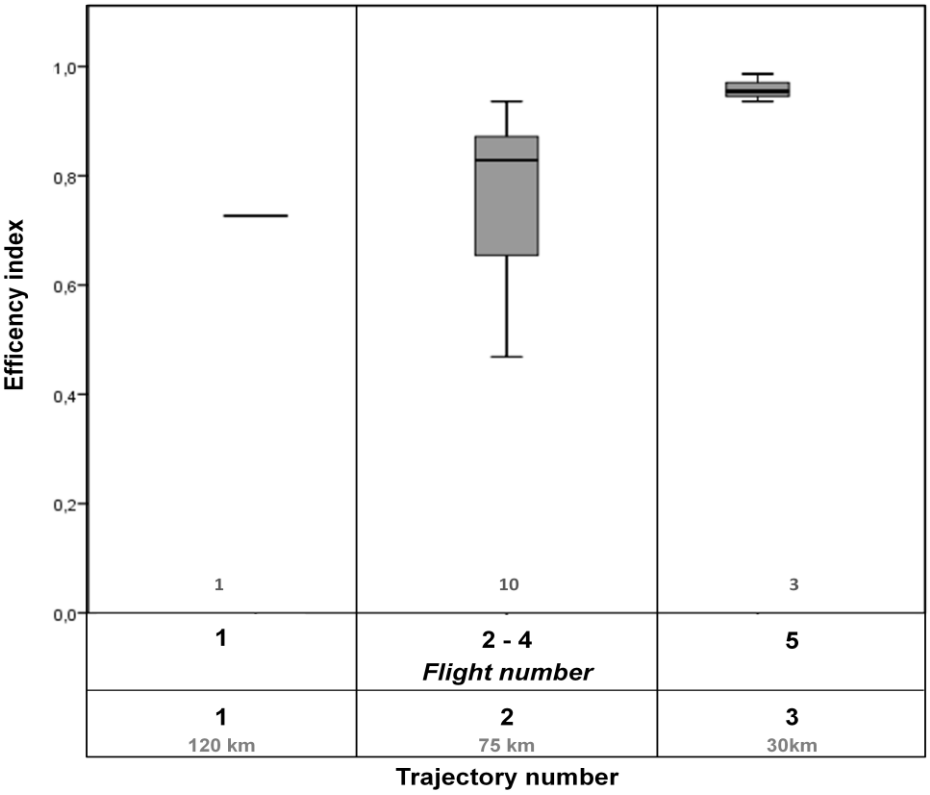

Figure 3.7. The efficiency indices of the GPS-wearing individuals (with complete tracks) in the flights on the three trajectories. An efficiency index of 1 represents a hundred percent efficient route.

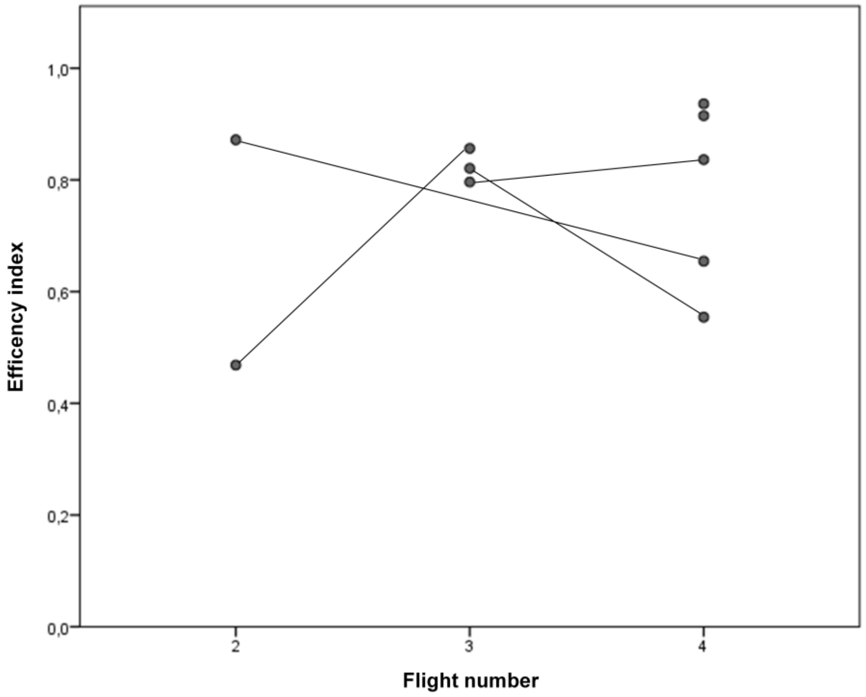

Figure 3.8. Measurements of individual efficiency indices of the GPS-wearing individuals in the second trajectory.

3.2.2.2 Movement steps characteristics

The movement step analyses were based on all fixes in the recorded tracks (total recorded tracks: 26, Appendix 19), without the excluded fixes (Appendix 17).

<u>Step characteristics and arrival time</u>

No contribution was found of flight speed, the orientation indices (turning angle and deviation from bee-line) or flight height in explaining the variance in arrival time (Table 3.3).

Table 3.3. Model outputs of the GzLMM analysis of the effect of the step characteristics on arrival time. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Flight number **(reference = 5)**		3.049	4	13	0.056
1	3.299				
2	2.616				
3	-0.091				
4	0.925				
Mean flight speed	-0.236	2.783	1	13	0.119
Deviation in flight speed	0.149	1.219	1	13	0.290
Mean turning angle	-0.041	2.571	1	13	0.133
Deviation in turning angle	0.026	1.597	1	13	0.229
Mean deviation bee-line		0.286	1	12	0.602[a]
Deviation in deviation bee-line		0.100	1	11	0.758[a]
Mean height	-0.008	2.091	1	13	0.172
Deviation in height	0.007	1.404	1	13	0.257

[a] These variables were excluded from the model one by one (deviation in deviation bee-line first and mean deviation bee-line second), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Effects on flight speed

In all three *GzLMM's* of the flight speed (described underneath), a significant effect of distance to the loft was found. However, the direction of the effect is inconsistent (positive in condition and landscape model, negative in weather model, Figure 3.9). An effect of flight number on flight speed was only detected in the weather model. Higher flight speeds were observed in flight 3 compared to flight 2 and flight 4 (Appendix 20).

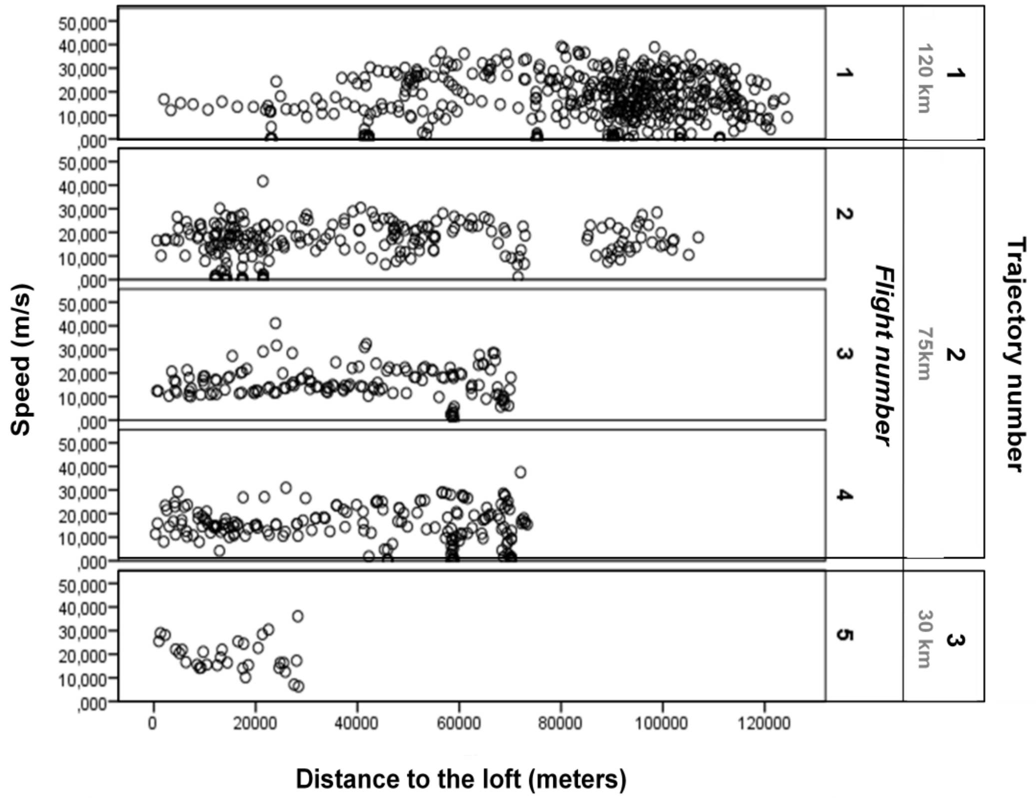

Figure 3.9. Flight speeds at different distances to the loft in the five GPS flights.

Condition

None of the conditional variables were significantly affecting flight speed (Table 3.4, Figure 3.10).

Table 3.4. Model outputs of the GzLMM analysis of the effect of the condition variables on flight speed. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values.

	Covariates	F	d.f. 1	d.f. 2	p
Moulting status		1.313	3	952	0.269[a]
Condition score		0.108	1	947	0.743[a]
Weight/size ratio – wing		0.335	1	950	0.563[a]
Weight/size ratio – wing^2		0.429	1	950	0.513[a]
Weight/size ratio – tarsus		1.903	1	948	0.283[a]
Weight/size ratio –tarsus^2		1.152	1	948	0.277[a]
Flight number **(reference = 5)**		1.187	4	955	0.315
1	-0.077				
2	-0.102				

	Covariates	**F**	**d.f. 1**	**d.f. 2**	**p**
Flight number (reference = 5)					
3	-0.194				
4	-0.136				
Distance to the loft	1.317E-6	5.273	1	955	0.022

[a] These variables were excluded from the model one by one (first condition score, second weight/size ratio tarsus and in squared term, third weight/size ratio wing and in squared term and lastly moulting status), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight number	**Mean**	**SE**
2	18.375	0.986
3	16.744	0.960
4	17.748	1.002

Comparisons flight numbers	**p**
2-3	0.837
3-4	0.939
2-4	0.939

Landscape

No effect of the landscape variables on flight speed was found (Table 3.5).

Table 3.5. Model outputs of the GzLMM analysis of the effect of the landscape variables on flight speed. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Landscape transition		0.623	2	953	0.536[a]
Dominant landscape type		0.693	2	951	0.500[a]
Flight number		1.187	4	955	0.315[a]
Distance to the loft	1.453E-6	8.247	1	959	0.004

[a] These variables were excluded from the model one by one (first dominant landscape type, second landscape transition, third flight number), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Weather

The flight speed differed with the relative wind direction. The higher the relative wind direction, so the more headwinds, the lower the flight speed (Table 3.6, Figure 3.10). Moreover, higher flight speeds were related to higher temperatures (Table 3.6, Figure 3.11).

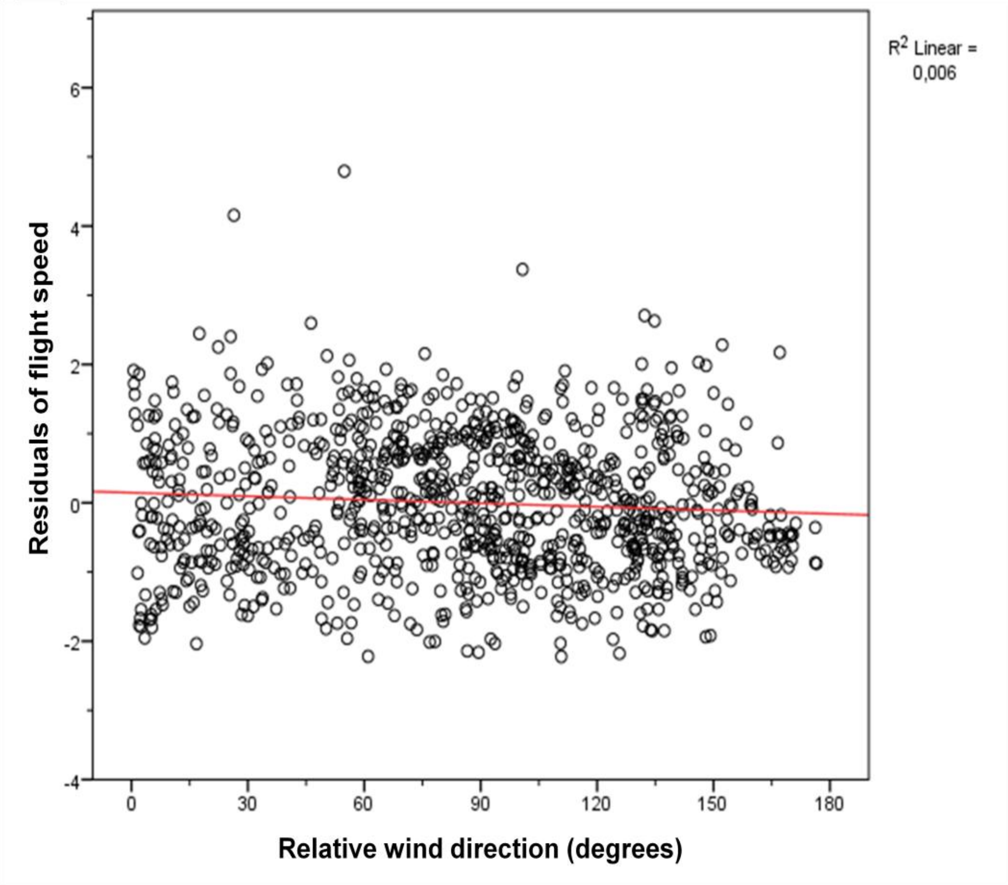

Figure 3.10. Residuals of flights speeds at different relative wind directions (wind direction relative to the bird's movement). A relative wind direction of 180 degrees is considered to be headwinds and a relative wind direction of 0 degrees is considered to be tailwinds.

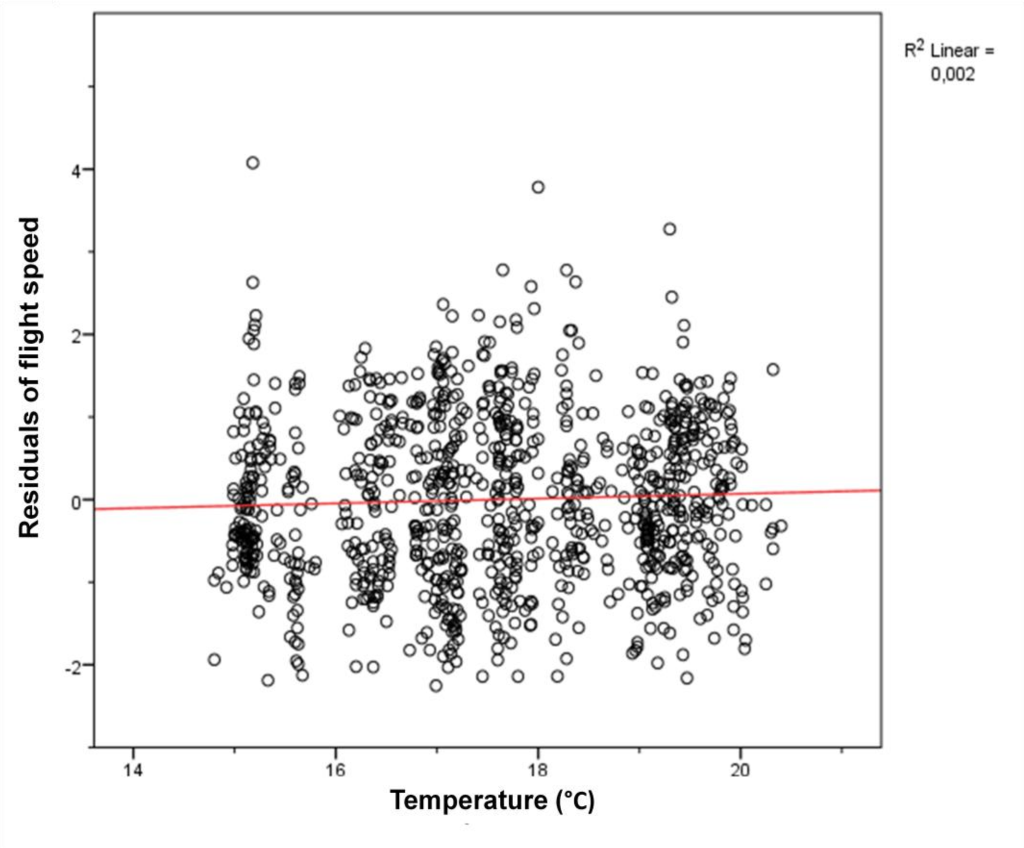

Figure 3.11. Residuals of flight speed related to the air temperature (°C).

Table 3.6. Model outputs of the GzLMM analysis of the effects of the weather variables on flight speed and of the additional pair-wise comparisons (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Temperature	0.154	30.195	1	953	<0.001
Wind speed		0.149	1	952	0.699[a]
Relative wind direction	-0.001	9.139	1	953	0.003
Wind speed * relative wind direction		0.320	1	951	0.572[a]
Flight number **(reference = 5)**		6.959	4	953	<0.001
1	0.050				
2	-0.427				
3	0.069				
4	-0.403				
Distance to the loft	-1.72E-6	5.487	1	953	0.019

[a] These variables were excluded from the model one by one (first wind speed * relative wind direction, second wind speed), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight number	**Mean**	**SE**
2	13.485	0.956
3	22.142	1.634
4	13.815	0.968

Comparisons flight numbers	**p**
2-3	0.001
3-4	0.002
2-4	0.948

Interaction variables

No interaction model was calculated, as only several weather variables were significant.

Effects on the turning angle

In the condition and landscape *GzLMM* (described underneath) an effect of distance to the loft was found. The further away from the loft the higher the turning angles, which corresponds with more tortuous routes (Figure 3.12). The effect of flight number on the turning angle was significant in all models. However, only in the weather and interaction model, significant differences in turning angles between the three flights of trajectory 2 were found in the pair-wise comparisons. Lower turning angles were observed in flight 3 compared to flight 2 and flight 4 (Appendix 20).

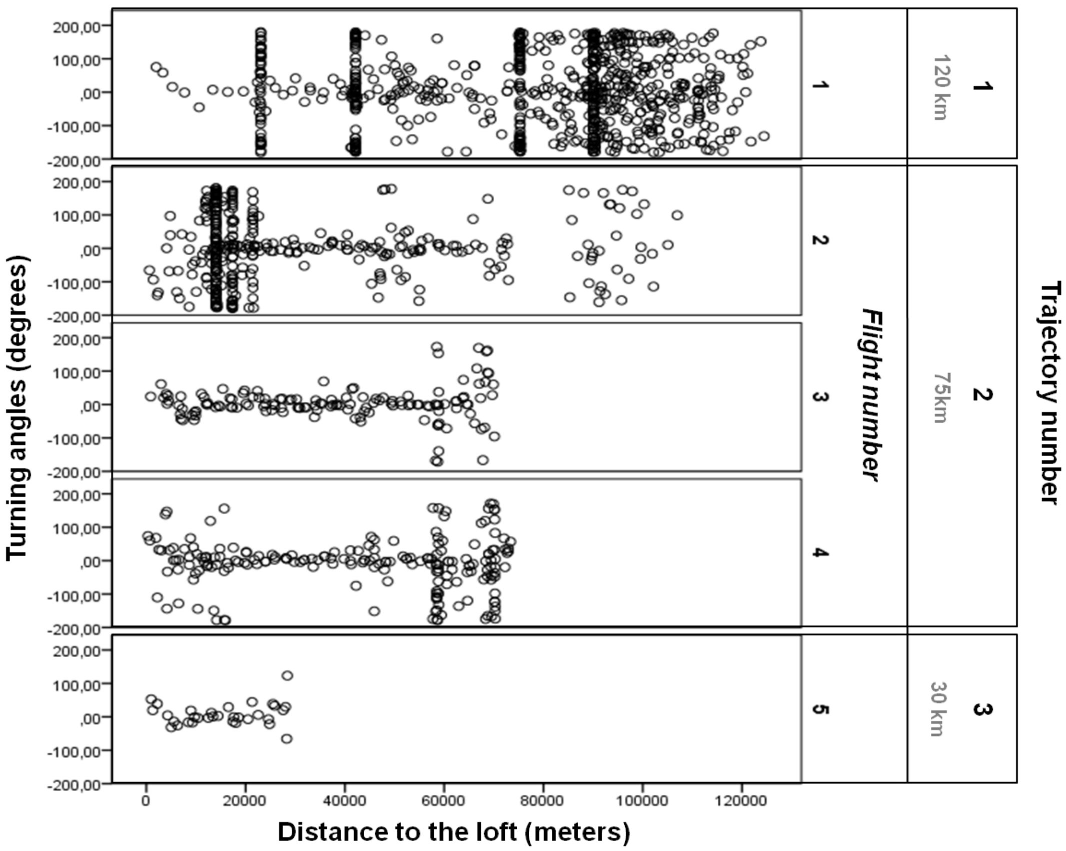

Figure 3.12. Turning angles (degrees) at different distances to the loft in the five GPS flights.

Condition

The weight/size ratios were affecting the turning angle significantly, both as the singular term and the squared term (Table 3.8). However, for the weight/size ratio – wing, the squared term had a slightly higher significance level compared to the singular term. The direction of the weight/size effect is inconsistent, higher ratios are related to both higher and lower turning angles (Table 3.8, Figure 3.13, 3.14).

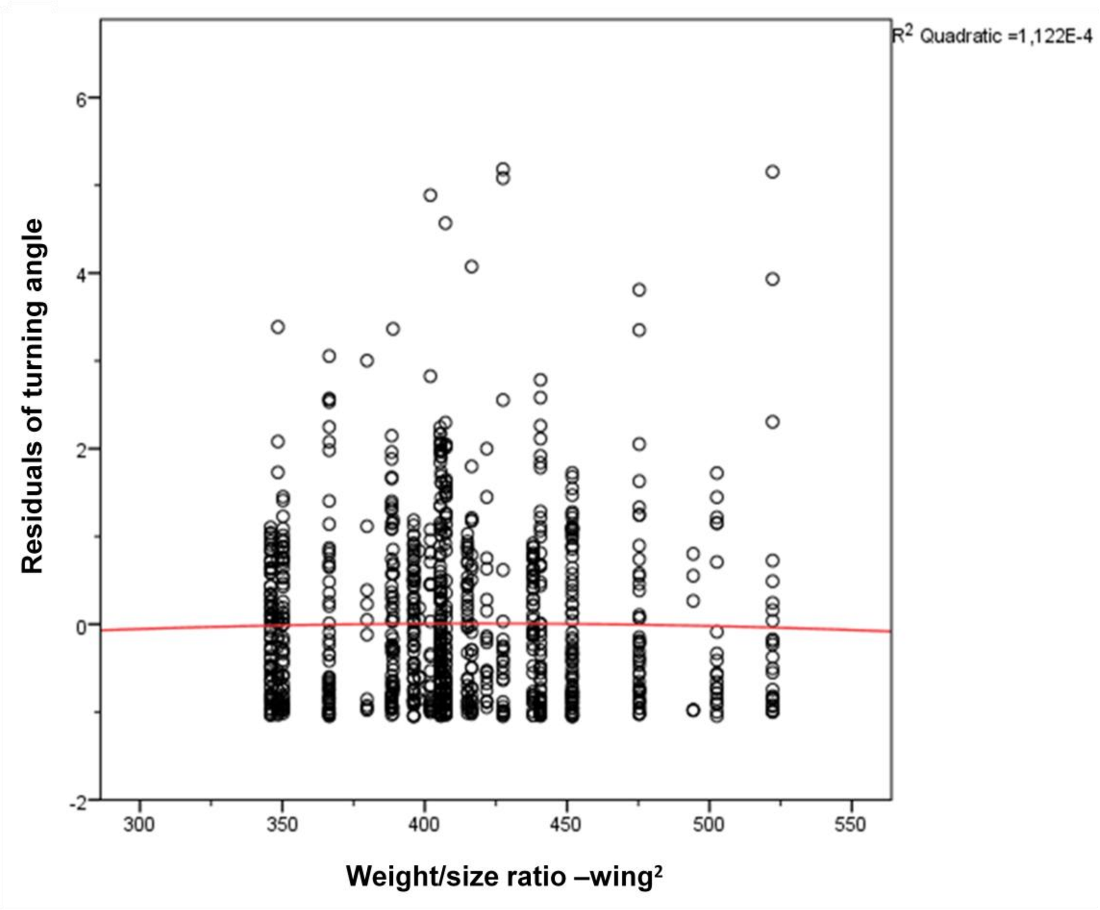

Figure 3.13. Residuals of turning angle related to the weight/size ratio – wing^2.

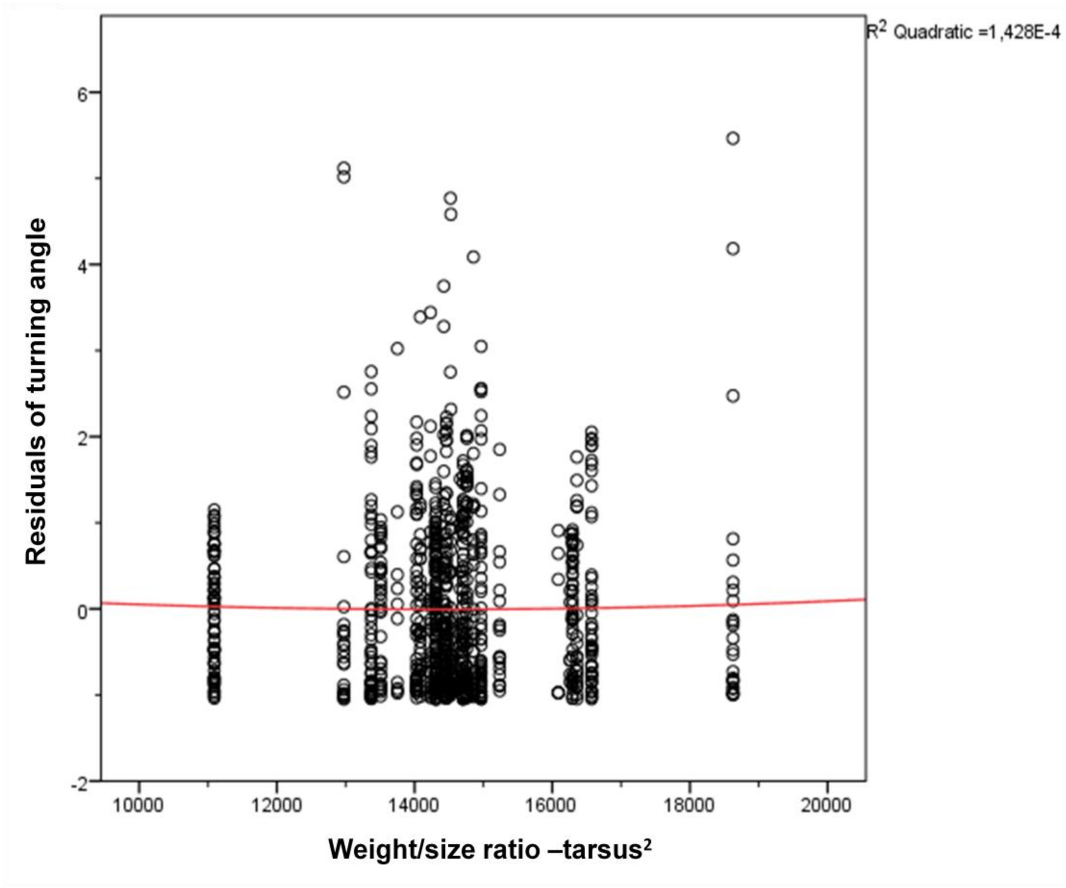

Figure 3.14. Residuals of turning angle related to the weight/size ratio – tarsus^2.

Table 3.8. *Model outputs of the GzLMM analysis of the effect of the conditional variables on turning angle and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.*

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Moulting status (reference = 3)		1.668	3	945	0.172
0	1.147				
1	0.405				
2	0.304				
Condition score		0.006	1	944	0.938[a]
Weight/size ratio – wing	9.596	4.683	1	945	0.031
Weight/size ratio – wing^2	-0.241	4.857	1	945	0.028
Weight/size ratio –tarsus	-1.164	4.718	1	945	0.030
Weight/size ratio –tarsus^2	0.005	4.748	1	945	0.030
Flight number **(reference = 5)**		4.619	4	945	0.001
1	1.653				
2	1.421				
3	0.746				
4	0.396				
Distance to home	4.261E-6	7.878	1	945	0.005

[a] This variable was excluded from the model, because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight number	**Mean**	**SE**
2	71.062	16.809
3	36.165	8.318
4	25.496	8.579

Comparisons flight numbers	**p**
2-3	0.164
3-4	0.633
2-4	0.180

Landscape

Turning angles were not affected by the landscape transitions or the landscape types in the buffer (Table 3.9).

Table 3.9. *Model outputs of the GzLMM analysis of the effect of the landscape variables on turning angle and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.*

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Landscape transition **(reference = urban area> non-urban)**		2.839	2	950	0.059
no transition	-0.422				
non-urban > urban area	-0.256				
Dominant landscape type		0.624	2	948	0.536[a]
Flight number **(reference = 5)**		3.298	4	950	0.011
1	0.977				
2	0.803				
3	0.221				
4	0.354				
Distance to home	4.492E-6	8.908	1	950	0.003

[a] This variable was excluded from the model, because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight number	**Mean**	**SE**
2	62.848	14.675
3	35.118	8.222
4	40.146	9.219

Comparisons flight numbers	**p**
2-3	0.352
3-4	0.892
2-4	0.560

Weather

Several weather parameters were affecting the turning angles significantly. Higher turning angles were observed with higher wind speeds (Table 3.10, Figure 3.15). In contrast, lower turning angles were related to higher relative wind direction, which equals more headwinds (Table 3.10, Figure 3.16). Lastly, also lower turning angles were observed with higher temperatures (Table 3.10, Figure 3.17).

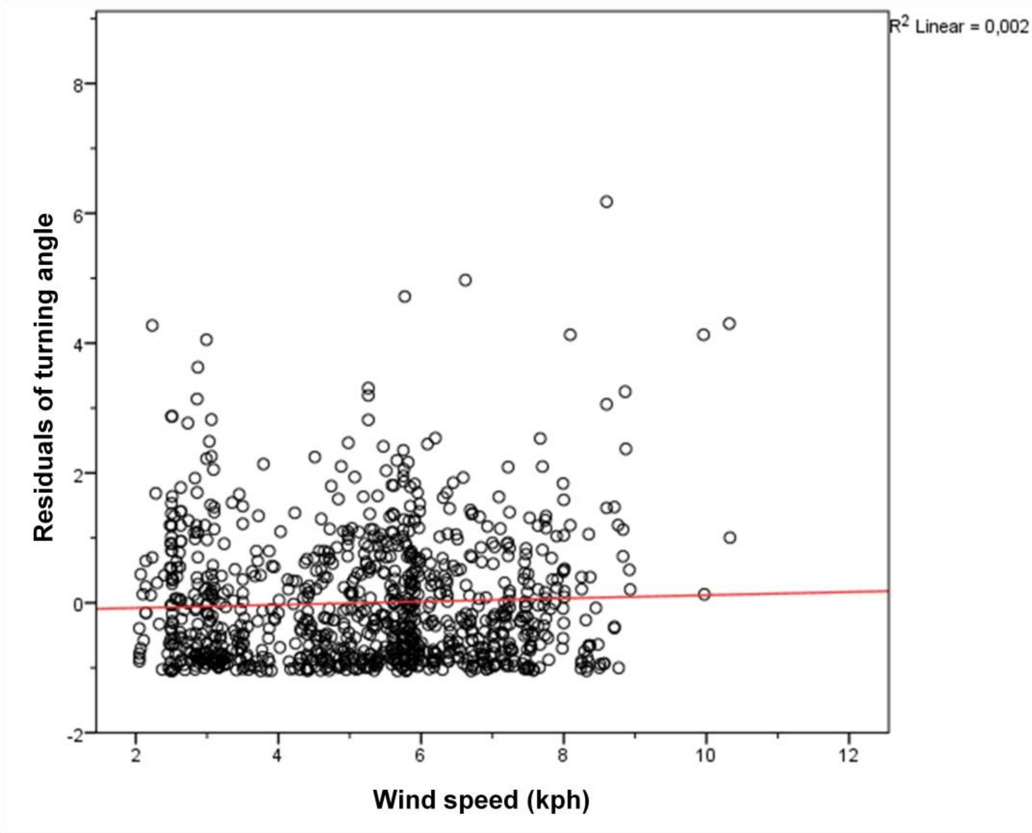

Figure 3.15. Turning angles in relation to wind speed (kph).

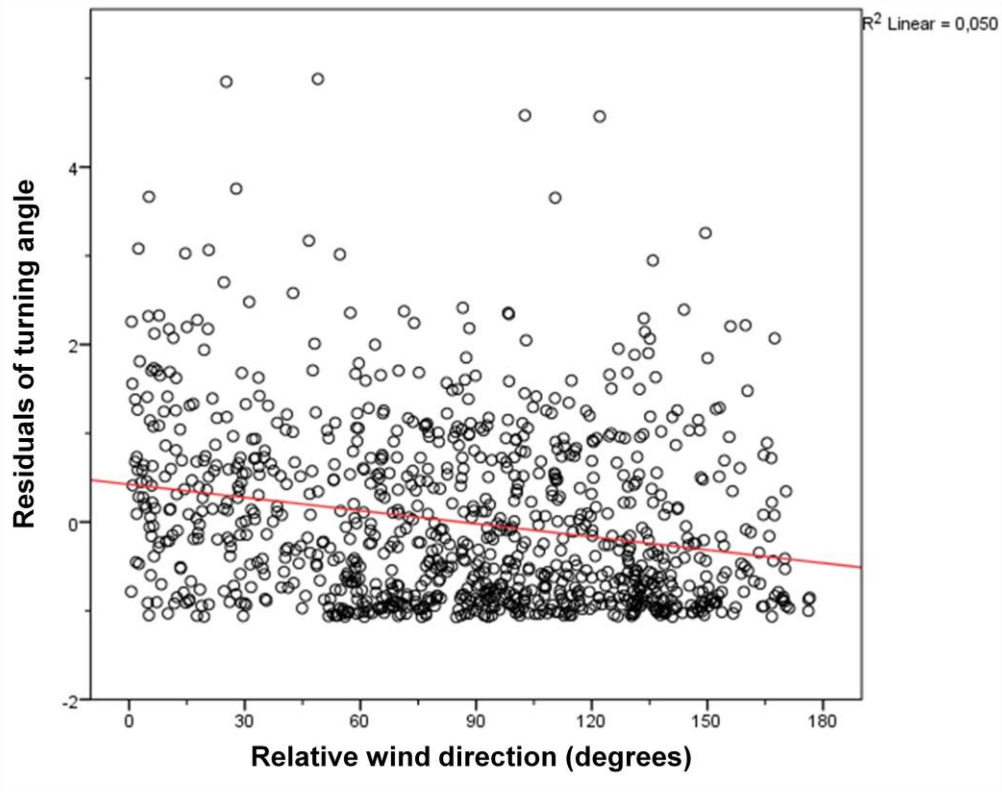

Figure 3.16 Turning angles in relation to relative wind direction (degrees). A relative wind direction of 180 degrees is considered headwind and a relative wind direction of 0 degrees is considered tailwind.

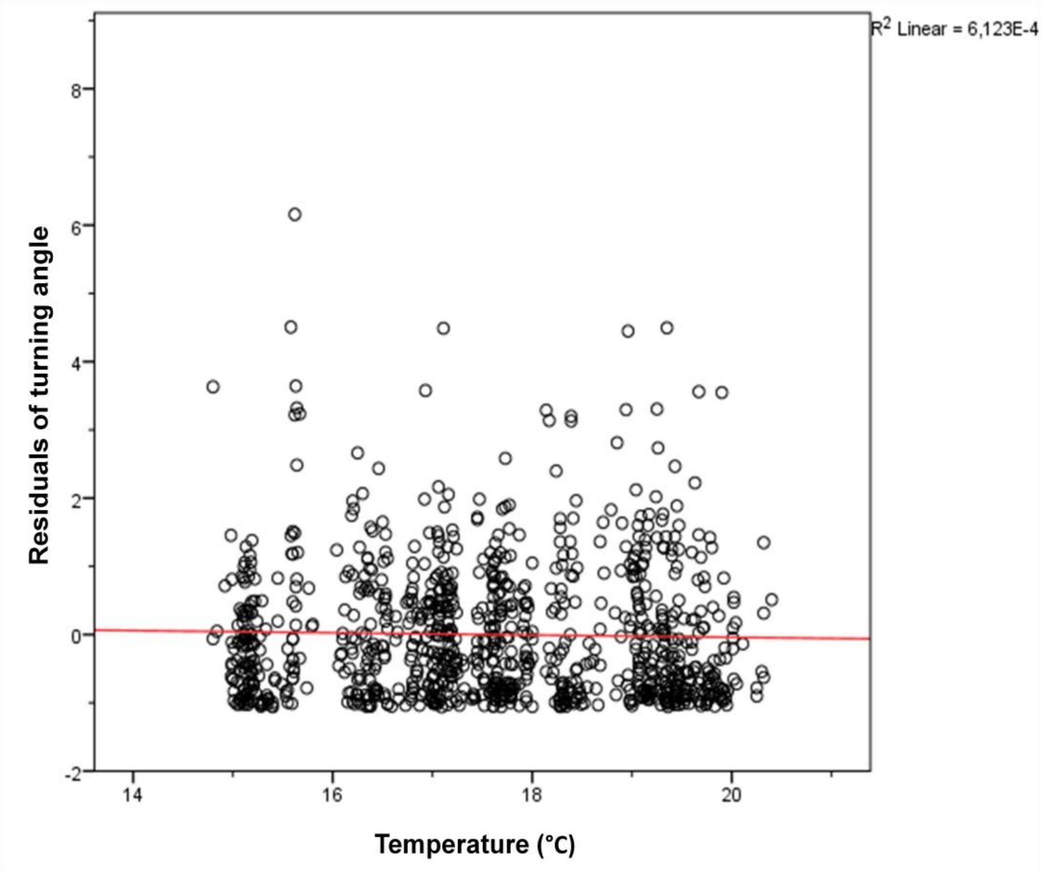

Figure 3.17 Turning angles in relation to air temperature (°C).

Table 3.10. *Model outputs of the GzLMM analysis of the effect of the weather variables on turning angle and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.*

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Temperature	-0.226	8.190	1	949	0.004
Wind speed	0.158	12.213	1	949	<0.001
Relative wind direction	-0.006	48.818	1	949	<0.001
Wind speed * relative wind direction		1.156	1	948	0.283[a]
Flight number (reference = 5)		7.837	4	949	<0.001
1	0.354				
2	1.139				
3	-1.254				
4	0.380				
Distance to home	3.979E-6	3.827	1	949	0.051

[a]This variable was excluded from the model, because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight number	**Mean**	**SE**
2	108.218	30.477
3	9.889	3.013
4	50.654	12.121

Comparisons flight numbers	**p**
2-3	0.019
3-4	0.019
2-4	0.223

Interaction variables

When including all significant variables of the condition, landscape and weather models into a new model as an interaction effect, it was significant, as well as the temperature and wind speed on itself. However, the direction of the effect of the temperature in the interaction model was contradicting with the findings of the weather model (Table 3.10 and 3.11). In the interaction model, higher temperatures were related to lower turning angles, whereas in the weather model the reverse was found. The direction of the effect of wind speed was the same as in the weather model, higher turning angles were related to higher wind speeds (Table 3.10 and 3.11). Moreover, in contrast to the results of the other models (Table 3.8 and 3.10), the relative wind direction and both the weight/size ratios are in the interaction model not significant anymore (Table 3.11).

Table 3.11. Model outputs of the GzLMM analysis of the effect of several variables, which were significant in earlier models, and their interaction on flight height, and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and P-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Temperature	-0.206	6.705	1	944	0.010
Relative wind direction	-0.001	0.395	1	944	0.530
Wind speed	0.233	18.268	1	944	<0.001

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Weight/size ratio – wing	3.901	1.809	1	944	0.179
Weight/size ratio – wing^2	-0.098	1.904	1	944	0.168
Weight/size ratio –tarsus	-0.564	1.934	1	944	0.165
Weight/size ratio –tarsus^2	0.002	1.947	1	944	0.163
Temperature * wind speed * relative wind direction *weight/size ratio – wing^2 * Weight/size ratio –tarsus^2	-8.266E-12	5.125	1	944	0.024
Flight number **(reference = 5)**		9.241	4	944	<0.001
1	0.412				
2	1.168				
3	-1.299				
4	0.695				
Distance to home	3.560E-6	2.928	1	944	0.087

Flight number	**Mean**	**SE**
2	106.034	29.524
3	9.001	2.710
4	66.134	18.294

Comparisons flight numbers	**p**
2-3	0.017
3-4	0.025
2-4	0.480

Effects on the deviation from the bee-line

In all three *GzLMM*'s (condition, landscape and weather) an effect of distance on the deviation in the bee-line was detected. Surprisingly, higher distances from the loft were related to lower deviation in the bee-line (Figure 3.18). Also, an effect of flight number was found in all models. Lower deviations from the bee-line were found in flight 3 compared to flight 2 and flight 4 (Appendix 20).

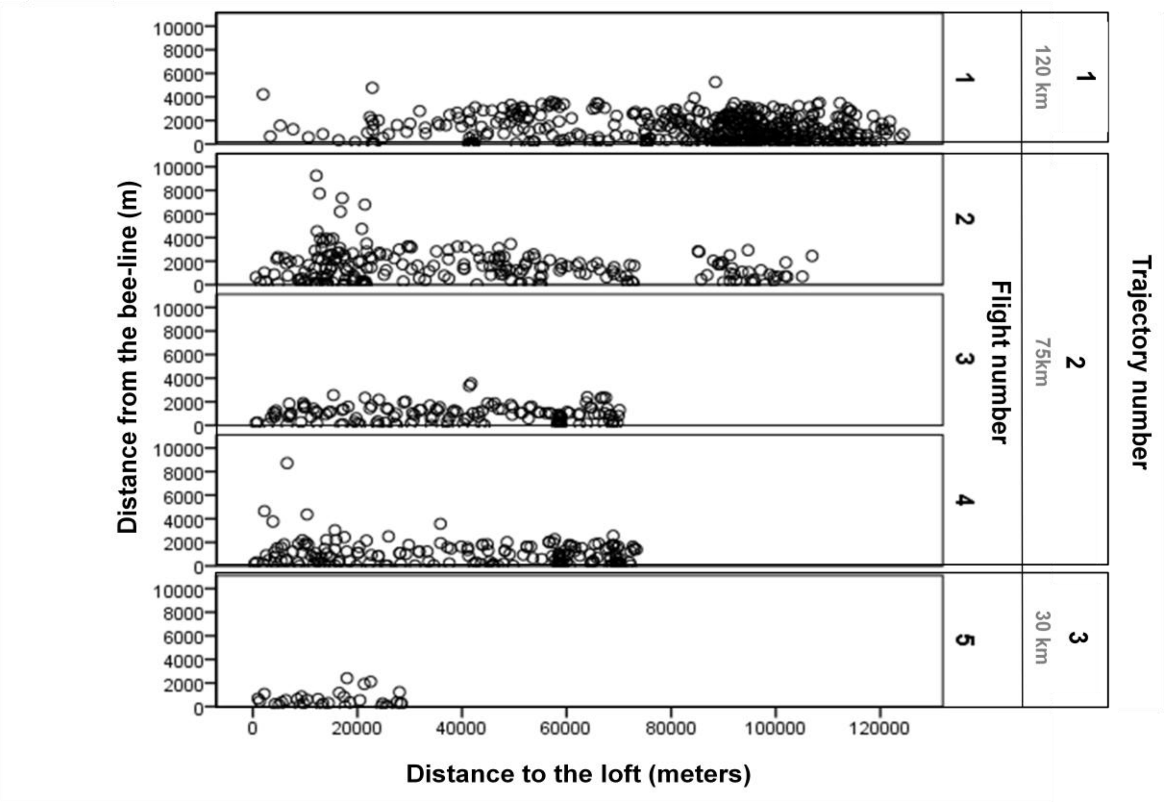

Figure 3.18. Deviation from the bee-line (in meters) at different distances to the loft in the five GPS flights.

Condition

No conditional variables were affecting the deviation of the bee-line (Table 3.12).

Table 3.12. Model outputs of the GzLMM analysis of the effect of the conditional variables on deviation from the bee-line and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Coefficient	F	d.f. 1	d.f. 2	p
Moulting status		1.769	3	952	0.151[a]
Condition score		0.324	1	950	0.569[a]
Weight/size ratio – wing		1.106	1	951	0.293[a]
Weight/size ratio – wing^2		0.055	1	949	0.815[a]
Weight/size ratio – tarsus		0.002	1	947	0.966[a]
Weight/size ratio – tarsus^2		0.005	1	947	0.946[a]
Flight number **(reference = 5)**		12.803	4	955	<0.001
1	1.175				

	Coefficient	F	d.f. 1	d.f. 2	p
Flight number (reference = 5)					
2	1.088				
3	0.587				
4	0.743				
Distance to home	-4.20E-6	14.185	1	955	<0.001

[a] These variables were excluded from the model one by one (first weight/size ratio tarsus and squared term, second weight/size ratio wing squared term, third condition score, fourth weight/size ratio wing, and lastly moulting status), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight number	Mean	SE
2	1469.918	139.940
3	890.617	91.984
4	1041.142	105.280

Comparisons flight numbers	p
2-3	0.003
3-4	0.465
2-4	0.038

Landscape

No effects of landscape transition and dominant landscape types on the deviation from the bee-line were found (Table 3.13).

Table 3.13. Model outputs of the GzLMM analysis of the effect of the landscape variables on deviation from the bee-line and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Covariates	F	d.f. 1	d.f. 2	p
Landscape transition		0.589	2	951	0.555[a]
Dominant landscape type		1.643	2	953	0.194[a]
Flight number (reference = 5)		12.803	4	955	<0.001
1	1.175				
2	1.088				
3	0.587				
4	0.743				
Distance to home	-4.201E-6	14.185	1	955	<0.001

[a] These variables were excluded from the model one by one (first landscape transition, second dominant landscape type), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight number	Mean	SE
2	1469.918	139.940
3	890.617	91.984
4	1041.142	105.280

Comparisons flight numbers	p
2-3	0.003
3-4	0.465
2-4	0.038

Weather

The deviation from the bee-line was significantly affected by wind speed, the higher the wind speed, the higher the deviation (Table 3.14, Figure 3.19).

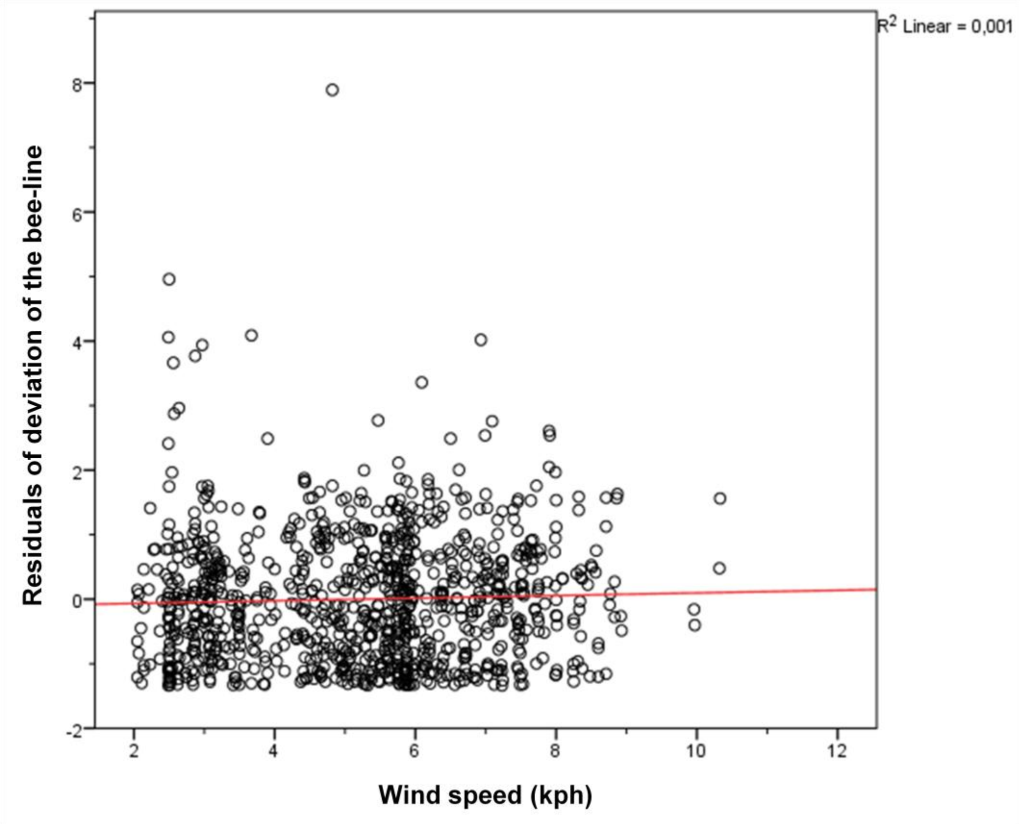

Figure 3.19. Deviation from the bee-line (in meters) in relation to wind speed (kph).

Table 3.14. Model outputs of the GzLMM analysis of the effect of the weather variables on deviation from the bee-line and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Temperature		0.042	1	951	0.838[a]
Wind speed	0.085	6.857	1	954	0.009
Relative wind direction		0.002	1	952	0.958[a]
Wind speed * relative wind direction		1.103	1	952	0.294[a]
Flight number **(reference = 5)**		15.660	4	954	<0.001
1	1.029				
2	1.105				
3	0.186				
4	0.482				
Distance to home	-5.673E-6	25.559	1	954	<0.001

[a] These variables were excluded from the model one by one (first temperature, second relative wind direction and wind speed * relative wind direction), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Flight number	Mean	SE
2	1750.862	195.654
3	698.457	94.104
4	938.673	96.474

Comparisons flight numbers	p
2-3	<0.001
3-4	0.102
2-4	0.003

Interaction variables
As only wind was affecting the deviation from the bee-line, no interaction model was executed.

Height
Only in the weather and interaction model (described underneath), an effect of distance to the loft on flight height was found. The further away from the loft, the lower the flight heights observed (Figure 3.20). In addition, in these models, flight height was also affected by flight number. On trajectory 2, the pigeons were flying significantly higher in flight 3 compared to flight 2 and flight 4 (Appendix 20).

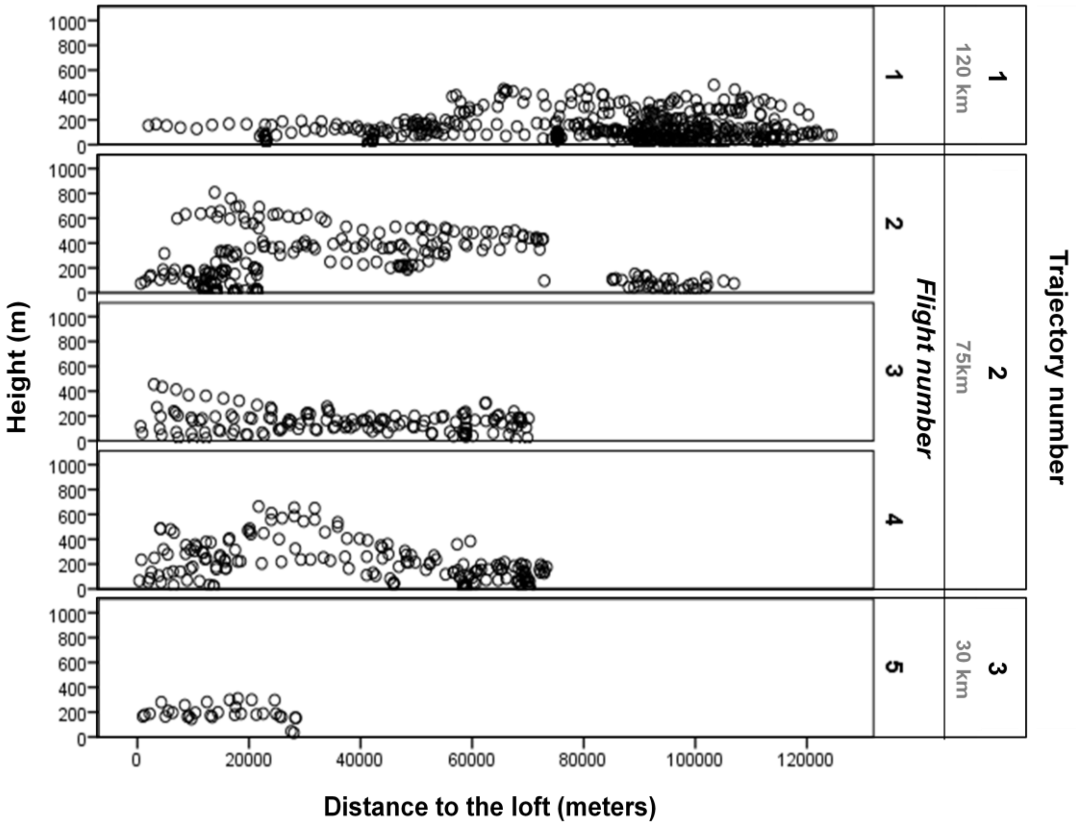

Figure 3.20. Flight height (in meters) at different distances to the loft in the five GPS flights.

Condition

No effect of condition on flight height was found (Table 3.15).

Table 3.15. Model outputs of the GzLMM analysis of the effect of the conditional variables on flight height. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Moulting status (reference = 3)		1.421	3	948	0.235
0	-0.258				
1	-0.562				
2	-0.030				
Condition score	0.030	0.038	1	948	0.846
Weight size ratio – wing	0.497	0.021	1	948	0.884
Weight size ratio – wing^2	-0.013	0.023	1	948	0.880
Weight size ratio – tarsus	0.028	0.874	1	948	0.350
Weight size ratio – tarsus^2		1.178	1	947	0.278[a]
Flight number (reference = 5)		1.7492	4	948	0.202
1	-0.501				
2	0.182				
3	-0.347				
4	0.019				
Distance to home	1.316E-6	2.166	1	948	0.141

[a] This variable was excluded from the model, because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Landscape

The landscape types, above which the pigeons were flying, were affecting the flight heights differently. Higher flight heights were observed above ‘’mixed landscape types’’. This was significantly higher compared to the flight height above shrub/cropland (Table 3.16, Figure 3.21). In addition, the flight height was significantly lower in transition from urban area to non-urban area in contrast to no transition (Table 3.16, 3.22).

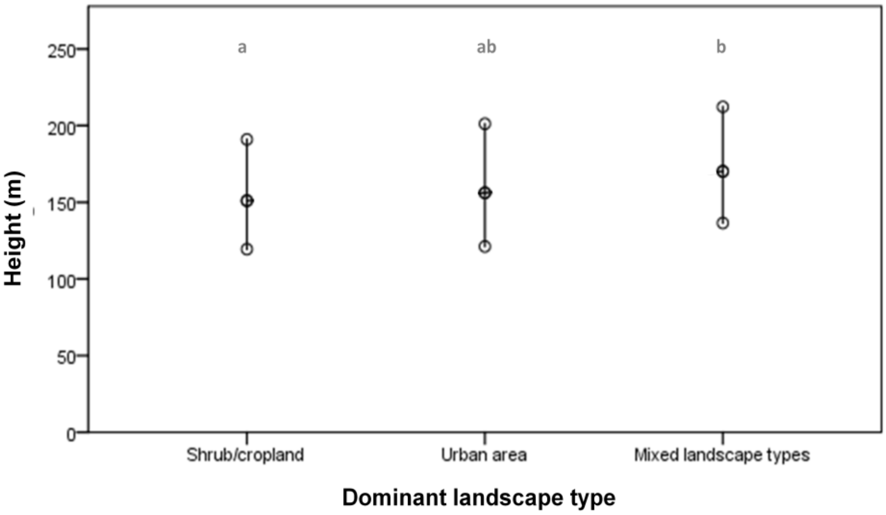

Figure 3.21. Flight height (in meters) in relation to the dominant landscape type of the buffer. Significant differences are indicated with alphabetic letters (top of graph).

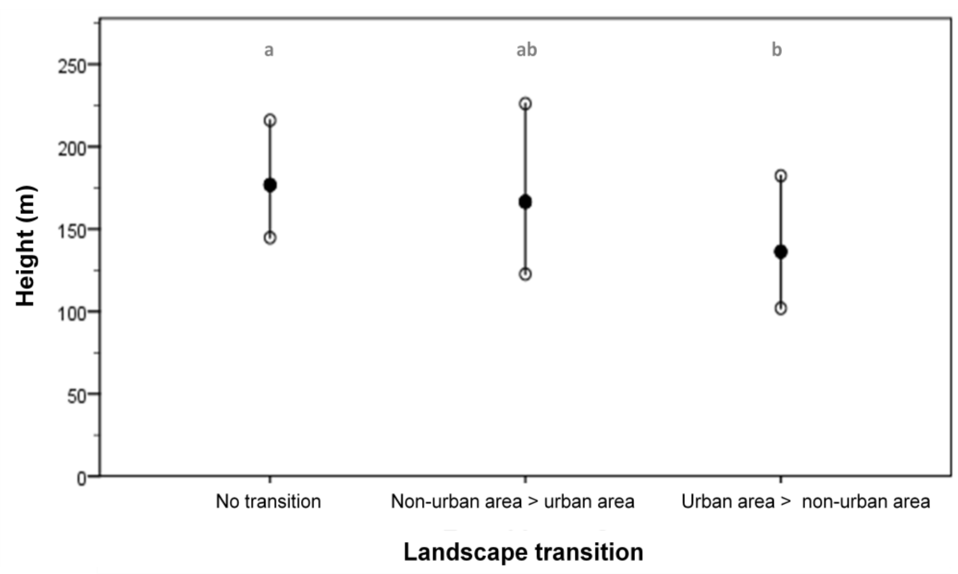

Figure 3.22. Flight height (in meters) in relation to the landscape transitions. Significant differences are indicated with alphabetic letters (top of graph).

Table 3.16. Model outputs of the GzLMM analysis of the effect of the landscape variables on flight height and of the additional pair-wise comparison (Sequential Sidak) for dominant landscape type. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the dominant landscape type the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Landscape transition **(reference = urban area > non-urban area)**		3.015	2	956	0.050
no transition	0.260				
non-urban area > urban area	0.200				
Dominant landscape type **(reference = mixed landscape types)**		3.100	2	956	0.045
schrub/cropland	-0.119				
urban area	-0.086				
Flight number		1.918	4	952	0.105[a]
Distance to home		1.600	1	951	0.206[a]

[a] These variables were excluded from the model one by one (first distance to home, second flight number), because the variable effect was not significant and did not improve the model fit. The results for the other variables in the table are from the model without these excluded variables.

Dominant landscape types	**Mean**	**SE**
Shrub/cropland	151.019	18.071
Urban area	156.139	20.170
Mixed landscape types	170.181	19.144

Comparisons dominant landscape types	**p**
Shrub/cropland – urban area	0.761
Urban area – mixed landscape types	0.637
Shrub/cropland – mixed landscape types	0.046

Landscape transition	**Mean**	**SE**
No transition	176.813	18.014
Non-urban area > urban area	166.498	25.945
Urban area > non-urban area	136.311	20.196

Comparisons landscape transition	**p**
[No transition] – [non-urban area > urban area]	0.667
[non-urban area > urban area] – [urban area > non-urban area]	0.471
[No transition] – [urban area > non-urban area]	0.024

Weather

Remarkably, significantly higher flight heights were found under higher relative wind directions, so higher flight heights under more headwinds (Table 3.17, Figure 3.23). Also, higher temperatures were related to higher flight heights (Table 3.17, Figure 3.24).

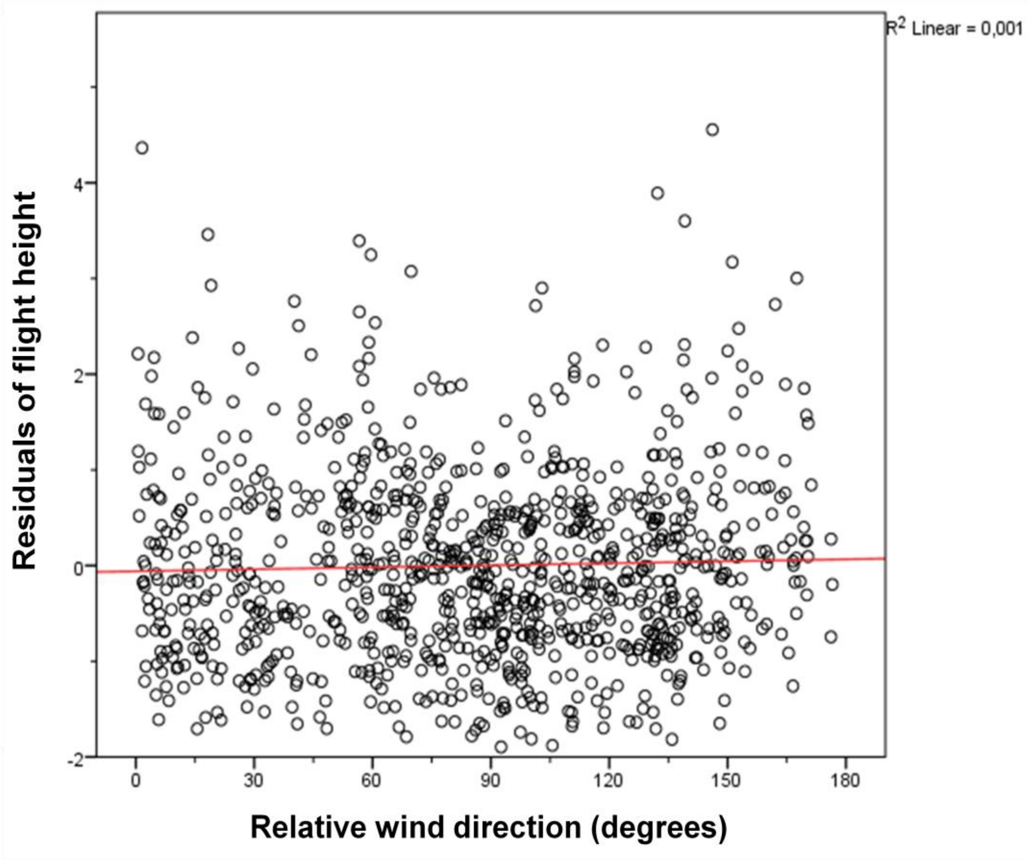

Figure 3.23. Flight height in relation to relative wind direction. A relative wind direction of 180 degrees is considered headwind and a relative wind direction of 0 degrees is considered tailwind.

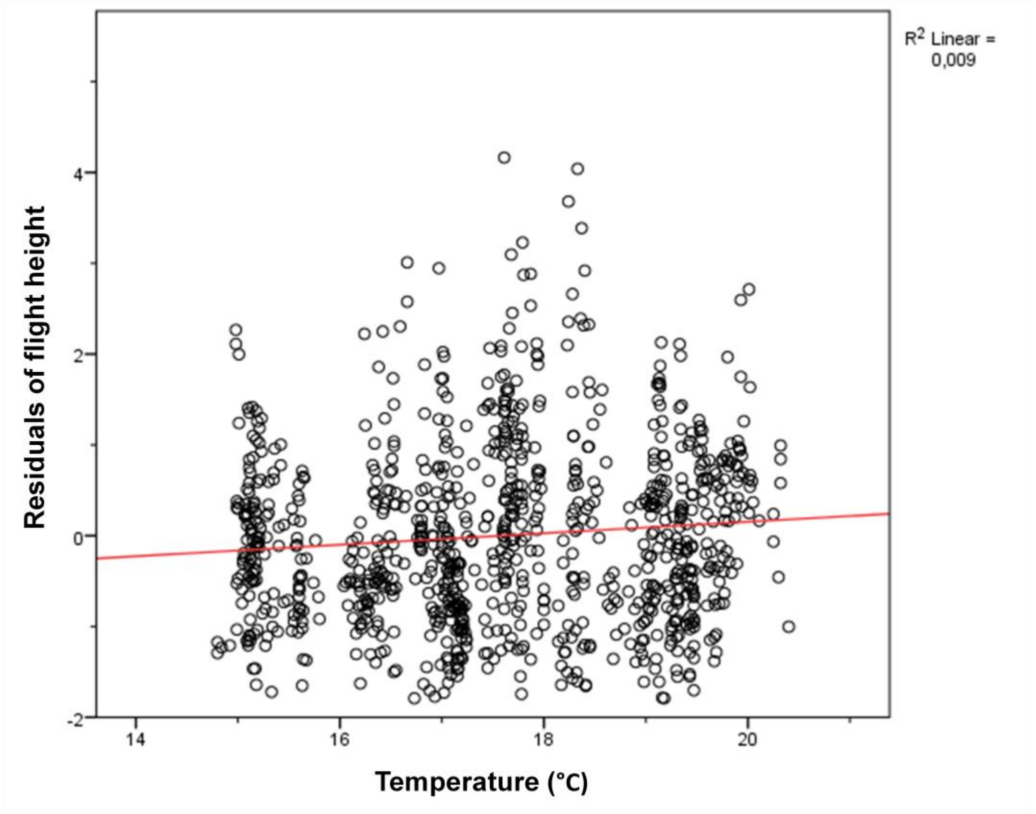

Figure 3.24. Flight height in relation to air temperature (°C).

Table 3.17. Model outputs of the GzLMM analysis of the effect of the weather variables on flight height and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and p-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Temperature	0.662	229.774	1	951	<0.001
Wind speed	0.029	0.826	1	951	0.364
Relative wind direction	0.005	14.669	1	951	<0.001
Wind speed * relative wind direction	0.000	3.238	1	951	0.072
Flight number **(reference = 5)**		15.725	4	951	<0.001
1	0.433				
2	-0.995				
3	1.251				
4	-0.958				
Distance to home	-9.626E-6	71.102	1	951	<0.001

Flight number	**Mean**	**SE**
2	61.684	12.469
3	583.034	123.723
4	63.987	11.954

Comparisons flight numbers	**p**
2-3	<0.001
3-4	<0.001
2-4	0.884

Interaction variables:

When including all significant variables of the condition, landscape and weather models into a new model as an interaction effect, the interaction was significant, as well as the temperature and relative wind direction on itself. The direction of the effect of temperature on height was the same as found in the weather model (Table 3.17 and 3.18). However, the direction of the effect of the relative wind direction in the interaction model was contradicting with the findings of the weather model (Table 3.17 and 3.18). In the interaction model, I did find lower flight heights with higher relative wind directions (more headwinds). Also interesting is the effect of the dominant landscape type, which is, in contrast to what was found in the landscape model (Table 3.16), not significant in the interaction model (Table 3.17).

Table 3.18. Model outputs of the GzLMM analysis of the effect of several variables, which were significant in earlier models, and their interaction on flight height, and of the additional pair-wise comparison (Sequential Sidak) for flight number. The model results include coefficients, F-values, degrees of freedom (d.f.) and P-values, and for the flight number the estimated marginal means, standard errors and p-values of the pair-wise comparisons.

	Coefficient	**F**	**d.f. 1**	**d.f. 2**	**p**
Temperature	0.485	94.525	1	948	<0.001
Relative wind direction	-0.034	32.641	1	948	<0.001
Dominant landscape type **(reference = mixed landscape types)**		0.797	2	948	0.451
Shrub/cropland	0.043				
Urban area	0.167				
Temperature * relative wind direction * dominant landscape type		15.565	3	948	<0.001
Wind speed * relative wind direction * dominant landscape type = shrub/cropland	0.002				
Wind speed * relative wind direction * dominant landscape type = urban area	0.002				
Wind speed * relative wind direction * dominant landscape type = mixed landscape types	0.002				
Flight number **(reference = 5)**		21.311	4	948	<0.001
1	0.303				
2	-1.133				
3	1.014				
4	-1.299				
Distance to home	-1.036E-5	85.596	1	948	<0.001

Flight number	**Mean**	**SE**
2	58.832	10.629
3	503.682	92.847
4	49.813	9.075

Comparisons flight numbers	**p**
2-3	<0.001
3-4	<0.001
2-4	0.471

Discussion

The aim of this study was to determine the contribution of pre-flight physical condition to the flight performances of pigeons under different environmental conditions. As it is already known from multiple pigeon- and migratory studies, weather is of major influence on flight performance (e.g. Alerstam, 1979a, 1979b). This was also confirmed by my study, showing some expected relationships between, for instance, the wind conditions and the pigeons' flight speed. In contrast, fewer studies have been done on the influence of the pigeon's physical condition and the landscape composition on the flight performance. Though, influences were expected, as the landscape is of importance for the pigeon's navigation, and the pigeon's physical condition can restrict the flight ability, and thereby affect the flight performance. However, these influences could not be ascertained by the results of my study, as most of the effects were non-significant or of low effect size. This chapter will continue with discussing, first, the overall performance of the pigeons in the dummy flights and GPS flights. Thereafter, the results of the track analyses are reviewed.

Effects of the GPS ring

There was no evidence of adverse effects of the dummy rings on the flight performance of the pigeons in the dummy flights, as no significant differences in arrival time were found between the pigeons with and without a dummy ring, neither over all flights, nor within flights. Similarly, no significant differences in arrival time were found between the pigeons with and without GPS ring, over all GPS flights. However, in the first GPS flight, the GPS and non-GPS group did differ significantly in arrival time. This was also visible when looking at the occurrence of extreme delays and lost pigeons. There are only a few studies, which also report disadvantageous effects of a transmitter load on the flight performance of pigeons. For instance, Gessaman & Nagy (1988) and Irvine, Leckie, & Redpath (2007) found that backpack transmitters were significantly reducing the flight velocity in pigeons. However, Irvine et al. (2007) also reported that tail-mounted transmitters were less affecting the pigeon's flight performance. In general, other bird tracking studies do not indicate negative effects of transmitters on short-term flight performance (manoeuvrability, velocity and acceleration, Barron, Brawn, & Weatherhead, 2010). However, several studies did found an effect of transmitters on energy expenditure, although this effect was small (Barron et al., 2010). Gessaman et al. (1991) studied the effect of transmitters on the energy expenditure of pigeons, but they were not able to draw any firm conclusions. In this study, no measurements on energy expenditure were done, so a detrimental effect of wearing a GPS ring on energy expenditure cannot be excluded as explanation of the later arrival times of the GPS wearing pigeons in the first GPS flight.

Whether it is likely that our GPS rings were having an effect on the flight performance is dependent on the ring characteristics. The factors that determine the impact of a transmitter are the mass and method of attachment (Kenward, 2001). Effects of the weight of our GPS rings on flight performance is less likely, as it is much lower (0.8% of the body weight) than that of the transmitters used in other pigeon tracking studies (1-5% of the body weight, Gessaman & Nagy, 1988; Gessaman et al., 1991; Irvine et al., 2007; Tyson, 2013), although some report some reverse effects of the transmitters. Moreover, the weight of our GPS rings was far below the threshold of 5% of the body weight, which is the general, but not unanimously accepted (Barron et al., 2010; Irvine et al., 2007) rule of thumb on how much a bird can carry (Kenward, 2001; Scullion, 2016). However, the method of attachment of the transmitter might be even more important as it can affect the balance and aerodynamics of the bird (Gessaman & Nagy, 1988; Irvine et al., 2007). So, a poor or incorrect fitting can affect the behaviour of the pigeon. Most of the radio transmitters are attached to the back by a harness or glue, as collars or tail mounts (Kenward, 2001). Our GPS ring, instead, was attached to the left leg, where it was not fixed, but was able to move. The ring is especially designed for pigeon tracking. Nonetheless, I could not find any publication of pigeon tracking studies using this type of devices and reporting on the effects of the rings on the performance of the pigeons. However, if the loose fitting of the GPS rings has had any severe effects on the pigeon's flight performance, you would expect to see differences between the ring wearing and the non-ring wearing individuals in all flights. However, I did not observe this. It could be that an effect of the ring is only present under certain circumstances, e.g. a larger distance from home, which might demand more from pigeons with an extra load (Gessaman & Nagy, 1988). This might have been the case in the first GPS flight, as the pigeons were released at 120 kilometres from the loft, which was the furthest away in my study. Moreover, the fact that the release site in the first GPS flight was unfamiliar for the pigeons might have had an additive influence, as this can decrease the initial orientation and thereby increase the flight duration (Kowalski & Wiltschko, 1987).

In summary, detrimental effects of the GPS ring on energy expenditure or short-term flight performance, by the way of attachment of the ring, cannot be completely excluded. However, there are no reasons to assume that the GPS rings have had a strong impact on the pigeons' welfare or has affected the outcome of this study severely, as there were no differences in flight performance found between the ring-wearing and non-ring wearing pigeons over all flights and within most of the flights.

Flight performances and route efficiency

No improvement in arrival times along the dummy flights was expected, as this release site and region were familiar to the pigeons through earlier training flights. It is therefore likely that the development of stereotyped routes already have taken place. However, there was a decrease in arrival time observed from dummy flight 1 to dummy flight 3. It could be that the development of stereotyped routes was still going, accompanied with improved homing, as, for example, observed by Armstrong (2009). On the other hand, another possible explanation of the decrease in arrival time from dummy flight 1 to dummy flight 3 is the training regime of the pigeons. Although there was no difference in the average arrival time found between dummy and non-dummy group in the first flight, the dummy group seems to have a higher variety in arrival time in this flight. When analysing the arrival group data, it is noticed that in the first dummy flight, several dummy-wearing pigeons were arriving extremely delayed. This was not observed in the proceeding dummy flights. This difference in the first dummy flight could be due to the flight experience of the pigeons in the dummy group and non-dummy group, as this differed. Due to an organizational error, the dummy group consisted of somewhat younger pigeons, who had less flight experience and did not participate in races before, in contrast to the more older birds from the non-dummy group. During the execution of the dummy flights, we noticed that when arriving home, some dummy wearing individuals were staying on the roof for quite a long time, before entering the loft. As the electronic recognition system only registers a pigeons which enters the loft, individuals who not enter the loft immediately when arriving on the loft site can have artificially inflated arrival times. It is plausible that while the flight were advancing, the birds became more trained in entering the loft rapidly, instead of a factual shortening of the flight duration.

Although, the arrival times of the pigeons in the first GPS flight of trajectory 2 (GPS flight 2) were somewhat higher and more ''extreme delays'' were recorded, compared to the other two GPS flights at the same trajectory, no overall significant differences in arrival times were found. An improvement was also not observed when considering the efficiency index (EI). This finding is in contrast to what was expected and observed by in other studies (Guilford & Biro, 2014), namely an improvement in the arrival times of the GPS flights on trajectory 2, as this release site was not used before and unfamiliar to the pigeons. In contrast, no improvement of the route efficiency was also observed by (Wiltschko et al., 2007). Guilford & Biro (2014) suggested, as a possible explanation of this finding, that the pigeons might were already familiar with the region, as they have had local training flights, which likely crossed the experimental release site or neighbouring area. If the pigeons had already formed to a certain extent a familiar route, it might explain that no major improvement in route following was found in this experiment. This could also be the case in my study, as the pigeons have had a few longer training flights before of which the route might have crossed the release site of trajectory 2. However, the average EI in trajectory 2 was 0.77, which is a bit lower than the average observed route efficiencies when route familiarity was at its maximum (0.83-0.85), reported in earlier studies (e.g. Armstrong et al., 2008; Mehlhorn & Rehkaemper, 2016). It is therefore possible that route development still was going on, however, it is then unclear why no obvious learning pattern was observed. Another possibility is that less route learning and improvement is caused by the landscape composition. As suggested by Armstrong et al. (2008), the following of a familiarised route is easier and more faithful in edge containing landscapes with not too much complexity. The influence of the landscape on the step characteristics of the flight tracks in this study, will be discussed further on in this chapter. Lastly, it could also be that route following is less general than expected, as there are different ways of navigation and there are environmental differences between regions, as also suggested by Guilford & Biro (2014).

Overall, the EI in the GPS flights was on average 0.81, which is similar to the average EI (0.83-0.85), observed in other studies (Armstrong et al., 2008; Mehlhorn & Rehkaemper, 2016). In GPS flight 5, the efficiency indices observed were the highest of all flights. Also, almost all pigeons arrived ''on time'' in this flight. In contrast, the performance in GPS flight 1 was much worse, a higher amount of ''extreme delays'' were observed and some pigeons got lost. Therefore, almost none EI's could be calculated for this flight, as a complete track is needed for the EI calculation. The losses were not exceptional for my study. Losses are recorded in some other studies, like (Foà, Benvenuti, Ioalé, & Wallraff, 1984), and are also experienced during pigeon races (WOWD, 2010). There are several possible causes of the losses, including predation, for instance by sparrow hawks, and collisions with power lines and cables, and traffic (Bevanger, 1998; WOWD, 2010). Also, unfavourable weather conditions and gravity anomalies can cause the pigeons to lose their homeward orientation (e.g. Dornfeldt, 1991), although no indications of highly unfavourable weather and gravity conditions on the day of the first GPS flight were observed (Appendix 3).

Contribution of flight speed, orientation and height in flight performance

Flight performance is determined by flight speed and orientation, and can be influenced by flight height. Logically, earlier arrivals are related to higher flight speeds, and smaller turning angles and lower deviation from the bee-line, as this indicate a straighter route to home. Although, both, flight speed and orientation, are expected to influence the homing time, it has been suggested that differences in arrival time are mainly caused by differences in orientation and not so much by differences in flight speed among the pigeons, as this difference is small (WOWD, 2010). Also Matthews (1951) indicated that differences in homing time mainly reflect the extent of deviation from the straight track to home or the amount of stops on the way. However, besides these notations, the real extend to which both parameters make up the flight performance, is to my knowledge, so far unpublished. Therefore, I tested the effect of the mean and deviation in flight speed, turning angle, deviation from the bee-line and flight height in the flights, on the arrival time of the GPS wearing individuals. Surprisingly, none of the variables had a significant influence on arrival time. This is in contrast to what was found by Li et al. (2016), which reported a significantly higher arrival time with higher distances from the bee-line (fixed). No other publications could be found to compare my results with. However, it is not very likely that none of the variables are influencing the flight performance, as flight speed, orientation and flight height are the only flight parameters which can vary in a flight and therefore the only factors which can cause variation in flight performance. So, it is more likely that this outcome is the result of the low sample sizes, as the number of recorded tracks in each of the flights was only 5 (GPS flight 2-5) or 7 (GPS flight 1). Moreover, there was quite some variation in the mean and deviation of most of the step characteristics, in each of the flights. So, the extent to which flight speed and orientation are determining the overall flight performance (arrival time) remains obscure and needs further investigation.

Effects of flight characteristics on step characteristics

It was uncertain if and to what extent an effect of the remaining distance to the loft during the flight on flight performance could be expected. Michener & Walcott (1967) reported an improved in orientation within a few kilometres of the loft. In contrast, a more stable flight speed over the flight was reported by Tyson (2013). However, a ''distance to the loft effect'' on flight performance is not widely reported. In most of the models in this study an effect of distance to the loft on the step characteristics (flight speed, turning angle, deviation bee-line and flight height) was found. However, the direction of the effect was often unclear. Regarding the flight speed the results in the various models were contradicting; the further away from the loft, the higher and lower the flight speed. As I only analysed the active flight track (so without start and end of the flight), I would expect to observe a steady flight speed, as found by Tyson (2013). Although Tyson (2013) report this for a flock flight, they also describe the wing beat frequency and body acceleration of individual flyers, which is related to the flight speed. The results of this analysis were showing a rather similar pattern, with a lower and stable wing beat frequency and body acceleration in middle of the flight. These steady values indicate a steady horizontal flight. As I did observe differences in speed along the flight track, it might indicate that some of the flights in my study were less steady. However, whether this was really the case and what could be the cause of this behaviour is unclear, but it might be related to the weather conditions (which is discussed underneath) as Tyson (2013) report this for flights without any wind conditions. Also the models for the orientation indices were showing contradicting results; the further away from the loft the larger the turning angles, but also, the lower the deviation from the bee-line. So, this is not totally in line with the expectations, based on the reported distance effect by Michener & Walcott (1967). It might be that the orientation is less related to the distance to the loft remaining, and more to the conditions encountered during the flight (as discussed underneath). Lastly, for flight heights, only one of the four models (condition, landscape, weather and interaction model) found an effect of the distance to the loft. In that model, higher distances from the loft were related to lower flight heights. Moreover, the effect sizes of the results were often rather small. So, although flight speed, orientation and height were in some cases found to be different at different distances from the loft, no major uniform distance effect was determined, at least not for the distances tested in this study (up to 120 km).

An effect of the flight number was found in some of the models, comprising a difference between flight 3, and flight 2 and flight 4 of trajectory 2. Higher flight heights and flight speeds and lower turning angles and deviation from the bee-line were observed in flight 3, indicating a better homing and route efficiency in this flight. Although, a lower mean arrival time and higher EI were also observed in flight 3 compared to flight 2 and 4, these difference was not statistically proven. As discussed earlier, it was expected to observe an improvement in flight performance along the flights of trajectory 2. Also, this analysis of the flight performance according to the step characteristics does not confirm this.

Effect of physical condition on step characteristics

In contrast to what was expected, body condition had little if any effect on the step characteristics and arrival time in the GPS flights. The only effect that was detected was of body condition index (weight/wing length and weight/tarsus length) on the turning angle. I expected an optimum weight/size ratio, which allows an optimal flight speed and orientation. However, the results were contradicting: an optimum weight/wing length was related to higher turning angles, indicating more tortuous routes, whereas an optimum weight/tarsus length was related to lower turning angles, indicating less tortuous routes. It has to be noticed that both of these effects were small. An effect of weight on orientation was also found in red knots, showing that higher weights can affect the ability to turn (Dietz et al., 2007), although their data were explained by a sigmoid function instead of a quadratic function. The expected quadratic function was mostly based on a study of Klaassen (1996), indicating the relationship between the total fuel storage in birds and the energetic costs of it and that this can affect flight speed. This study was on migrating birds. Migrating birds undergo seasonal changes, including an major increase in their body mass as a preparation for the migration (Lindström & Piersma, 1993). It is suggested that the total fuel storage before the flight is determined by the trade-off between the energetic cost of a fuel load and the duration and risk of migration (Klaassen, 1996). In contrast, homing pigeons do not undergo such major mass changes before a racing flight. Homing pigeons are often compared to athletes, trained to perform at any time (Sharp, 2012). It might be that the influence of their body weight is therefore less, as the range of weights are less. Besides, it could also be that the distance flown in this study is not long enough to observe any differences in performances due to weight/size differences.

Individual differences in re-growth of the feathers during moult can have implications for the flight performance. For instance, moult can affect flight performance by reducing flight speed and manoeuvrability (Hedenström & Sunada, 1999; Swaddle & Witter, 1997; Swaddle, Witter, Cuthill, Budden, & McCowen, 1996). It was expected that most severe effects would occur in the middle stages of moult, as, among others, observed in Harris' hawks (5-8 primary feather, Hedenström & Sunada, 1999; Swaddle & Witter, 1997; Tucker, 1991). In contrast, I did not find any significant effects of the moulting status on the step characteristics, and thus not on the flight performance along the track. Bridge (2003) suggested that the effects of moult might be minor and that birds can compensate for the loss of wing area. This might be an explanation for my results. Another possible explanations is that the different moult stages are not impacting the flight performance differently, but that moult in general reduces the flight performance. As the moulting period was completely overlapping the experiment, I could not compare the flight performance of pigeons in moult and outside the moulting period, to test this hypothesis. However, this would contradict with the finding that moulting status was significantly affecting the arrival times in the GPS flights. Later arrival times during moult were also reported by Gessaman & Nagy (1988). In contrast, to what was expected, namely a higher impact of moult in the middle stages, a significant difference was found in the change of the outer primaries; the arrival time of individuals with one old primary feather remaining was significantly later compared to individuals with two old primary feathers remaining. Changes in the middle part of the wing are assumed to affect the circulation of air and thereby the lift during the flight (Hedenström & Sunada, 1999). However, also the outer primaries are important for the flight performance, as they are known to be more resistant for aerodynamic forces, compared to the inner primaries, especially more towards the wing tip (Ennos, Hickson, & Roberts, 1995; Purslow & Vincent, 1978). It might be that in pigeons the change in outer primaries is affecting the flight performance by affecting the aerodynamic drag in the flight. This would be in line with difference observed between two and one old primary feather remaining. However, if this would be the case, you would expect the highest impact of the change of the last primary feather (moulting stage: zero primary feathers remaining), but this was not found. It also not explains why I did not observe a difference between three and two old primary feathers remaining. Swaddle & Witter (1997), which studied moult in starlings, did also not observed the pattern reported by Tucker (1991). They explain this by stating that there study was limited to three moulting stages. During the GPS flights of this study, the pigeons were in moulting stage: 0 primary feathers remaining till 3 primary feathers remaining, so also in my study not the full moulting period was covered. So, similar as in the study of Swaddle & Witter (1997), the results might be related to the limited range of moulting stages. However, my results of the effects of the different moulting stages are not really matching the tail of a U-shaped response to moult. Another explanation for the absence of this U-shaped trend can be the size of the moulting gaps. The renewal of the feathers during moult leaves gaps in the wing, thereby reducing the wing area (Lind, 2001), causing asymmetry (J. P. Swaddle & Witter, 1994), and increasing the induced drag factor (Tucker, 1991). Hedenström & Sunada (1999) indicate that, both, the size and location of the moulting gap is affecting flight performance. Logically larger gaps are having a larger affect on the flight performance than smaller gaps (Hedenström & Sunada, 1999). It could be the combination between moulting gap and its location have a clearer effect on the flight performance in my study. However, this could not be tested, as I did not record the length of the re-grown feathers.

In addition to moulting status, also the effect of a pigeon's condition score on its flight performance was tested. This was included in the study, as in pigeon breeding it is common to check the condition of the pigeon on it physical appearance. In this study, I wanted to do a first attempt to assess whether predicting the pigeons flight performance on basis of the appearance of its the physical condition is possible. The results show no effects of condition score on the step characteristics. In contrast, an effect of condition scores on arrival times was found; higher condition scores were related to faster arrival times. Although the effect size was rather small, this finding could suggest that examining a bird on external physical condition criteria by a pigeon holder with the right expertise can be useful in predicting flight performance. Although this is an interesting finding, further study is needed to elucidate the exact relationships.

Effect of the landscape on step characteristics

As pigeons originally live in well-structured landscapes and are known to be able to use linear landscape features for their navigation (Wallraff, 2001), an effect of the landscape on flight performance was expected, especially of urban areas, as less route learning was observed by Armstrong et al. (2008) in regions with urban area. However, in this study, landscape composition had little effect on the step characteristics. Only flight height was influenced by the landscape types, above which the pigeons were flying; higher flight heights were observed above landscapes that were qualified as mixed, compared to above shrub/cropland. In addition, lower flights heights were observed in the transition from urban to non-urban areas compared to no transitions. This is in contrast to what was expected, based on the results of Armstrong et al. (2008), namely less orientation and flight speed above urban areas, as there is less possibility to follow linear landscape features. My results for flight height still could be partly in line with this finding, as mixed landscape types are likely more complex than shrub/cropland, therefore assumed to be less suitable for navigation by linear landscape features. Flying higher over mixed landscape types might suggest that they make less use of the navigation on linear landscape features and more on compass navigation, as Lipp et al. (2004), for example, found that there a significant negative correlation between the flight altitude of pigeons and road following during the flight. However, the height differences are not major, as well as the effect size, which is actually very small. Moreover, this cannot explain why I did not find a difference in flight height between shrub/cropland and urban areas, as urban areas are considered to be even more complex. Moreover, as I did not find any effects of landscape on the other step characteristics, and the effects of flight height are small, it is questionable whether the landscape had a direct influence on the flight behaviour of the pigeons. For extended seas or mountain ranges direct changes in the flight behaviour of pigeons are observed in earlier studies (Bonadonna et al., 1997; Wagner, 1972; Wiltschko & Wiltschko, 2015). Also route following by linear landscape features have been observed before (Dell'ariccia et al., 2009; Guilford et al., 2004; Lipp et al., 2004). This might indicate that the landscape features are affecting the flight path of pigeons more, instead of the landscape types itself. Although, it is likely that landscape complexity can influence the use of these linear landscape features, as observed by Armstrong et al. (2008) and Lau et al. (2006), in my study no effects of more complex urban areas on the flight paths of the pigeons were observed. However, a clear difference between the study of Armstrong et al. (2008) and my study need to be pointed out, namely, I did not study the effect of urban area on the flight performance over all flights, as Armstrong et al. (2008) did, but analysed the effects on urban area on the flight performance within a flight. It might be that more urban areas is affecting the route development over flights, but not the flight characteristics along the track. However, further study with a more similar study set-up is needed to make such comparison. Lastly, another possible explanation for the absence of the landscape influences on the flight performance of the pigeons is the flight behaviour of the pigeons. It is known that pigeons have the tendency to fly in flocks (Gould, 2006; Mehlhorn & Rehkaemper, 2016). Studies on the difference between flock-flying and individuals flights, have found that individually flying pigeons preferred to follow roads and other linear landscape features to navigate home (Dell'Ariccia et al., 2008). Although we released the pigeons in pairs with an interval of 5 minutes, and sometimes waited longer to make sure the pigeons were out of sight before releasing the next pair, grouping could not be completely excluded. From the GPS data, I know that in some flights several pigeons have likely flown together, instead of in a pair or solely. Therefore, it could be that these pigeons have made less use of the landscape for navigation, but flew home by following a leader or a more compromised route (Dell'Ariccia et al., 2008; Flack et al., 2012).

Effect of weather conditions on step characteristics

Of all the three models (condition, landscape and weather), the variables in the weather model were impacting the step characteristics the most. Major effects of wind on flight performance were also expected as lots of literature has addressed the effect of wind on the bird's flight (e.g. Alerstam, 1979a, 1979b; Richardson, 1978). As expected, I observed lower flight speeds with headwind, which are providing more counterforce compared to tailwinds (Dornfeldt, 1991, 1996). Additionally, also higher flight heights were observed under headwinds. This is an odd finding as it is generally known that with headwinds pigeons fly lower (Klaus Dornfeldt, 1996; Tyson, 2013), like this is also found in one of my interaction models (described underneath). Moreover the effect size is small. Therefore, it is more likely that this result is more coincidental. The turning angles were not negatively affected by headwind. In contrast, even more straight routes were observed under headwinds. This is not in line with the findings of Tyson, (2013), indicating a less efficient route back to the loft in strong headwinds. Moreover it does not coincide with the anecdotal knowledge that when pigeons experience head- or crosswinds, they try to fly in the lee of buildings and forests to avoid the non-optimal conditions, thereby increasing their turning angles. This observation of straighter routes in headwind is also not totally clear and convincingly, as the effect size is rather small and no similar effect was found in the interaction model. As expected, a higher wind speed is causing the pigeon's to perform less in terms of their orientation and flight speed. Stronger wind can make it more difficult to compensate for the wind direction, potentially forcing the pigeons to deviate more from the straight route to home (WOWD, 2010). In none of the models, the interaction between wind speed and direction was found. This is remarkable, as this interaction is commonly accepted and very likely.

It was not expected to observe any temperature effects, as the air temperatures in the flights were in the range of what is considered to be normal (Schietecat, 1991 and Tambouryn, 1992 in (Winkel et al., 2008)). However, in this study, higher temperatures were related to higher flight speeds, lower turning angles and higher flight heights. So, temperature seems to improve flight performance, as the pigeons were flying faster and had less tortuous routes. It might be that the higher temperatures, in my study, were related to more optimal wind conditions, as indicated by Sparks et al. (2002) for their study in the United Kingdom. However, such trend is not immediately found in the analyses of my data. Moreover, Li et al. (2016) did not found an effect of temperature on arrival time. Although, Michener & Walcott (1967) did observe lower route deviation with higher temperatures, their conclusion is that they cannot think of a possible causal relationship between temperature and route deviation and that it is more likely to be a training effect. Moreover, also Dornfeldt (1991) denied a causal relation between navigation and air temperature. So, whether my results are indicating a causal relationship between temperature and flight performance is disputed. Additionally, it needs to be mentioned that all the weather effects were rather small. Moreover, the weather dataset used in this study was not fully optimal as it only provided data on weather measurements on the ground, instead of on the pigeons flight height. Additional weather data on higher altitudes could make the analyses more realistically, as these are the conditions that directly affect the pigeons' flight performance. This might also clarify the effects observed.

Interaction between condition and environmental variables

Only the interaction models for turning angle and flight height were run, as they could include variables of multiple categories, found significant in the condition, landscape or weather model. In both models, the interactions (turning angle-interaction model: Temperature * wind speed * relative wind direction * weight/size ratio – wing^2 * Weight/size ratio –tarsus^2, height-interaction model: Temperature * relative wind direction * dominant landscape type) were significant. This is in line with the idea that the movement performance of individuals is arising from an interaction of various internal and external factors (Nathan et al., 2008; Wilson et al., 2015).

Conclusions & recommendations

This study is one of the few studies which tries to elucidate the flight performance of pigeons, in terms of their flight speed, orientation and flight height, along their way home, and the factors influencing it. To conclude, it has been shown that these performance variables can vary over flight, as also within flights. Factors which are found to be responsible for the variation in flight performance, are mainly the wind conditions and temperature. For instance, high wind speeds cause pigeons to fly home less directly and more slowly. Moreover, higher temperatures seem to improve homing, as under this condition higher speeds, lower turning angles and higher flight heights were observed. In contrast, the landscape characteristics and body condition indices did not clearly influence flight performance, although small effects of the moulting status and condition score on arrival time were found. Although, these results were not all cogent, as effect sizes were small and the direction of the effect not in all cases clear, the present work is valuable preliminary study, showing that GPS tracker rings can be used to ascertain the flight performance of pigeons along the track. However, it also shows the weakness of the use of this type of GPS tracker rings, as the data can only be collected when the bird returns home, and the battery expenditure is maximal ten hours, which is not long enough to collect data over very long flights. Besides these practical implications, this study supports the idea that wind is very important for goal directed flights and provides insight in how pigeons respond to the weather conditions along the track. However, it also leaves ambiguity about the influence of the physical condition of the pigeon and the landscape on flight performance along the track, which therefore remains of interest for future study to further improve racing strategies in pigeon racing.

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Appendices

Appendix 1. Data of the pigeons participating in the dummy flights

Pigeon ID	Pair number	Ring number	Sex	Age (years)	Experience (group)[d]	Loft	Treatment group	**Flight 1**		**Flight 2**		**Flight 3**	
								25-August-2017		31-August-2017		7-September-2017	
								Stage of moult (number of remaining old primary feathers)	**Weight** (grams)	**Stage of moult** (number of remaining old primary feathers)	**Weight** (grams)	**Stage of moult** (number of remaining old primary feathers)	**Weight** (grams)
1	1	NL-16-1879061	Male	1	1	B	No dummy	2	417	2	440	2	449
2	1	NL-16-1879124	Male	1	1	L	Dummy	2	452	2	520[b]	1	477
3	2	B-13-6065302	Female	4	2	B	No dummy	3	395	3	420	3	416
4	2	NL-16-1879024	Female	1	1	L	Dummy	2	450	2	493	3	459
5	3	NL-13-1273920	Male	4	2	B	No dummy	3	475	2	480		
6	3	NL-16-1879068	Male	1	1	L	Dummy	3	463	3	520	2[c]	478[c]
7	4	NL-15-3512531	Female	2	2	L	No dummy	4	497	4	528	4	520
8	4	NL-16-1879019	Female	1	1	L	Dummy	3	434	3	483	2	422
9	5	NL-11-3020242	Male	6	2	B	No dummy	5	513	4	515	4	512
10	5	NL-16-1879051	Male	1	1	L	Dummy	4	481	4	497	4	507
11	6	NL-16-3617835	Female	1	1	B	No dummy	4	434	4	447	3	443
12	6	NL-16-1879109	Female	1	1	L	Dummy	3	422	3	472	3	448
13	7	NL-14-3418664	Male	3	2	B	No dummy	5	499	4	509	4	516
14	7	NL-16-1879299	Male	1	1	L	Dummy	4	477	4	560[b]	3	495
15	8	NL-16-3617813	Female	1	1	B	No dummy	5	502	5	509	4	516
16	8	NL-16-3617828	Female	1	1	L	Dummy	4	472	4	456	4	477
17	9	NL-14-1131406	Male	3	2	B	No dummy	5	487	4	506	4	496
18	9	NL-16-1879044	Male	1	1	L	Dummy	4	463	3	475	3	510
19	10	NL-11-1823489	Female	6	2	B	No dummy	5	482	5	480	5	469
20	10	NL-11-3020306	Female	6	2	L	Dummy	4	467	4	508	4	466
21	11	NL-11-3020294	Male	6	2	B	No dummy	6	452	5	465	3	474
22	11	NL-16-1879069	Male	1	1	L	Dummy	4	455	3	523[b]	3	476
23	12	B-13-6097795	Female	4	2	L	No dummy	5	481	5	467	4	520

								Flight 1		Flight 2		Flight 3	
								25-August-2017		31-August-2017		7-September-2017	
Pigeon ID	**Pair number**	**Ring number**	**Sex**	**Age** (years)	**Experience** (group) [d]	**Loft**	**Treatment group**	**Stage of moult** (number of remaining old primary feathers)	**Weight** (grams)	**Stage of moult** (number of remaining old primary feathers)	**Weight** (grams)	**Stage of moult** (number of remaining old primary feathers)	**Weight** (grams)
24	12	NL-11-3020282	Female	6	2	L	Dummy	4	459	4	490[b]	3	451
25	13	NL-12-3215964	Male	5	2	B	No dummy	4[a]	552	5	471	5	468
26	13	NL-16-1879162	Male	1	1	L	Dummy	3	461	3	461	2	469
27	14	NL-16-3617855	Female	1	1	B	No dummy	6	472	6	490	5	488
28	14	NL-16-1879092	Female	1	1	L	Dummy	4	433	4	498[b]	3	460
29	15	NL-11-3020236	Male	6	2	B	No dummy	4	528	4	544	3	496
30	15	NL-16-1879423	Male	1	1	L	Dummy	3	436	3	495[b]	2	453
31	16	NL-11-1823485	Female	6	2	B	No dummy	5	442	5	458	5	453
32	16	NL-16-1879009	Female	1	1	L	Dummy	4	429	4	464	3	442
33	17	NL-14-3418722	Male	3	2	B	No dummy	4[a]	501	5	503	5	515
34	17	NL-16-1879006	Male	1	1	L	Dummy	3	429	2	487[b]	2	451
35	18	B-13-6097722	Female	4	2	B	No dummy	5	431	5	479	5	463
36	18	NL-16-1879007	Female	1	1	L	Dummy	4	425	4	471[b]	4	417
37	19	NL-12-3215918	Male	5	2	B	No dummy	4	471	4	492	4	482
38	19	NL-16-1879042	Male	1	1	L	Dummy	3	413	3	495[b]	2	453
39	20	NL-15-3512548	Female	2	2	B	No dummy	5	425	5	438	5	449
40	20	NL-16-1879052	Female	1	1	L	Dummy	4	414	3	417	3	424

	Median	**Mean**	**Median**	**Mean**	**Median**	**Mean**
Dummy	4	446,75	3	489,25	3	461,75
No dummy	5	472,8	4-5	487	4	481,32

[a] *Likely wrong recordings, as the pigeons had 5 old primary feathers remaining in the proceeding flights.*

[b] *Possible mismeasurements while weighting.*

[c] *Due to the loss of his pair mate in the previous flight, this pigeon could not be released pair-wise. Therefore, the recordings of this pigeon was excluded from further analyses of the dummy data.*

[d] *Experience: **Group 1** = Daily training flights around the lofts, multiple training flights at 30 km of the lofts, and 3 training flights at 142 km of the lofts. No racing experience. **Group 2** = Experience with racing flights corresponding to their age. They have participated in multiple flights from 60 km up to 600 km. The last two years they did not participate in racing flights and only performed in daily training*

Appendix 2. Data of the pigeons participating in the GPS flights

									Trajectory 1		
									Flight 1		
									20-September-2017		
Pigeon ID	**Pair number**	**Ring number**	**Sex**	**Age** (years)	**Experience** (group)[a]	**Loft**	**Treatment group**	**GPS ring number** (when applicable, 22900...)	**Stage of moult** (remaining old primary feathers)	**Weight** (grams)	**Condition score** (1-10)
1	1	NL-16-1879109	Female	1	1	L	No GPS	-	2	405	5
2	1	NL-16-1879024	Female	1	1	L	GPS	392	1	426	6
3	2	NL-16-1879162	Male	1	1	L	No GPS	-	2	447	7
4	2	NL-16-1879124	Male	1	1	L	GPS	402	1	457	6
5	3	NL-16-3617828	Female	1	1	L	No GPS	-	3	461	7
6	3	NL-11-3020306	Female	6	2	L	GPS	395	3	450	8
7	4	NL-16-1879423	Male	1	1	L	No GPS	-	2	390	6
8	4	NL-16-1879042	Male	1	1	L	GPS	400	2	411	6
9	5	NL-11-3020282	Female	6	2	L	No GPS	-	3	439	7
10	5	NL-16-1879007	Female	1	1	L	GPS	387	3	408	6
11	6	NL-16-1879006	Male	1	1	L	No GPS	-	2	420	7
12	6	NL-16-1879022	Male	1	1	L	GPS	390	2	438	5
13	7	NL-16-1879092	Female	1	1	L	No GPS	-	3	428	6
14	7	NL-16-1879019	Female	1	1	L		391	2	402	5
15	8	NL-16-1879069	Male	1	1	L		-	3	446	6
16	8	NL-16-1879051	Male	1	1	L		399	3	445	5
17	9	NL-16-1879009	Female	1	1	L		-	3	353	5
18	9	NL-16-1879052	Female	1	1	L		397	2	393	7
19	10	NL-16-1879299	Male	1	1	L		-	3	477	6
20	10	NL-16-1879044	Male	1	1	L		403	2	484	7

	Median	Mean	Median
GPS	2	431,4	6
No GPS	3	426,6	6

[a] *Experience:* ***Group 1*** *= Daily training flights around the lofts, multiple training flights at 30 km of the lofts, and 3 training flights at 142 km of the lofts. No racing experience. G**roup 2** = Experience with racing flights corresponding to their age. They have participated in multiple flights from 60 km up to 600 km. The last two years they did not participate in racing flights and only performed in daily training flights around the lofts (except the pigeons born in 2015, they have performed in racing flights in 2015, and stopped afterwards) .*

Due to the loss of pigeons and some extreme delayed arrivals, the other flights were performed with lesser pairs. We kept as much as possible the pairs the same, but were forced to make a new pair (pair 11).

									Trajectory 2					
									Flight 2			**Flight 3**		
									27-September-2017			3-October-2017		
Pigeon ID	**Pair number**	**Ring number**	**Sex**	**Treatment group**	**Age** (years)	**Experience** (group)[a]	**Loft**	**GPS ring number** (when applicable, 22900...)	**Stage of moult** (remaining old primary feathers)	**Weight** (grams)	**Condition score** (1-10)	**Stage of moult** (remaining old primary feathers)	**Weight** (grams)	**Condition score** (1-10)
1	1	NL-16-1879109	Female	No GPS	1	1	L	-	2	419	6	2	408	5
2	1	NL-16-1879024	Female	GPS	1	1	L	392	1	421	6	1	422	6
3	2	NL-16-1879162	Male	No GPS	1	1	L	-	1	443	6	1	442	7
4	2	NL-16-1879124	Male	GPS	1	1	L	402	1	438	6	1	459	6
15	8	NL-16-1879069	Male	No GPS	1	1	L	-	2	461	6	1	421	6
16	8	NL-16-1879051	Male	GPS	1	1	L	399	3	446	6	3	451	7
9	5	NL-11-3020282	Female	No GPS	6	2	L	-	3	433	6	2	426	6
10	5	NL-16-1879007	Female	GPS	1	1	L	387	3	404	5.7	2	411	5
19	10	NL-16-1879299	Male	No GPS	1	1	L	-	2	482	6	2	473	7
20	10	NL-16-1879044	Male	GPS	1	1	L	403	2	466	6	2	459	6
13	11	NL-16-1879092	Male	No GPS	1	1	L	-	2	441	6	2	432	6
18	11	NL-16-1879052	Male	GPS	1	1	L	397	2	402	6	2	392	6

	Median	**Mean**	**Median**	**Median**	**Mean**	**Median**
GPS	2	429,5	6	2	432,33	6
No GPS	2	447,6	6	2	433,67	6

[a] Experience: **Group 1** = Daily training flights around the lofts, multiple training flights at 30 km of the lofts, and 3 training flights at 142 km of the lofts. No racing experience. **Group 2** = Experience with racing flights corresponding to their age. They have participated in multiple flights from 60 km up to 600 km. The last two years they did not participate in racing flights and only performed in daily training flights around the lofts (except the pigeons born in 2015, they have performed in racing flights in 2015, and stopped afterwards) .

After flight 3 of trajectory 2, one more pigeon was missing. Therefore, we had to change pair 11, by which the only option was a female/male pair (pair 12).

									Trajectory 2			**Trajectory 3**		
									Flight 4			**Flight 5**		
									13-October-2017			17-October-2017		
Pigeon ID	**Pair number**	**Ring number**	**Sex**	**Treatment group**	**Age** (years)	**Experience** (group)[a]	**Loft**	**GPS ring number** (when applicable, 22900...)	**Stage of moult** (remaining old primary feathers)	**Weight** (grams)	**Condition score** (1-10)	**Stage of moult** (remaining old primary feathers)	**Weight** (grams)	**Condition score** (1-10)
1	1	NL-16-1879109	Female	No GPS	1	1	L	-	1	425	6	1	409	5
2	1	NL-16-1879024	Female	GPS	1	1	L	392	0	432	6	0	417	6
3	2	NL-16-1879162	Male	No GPS	1	1	L	-	1	471	7	0	458	7
4	2	NL-16-1879124	Male	GPS	1	1	L	402	0	482	7	0	478	7
15	8	NL-16-1879069	Male	No GPS	1	1	L	-	0	430	7	0	427	7
16	8	NL-16-1879051	Male	GPS	1	1	L	399	2	505	5	1	495	6
9	5	NL-11-3020282	Female	No GPS	6	2	L	-	2	448	6	2	435	5
10	5	NL-16-1879007	Female	GPS	1	1	L	387	2	421	6	2	413	6
19	10	NL-16-1879299	Male	No GPS	1	1	L	-	2	498	7	1	483	7
20	10	NL-16-1879044	Male	GPS	1	1	L	403	1	485	7	0	470	7
RESERVE	12	NL-16-1879066	Female	No GPS	1	1	L	-		506		1	457	6
18	12	NL-16-1879052	Male	GPS	1	1	L	397	1	423	7	1	419	6

	Median	**Mean**	**Median**	**Median**	**Mean**	**Median**
GPS	1	465,4	6,5	0,5	448,67	6
No GPS	1	463	7	1	444,83	6,5

[a] Experience: **Group 1** = Daily training flights around the lofts, multiple training flights at 30 km of the lofts, and 3 training flights at 142 km of the lofts. No racing experience. **Group 2** = Experience with racing flights corresponding to their age. They have participated in multiple flights from 60 km up to 600 km. The last two years they did not participate in racing flights and only performed in daily training flights around the lofts (except the pigeons born in 2015, they have performed in racing flights in 2015, and stopped afterwards).

Measurements that were taken once before the start of the GPS flights:

Pigeon ID	**Pair number**	**Ring number**	**Sex**	**Treatment group**	**Wing length** (cm)	**Tarsus length 1** (cm)	**Tarsus length 2** (cm)	**Tarsus length 3** (cm)	**Average tarsus length** (cm)
1	1	NL-16-1879109	Female	No GPS	22,4	3,728	3,299	3,428	3,485
2	1	NL-16-1879024	Female	GPS	21,4	4,282	3,106	3,28	3,556
3	2	NL-16-1879162	Male	No GPS	22,5	3,828	3,366	3,313	3,502
4	2	NL-16-1879124	Male	GPS	21,5	3,872	3,718	3,716	3,769
5	3	NL-16-3617828	Female	No GPS	21,1	3,828	3,302	3,49	3,540
6	3	NL-11-3020306	Female	GPS	21,5	3,726	3,536	3,314	3,525
7	4	NL-16-1879423	Male	No GPS	21,6	4,026	3,258	3,426	3,570
8	4	NL-16-1879042	Male	GPS	22,1	3,762	4,126	3,82	3,903
9	5	NL-11-3020282	Female	No GPS	21,9	3,865	3,132	3,131	3,376
10	5	NL-16-1879007	Female	GPS	20,5	4,076	3,053	3,103	3,411
11	6	NL-16-1879006	Male	No GPS	22,5	3,886	3,403	3,471	3,587
12	6	NL-16-1879022	Male	GPS	23,1	4,282	3,401	3,62	3,768
13	7	NL-16-1879092	Female	No GPS	21,5	4,112	3,258	3,386	3,585
14	7	NL-16-1879019	Female	GPS	21,5	3,433	3,052	3,257	3,247
15	8	NL-16-1879069	Male	No GPS	21,4	4,064	3,672	3,622	3,786
16	8	NL-16-1879051	Male	GPS	22,1	4,01	3,652	3,439	3,700
17	9	NL-16-1879009	Female	No GPS	21,5	4,202	3,09	3,042	3,445
18	9	NL-16-1879052	Female	GPS	21	3,688	3,102	3,068	3,286
19	10	NL-16-1879299	Male	No GPS	22,4	3,892	3,486	3,362	3,580
20	10	NL-16-1879044	Male	GPS	22,2	4,278	3,812	4	4,030

No data of pigeon with ring number ‘’NL-16-1879066’’, as this one was used as a reserve in the last GPS flight.

Appendix 3. Weather conditions flights

An impression of the weather conditions at the release sites for the test-, dummy- and GPS flights, as shown here in this appendix, were provided by the ‘’Instituut Wedvlucht Begeleiding’’ (IWB).

Test flight

Average air temperature (°C)	**Cloudiness**	**Relative humidity** (%)	**Precipitation**	**Wind direction**	**Wind speed** (mps)
20.5	7 octa’s = almost completely clouded	69	no	South/South-East	3.5

Dummy flights

Flight number	**Average air temperature** (°C)	**Cloudiness**	**Relative humidity** (%)	**Precipitation**	**Wind direction**	**Wind speed** (mps)
1	18.4	7 octa’s = almost completely clouded	71	no	East/South-East	1.7
2	20.4	6 octa’s = heavenly clouded	75.5	no	South-West	3.2
3	15.9	8 octa’s = completely clouded	76	Almost nil	South-West	3.8

GPS flights

Flight number	**Average air temperature** (°C)	**Cloudiness**	**Relative humidity** (%)	**Precipitation** (mm)	**Wind direction**	**Wind speed** (mps)
1	14.5	6 octa’s = heavenly clouded	80	no	Sout-West	2.6
2	13.8	5 octa’s = partly till heavenly clouded	84	no	East/South-East	1.9
3	13.5	5/6 octa’s = partly till heavenly clouded	74	0.1	West	
4	15.3	6 octa’s = heavenly clouded			South-West	

* No data obtained for flight 5 of the GPS flights.

Appendix 4. Characteristics of the release site of the test flight

Coordinates location (decimal degrees): 51.357281, 4.639916
Address: Ringlaan, 2960 Brecht, Belgium
Distance from lofts (km): 23

Reference map: Google, 2017

Appendix 5. Data of the pigeons participating in the test flight and flight results

Due to an error in the electronic recognition system at the entrance of the lofts, no arrival times were registered in the test flight. However all pigeons arrived home within 35 minutes after release, except for the pigeon with the ringnumber ''NL-11-3020306'', which took more time to arrive home.

Sex	**Ring number**	**Group number release**	**Release time**	**Treatment group**	**Stage of moult** (number of remaining old primary feathers)	**Weight** (grams)
Male	NL-14-3418722	1	15:05	No dummy	5	499
Female	NL-16-3617813	1	15:05	No dummy	5	519
Female	B-13-6065302	1	15:05	No dummy	3	394
Female	NL-15-3512548	1	15:05	No dummy	5	417
Female	NL-16-3617855	1	15:05	No dummy	6	464
Male	NL-16-1879042	1	15:05	Dummy	3	417
Male	NL-16-1879124	1	15:05	Dummy	2	445
Male	NL-16-1879162	1	15:05	Dummy	3	464
Male	NL-16-1879006	1	15:05	Dummy	3	426
Male	NL-16-1879022	1	15:05	Dummy	3	456
Female	NL-15-3512531	2	15:12	No dummy	4	541
Female	B-13-6097795	2	15:12	No dummy	5	509
Female	NL-11-1823485	2	15:12	No dummy	5	445
Female	NL-16-3617835	2	15:12	No dummy	4	450
Female	NL-11-1823489	2	15:12	No dummy	5	487
Female	NL-16-1879009	2	15:12	Dummy	4	444
Female	NL-16-1879052	2	15:12	Dummy	4	416
Female	NL-16-3617828	2	15:12	Dummy	4	474
Female	NL-16-1879019	2	15:12	Dummy	4	431
Female	NL-11-3020282	2	15:12	Dummy	4	452
Female	NL-11-3020236	3	15:20	No dummy	4	530
Female	NL-14-3418664	3	15:20	No dummy	5	481
Female	NL-11-3020242	3	15:20	No dummy	5	511
Female	B-13-6097722	3	15:20	No dummy	5	437
Female	NL-11-3020306	3	15:20	No dummy	4	477
Female	NL-16-1879051	3	15:20	Dummy	4	492
Female	NL-16-1879044	3	15:20	Dummy	4	450
Female	NL-16-1879109	3	15:20	Dummy	3	434
Female	NL-16-1879092	3	15:20	Dummy	4	466
Female	NL-16-1879007	3	15:20	Dummy	4	423
Male	NL-16-1879061	4	15:33	No dummy	2	242
Male	NL-14-1131406	4	15:33	No dummy	5	482
Male	NL-11-3020294	4	15:33	No dummy	5	459

Sex	**Ring number**	**Group number release**	**Release time**	**Treatment group**	**Stage of moult** (number of maining old primary feathers)	**Weight** (grams)
Male	NL-12-3215918	4	15:33	No dummy	4	462
Male	NL-13-1273920	4	15:33	No dummy	3	466
Male	NL-12-3215964	4	15:33	No dummy	5	476
Male	NL-16-1879423	4	15:33	Dummy	3	438
Male	NL-16-1879299	4	15:33	Dummy	4	483
Male	NL-16-1879068	4	15:33	Dummy	3	470
Male	NL-16-1879069	4	15:33	Dummy	4	453
Female	NL-16-1879024	4	15:33	Dummy	2	455

Appendix 6. Characteristics of the release site of the dummy flights

Coordinates location (decimal degrees):	51.309286, 4.555601
Address:	2930 Brasschaat, Belgium
Distance from lofts (km):	30

Reference map: Google, 2017

Appendix 7. Behavioural observations

Although the results of the dummy flights are not showing effects of the dummy rings on the performance of the pigeons, we did observe ring-related behaviour, including pecking towards the ring and pulling up the leg. This might indicate discomfort of the ring and could thereby have welfare consequences. By means of behavioural observations, I wanted to determine the frequency of occurrence of this behaviour and the development of the behaviour over time. Expected was that the ring-related behaviour was mainly present at the first day, when the pigeons were introduced to the dummy ring, and decreased over-time due to habituation. The procedure followed during the behavioural observations is described in detail in this appendix.

Set-up observations

In order to record the pigeons' behavioural state (for example sitting or walking), as well as the events (for example aggressive behaviour towards one another or pecking towards the ring), focal animal sampling was used. In this sampling method information on what an individual is doing for a certain time period is gathered. For the behavioural observations female homing pigeons were used, which were not involved in the other parts of this study, and therefore did not wear a dummy ring before. To determine the effect of the GPS ring on the pigeon's behaviour, different treatments were included in the behavioural observations: pigeons with a dummy ring (rings was attached to the right leg of pigeon) and pigeons without. Pigeon breeders with experience with GPS-rings suggested to put a rubber tube underneath the dummy ring to reduce the movement of the ring on the leg, thereby diminishing the discomfort for the pigeon. To study the effectiveness of this measure, I included this option in the behavioural observations. Thereby, three sub-groups were formed: a group without a ring, a group with a dummy ring and a group with a dummy ring with rubber lining. Each of the sub-groups included 7 individuals (Table 1). The observations were done in a group setting. In this way also possible interactions between the pigeons were included. In order to be able to distinguish the individuals within the group, individuals were marked by coloured numbered tape around foot ring or dummy ring (no ring: yellow marking, ring: pink marking, ring with rubber lining: green marking).

Table 1. The three sub-groups that were included in the observations: no ring, ring and ring with rubber lining, and the ring numbers of the birds in each group.

No ring		**Ring**		**Ring with rubber lining**	
ID	**Foot ring number**	**ID**	**Foot ring number**	**ID**	**Foot ring number**
1	B-13-13936	1	NL-15-1778566	1	NL-16-4247871
2	NL-16-1879479	2	NL-16-1879325	2	NL-16-1597058
3	B-13-13363	3	NL-16-1597149	3	NL-16-1879040
4	NL-16-1597102	4	NL-15-3512547	4	NL-16-1879465
5	NL-14-1937666	5	NL-16-1596244	5	NL-16-1879053
6	NL-14-6304916	6	NL-11-6082883	6	NL-16-1596976
7	NL-14-6296751	7	NL-15-1894965	7	NL-16-1897130

Each individual's behaviour was observed continuously for 3 minutes. All observations were executed by the same person. During the observation, the type of behaviours that were shown and the duration were noted by using an ethogram (underneath) and protocol (page 29-38). After each observation, a new individual was observed. Search time for a new individual sometimes cost several minutes. In total, 3 observational rounds were executed on a day, except for the first day. Then 2 observational rounds were executed due to organizational issues. As I wanted to observe the development of the behaviour over time, I have repeated these observations three times: on day 1, day 4 and day 8. Observations were taking place from 12:45 till 17:30 on the following dates:

Day 1 – 20 October 2017
Day 4 - 23 October 2017
Day 8 - 27 October 2017

Ethogram

Type of behaviour	Behaviour	Description of behaviour	Abbreviation
Solitary	Sitting	Pigeon sits/lays on the litter layer or in the cupboard. No other activity is displayed	S
	Standing with two legs	Pigeon stands with both of his legs reaching the ground. No other activity is displayed	STL
	Standing on leg with ring	Pigeon stands with one leg pulled up, leg with ring is down. No other activity is displayed	SLR
	Standing on leg without ring	Pigeon stands with one leg pulled up, leg without ring is down. No other activity is displayed	SLWR
	Walking	Pigeon moves from one place to another by walking	W
	Flying	Pigeon moves from one place to another by flying	F
	Grooming itself	Pigeon preens its own feathers by using its beak	GI
Food-related	Eating	Pigeon ingests food	E
	Drinking	Pigeon stands at the water dispenser and ingests water	D
	Foraging	Pigeon is walking, picking and routing the litter layer in search for food	FO
Social	Grooming other	Pigeon preens another pigeon’s feathers by using its beak	GO
	Getting groomed	The pigeon’s feathers are preened by another pigeon, using its beak	GG
Aggressive	Chasing of other pigeon	Pigeon runs after another pigeon	CO
	Chased by other pigeon	Pigeon is run after by another pigeon	CB
	Pecking other pigeon	Pigeon pecks another pigeon	PO
	Pecked by other pigeon	Pigeon gets pecked by a pigeon	PB
Ring-related	Pecking ring	Pigeon pecks towards the ring	PR
	Dragging leg	Pigeon is dragging its leg with the ring	DL
	Pulling leg	Pigeon is pulling its leg up with the ring	PL
	Other behaviour	All other behaviour which is not covered by the above mentioned types of behaviour	OB

Data analyses

All observed behaviour during the observations was classified into the pre-defined groups, including solitary-, food-related-, social-, aggressive-, ring-related behaviour and other behaviours (included in the ethogram, described above). In the analyses of the occurrence of certain types of behaviour in the three different study groups, ring, no ring and ring with rubber lining, the focus was on the ring-related behaviour, as this was the main interest for the observations. Since the amount of ring-related behaviour was small, zero data were plentiful. Since the zero data is also very important, indicating no ring-related behaviour, I decided to transfer the data into present/absent data. Unfortunately, the statistical model for analyzing this data was not working properly, likely due to the low amount of ring-related behaviour.

Results

Percentage of total time

At every observational day, ring-related behaviour was observed, although it was in low amounts. Therefore the percentage of ring-related behaviour of the total observation time at each day, was low (Figure 1). However, a difference in amount of ring-related behaviour was observed between the groups, as expected, the ‘’no ring’’ group showed a lesser amount of ring-related behaviour. Although this group don’t wear a dummy ring, some ring-related behaviour was recorded at the first two observational days. This concerns pecking towards the foot ring. Due to the high amount of zero data and the statistical analysis of this, it was decided to transform the data into presence/absence data, as discussed underneath.

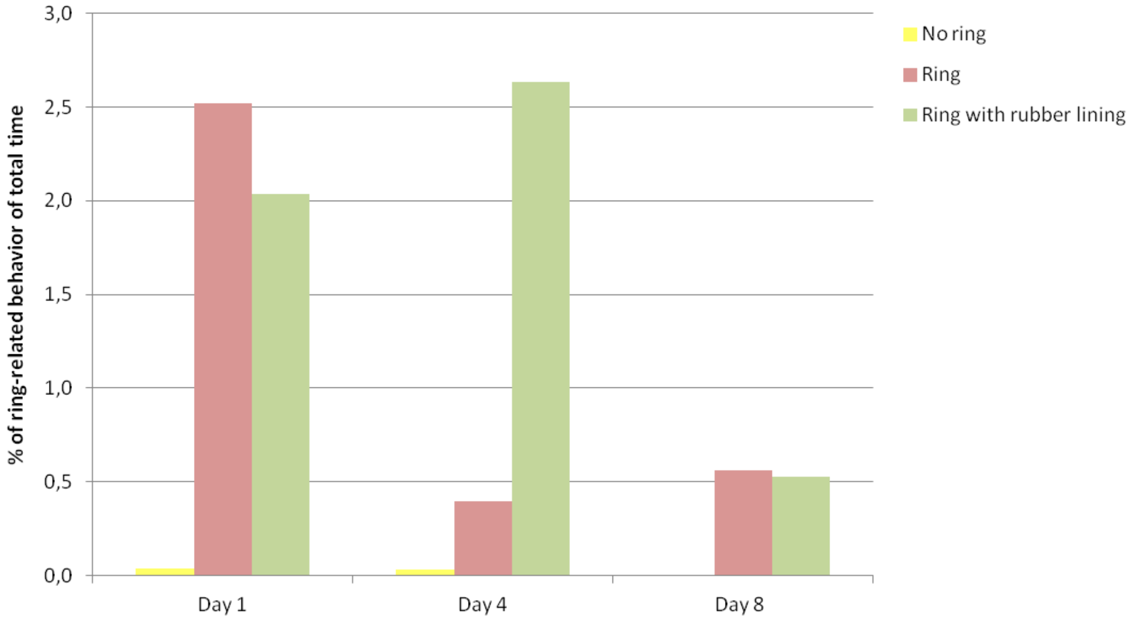


Figure 1. Percentage of ring-related behaviour of total observed behaviour per treatment group and observational day.

Presence/absence ring-related behaviour

When transforming the data into presence/absence data, it was observed that more ring-related behaviour was shown by the individuals wearing a ring with or without a rubber lining (Figure 2). Furthermore, no clear change of the ring-related behaviour over the different days could be established (Figure 2).

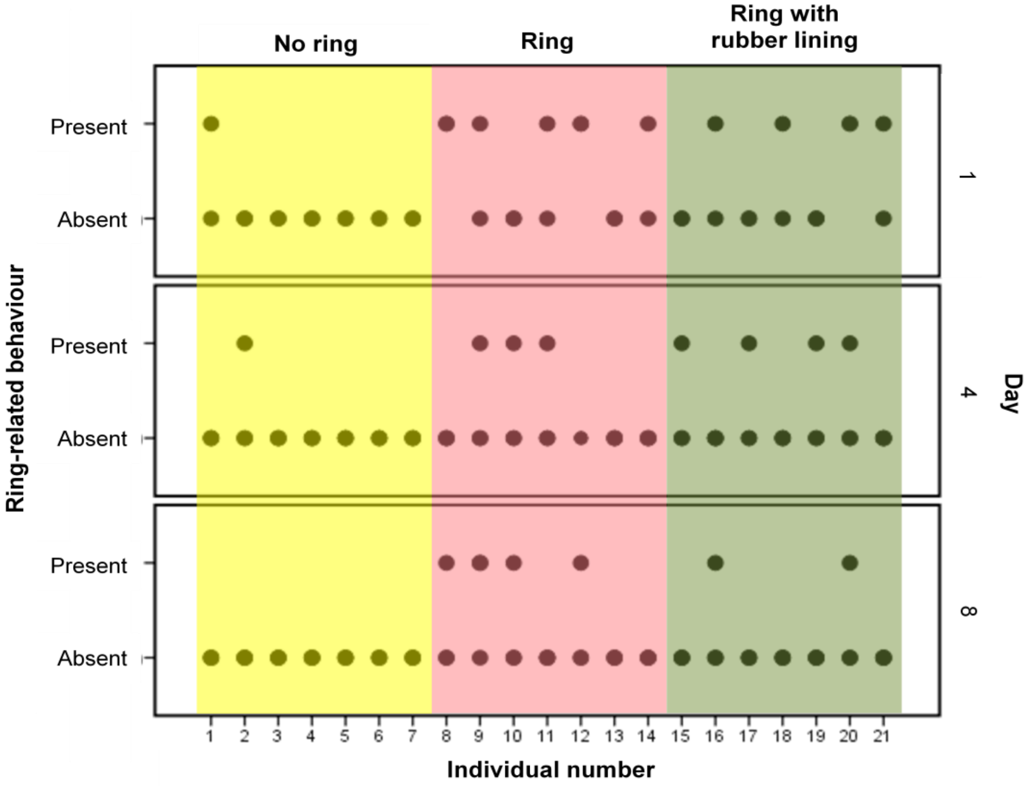


Figure 2.The presence or absence of ring-related behaviour per individual of each treatment group on each of the observational days.

Discussion/conclusion

Although differences in the presence of ring-related behaviour between the individuals with and without a dummy ring were observed, it could not be statistically tested. Moreover, the amount of ring-related behaviour was small. Although others suggested that rubber lining under the GPS ring can reduce the discomfort, we could not confirm this assumption in our observational study. However, it could be that the lack of improvement by the rubber lining is caused by the finding that the rubber lining was not exactly fitted on the leg of the pigeon and up- and downwards movements of the ring were still possible. It might be that with other rubber linings, that prevent movements, this measure is more effective. Whether this is the case and if this is a good mitigating measure, have to be further studied. In conclusion, wearing a GPS ring might cause some discomfort to the pigeon. However, the amount of ring-related behaviour is small. Together with the absence of abnormalities in the test flight, we conclude that the rings are not causing major abnormalities in the pigeons' behaviour and that GPS flights can be performed without serious welfare consequences for the pigeons. However, the behaviour of the pigeons, wearing a ring, need to be continually monitored and compared to pigeons without a ring to be able to intervene when negative changes in the behaviour occur.

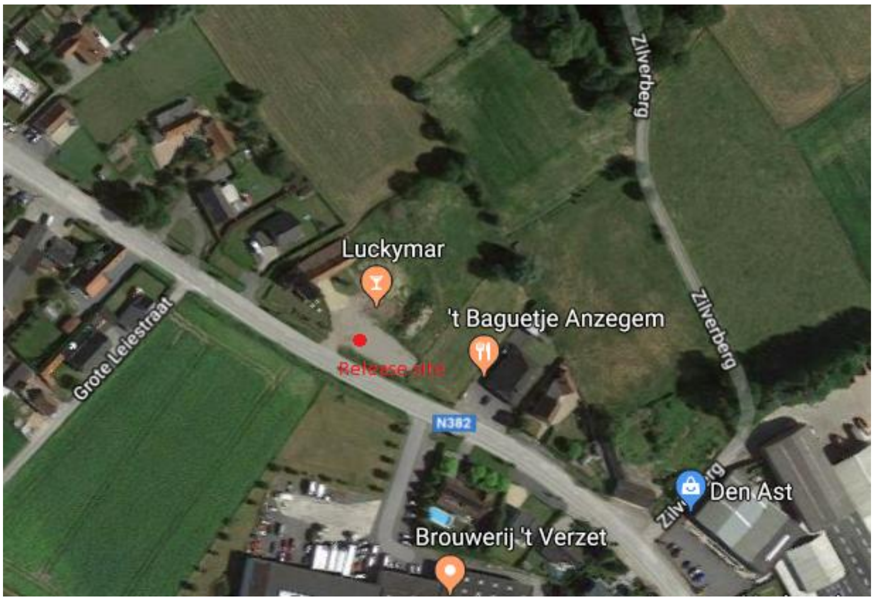
Appendix 8. Characteristics of the release sites of the GPS flights

Flight 1 – trajectory 1

Coordinates location (decimal degrees): 50.8550407, 3.4590569

Address: Grote Leiestraat 74-80, 8570 Anzegem, Belgium

Distance from loft (km): 118



Reference map: Google, 2017

Flight 2 – trajectory 2

Coordinates location (decimal degrees): 50.918028, 4.398612

Address: Albert I Laan, 1800 Vilvoorde, Belgium

Distance from loft (km): 75

Reference map: Google, 2017

Flight 3 – trajectory 2

Coordinates location (decimal degrees): 50.934997, 4.453398

Address: Houtemsesteenweg, 1800 Vilvoorde, Belgium

Distance from loft (km): 75

Reference map: Google, 2017

Flight 4 – trajectory 2

Coordinates location (decimal degrees): 50.918028, 4.398612

Address: Albert I Laan, 1800 Vilvoorde, Belgium

Distance from loft (km): 75

Reference map: Google, 2017

Flight 5 – trajectory 3

Coordinates location (decimal degrees): 51.309286, 4.555601

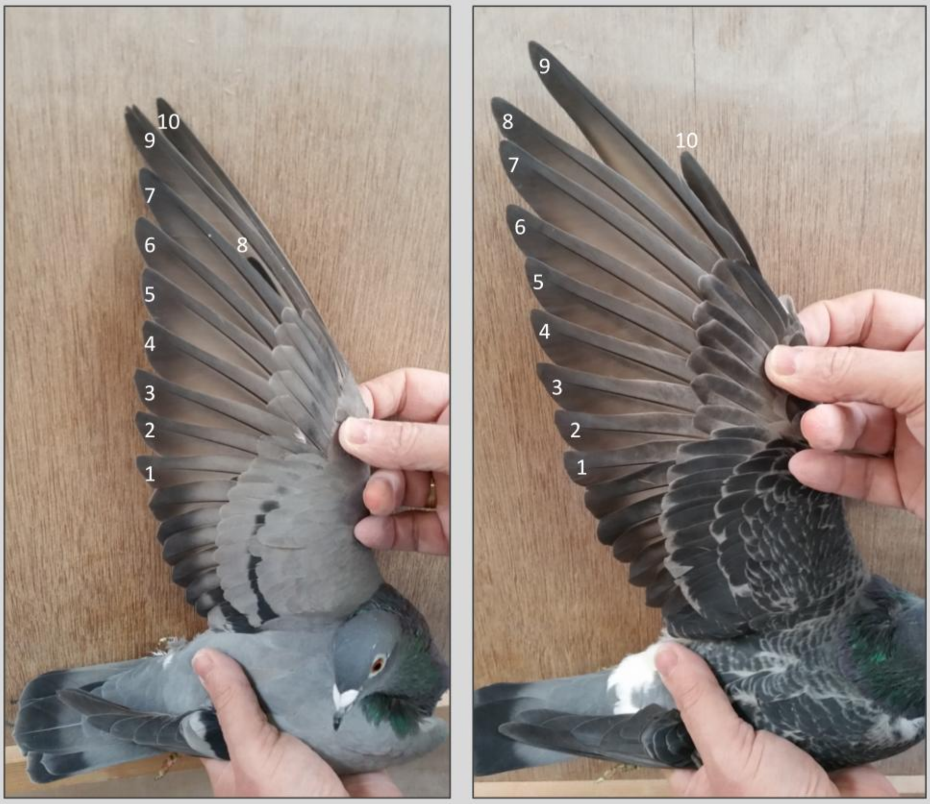
Address: 2930 Brasschaat, Belgium

Distance from lofts (km): 30

Reference map: Google, 2017

Appendix 9. Determination moulting status

Moulting status was recorded by determining the number of old primary feathers remaining. The figure in this appendix is showing an example of the moulting status of two individuals, one with 2 old primary feathers and one with none left.



2 old primary feathers remaining,
8th feather on 1/3.

0 old primary feathers remaining,
10th feather halfway.

Appendix 10. Accuracy tests

The level of accuracy of all the GPS tracking rings (Skyleader) was determined by executing multiple tests on location, height and speed. All tests were executed twice, before and after the flights. So, the stability of measurements over time could be determined. The procedure followed during the accuracy tests is described in detail in this appendix.

Set-up

Recording location

First, the accuracy of the recording of the location was tested by placing the GPS rings on a RDW registration point (a location for which the coordinates are officially fixed) for 30 minutes and comparing the recorded positions to the RDW registered location (DM 51.985796, 5.633538). Secondly, the accuracy of measurements was determined by comparing the measurements with those of an exact GPS device (DM 51.987780, 5.665950, RTK GNNS, Topcon Hiper V). In addition, I tested the maximum life span of the battery and the accuracy of data recording over a longer time span, by placing the GPS tracker rings on a fixed location for a minimum of 12 hours and comparing the results with the location measurements of a GPS device (Before: DM 51.609222, 5.148889, after: DM 51.848495, 4.889131, Garmin 60CSx and Garmin eTrex Legend HCx).

Recording height

I tested the accuracy of the height recordings by placing the GPS rings for 30 minutes on the outside area of the highest level of an apartment building and compared the results with the measurements of the height made by a GPS device (DM 51.983472, 5.664056, Garmin 60CSx and Garmin eTrex Legend HCx). This provides information on the accuracy of the height measurements on a fixed position. Additionally, the height measurements of the GPS tracking rings were compared with the measurements of a GPS logger during a flight of a glider (Sample frequency: 1Hz), to test the accuracy of the measurements during movement. Due to problems with the GPS logger of the glider, this accuracy measurement could only be executed completely before the flights.

Recording speed

The speed measurements were analysed by placing the GPS rings in a car. Several measurement at different speeds were made. The data of the GPS rings were compared to the speed indicated by a GPS navigation device (Garmin), after which the deviation was calculated. This measurement was only executed after the flights.

Data analyses

When data before and after flight were available, the test results were statistically analysed. For the life-span battery data, this was done by a paired sample t-test. For the accuracy tests, Wilcoxon signed rank tests were performed, as these data were not normally distributed. Before the height data were analysed, several unrealistic measurements were deleted. This was only the case in the test on the fixed location.

Results

Lifespan battery

No significant differences were detected between the total recorded time before (x̅ =615 minutes) and after (x̅ =515 minutes) the flights of (t=2.087, d.f.=5, p=0.091, Figure 1).

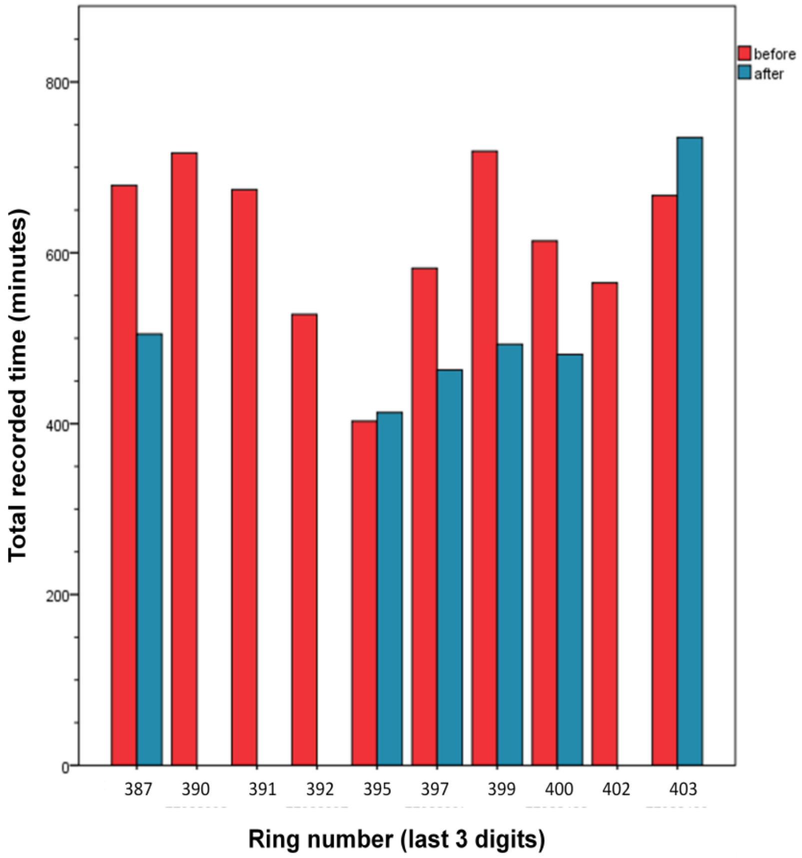


Figure 1. Total recorded time (in minutes) per ring, before and after the execution of the flights.

Location recording – long timespan

Deviation in latitude

The deviation in latitude recordings of our GPS rings from the recordings by a GPS device, was significantly higher before the flights (x̅ =417 metres) compared to after (x̅ =10 meters) (Z=-29.755, p<0.001, Figure 2).

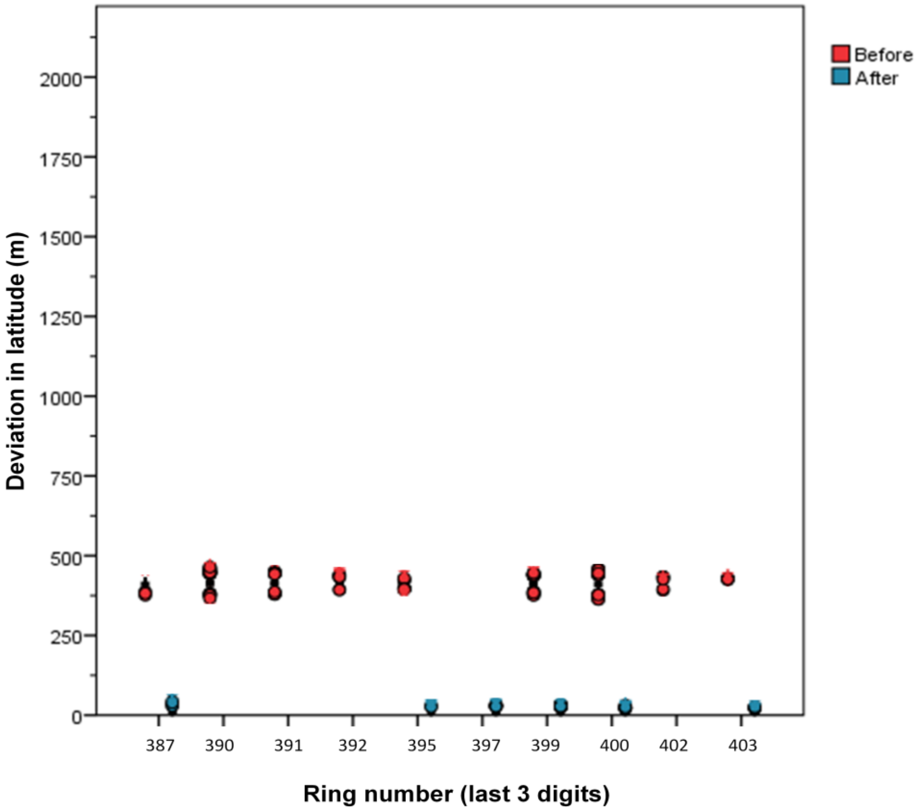


Figure 2. Deviation in latitude, before and after the flights, for each of the GPS rings, in meters relative to the recordings of a GPS device.

Deviation in longitude

A same pattern as with the latitude deviation was observed for the longitude deviation. The deviation in longitude recordings of our GPS ring from the recordings of a gps device, was significantly higher before (x̅ =432 meters) compared to after the flights (x̅ = 10 meters) (Z=-29.755, p<0.001, Figure 3)

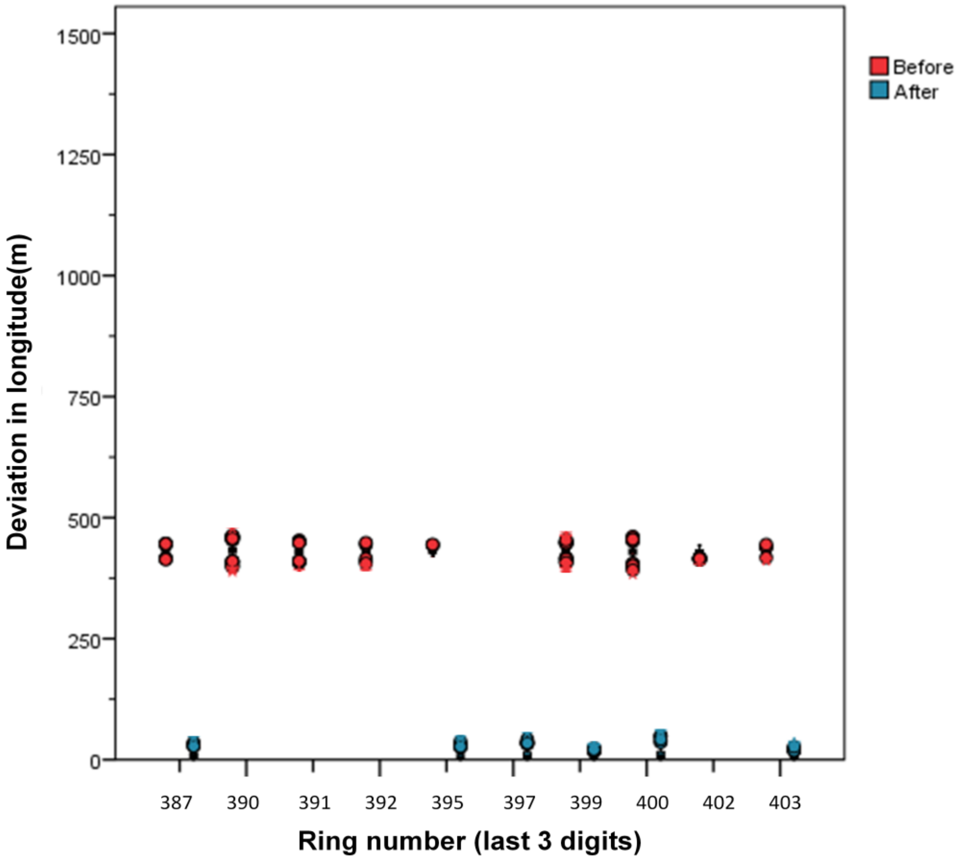


Figure 3. Deviation in longitude, before and after the flights for each of the GPS rings expressed in meters relative to the recordings of a GPS device.

The total deviation of the recorded locations differed also between the before and after flight measurements, in the ‘before test’ (x̅ =15, SD=22 meters), 95% of the recordings had less than 749 meters deviation and in the ‘after test’ (x̅ =678, SD=106 meters), 95% of the recordings had less than 38 meters deviation.

Location recording – RDW registration point

Deviation in latitude

There was no significant difference in latitude deviation from the RDW registration point, before ($\overline{x}$ =33 meters) or after the flights ($\overline{x}$ =36 meters) (Z=-1,535, P=0.125, Figure 4).

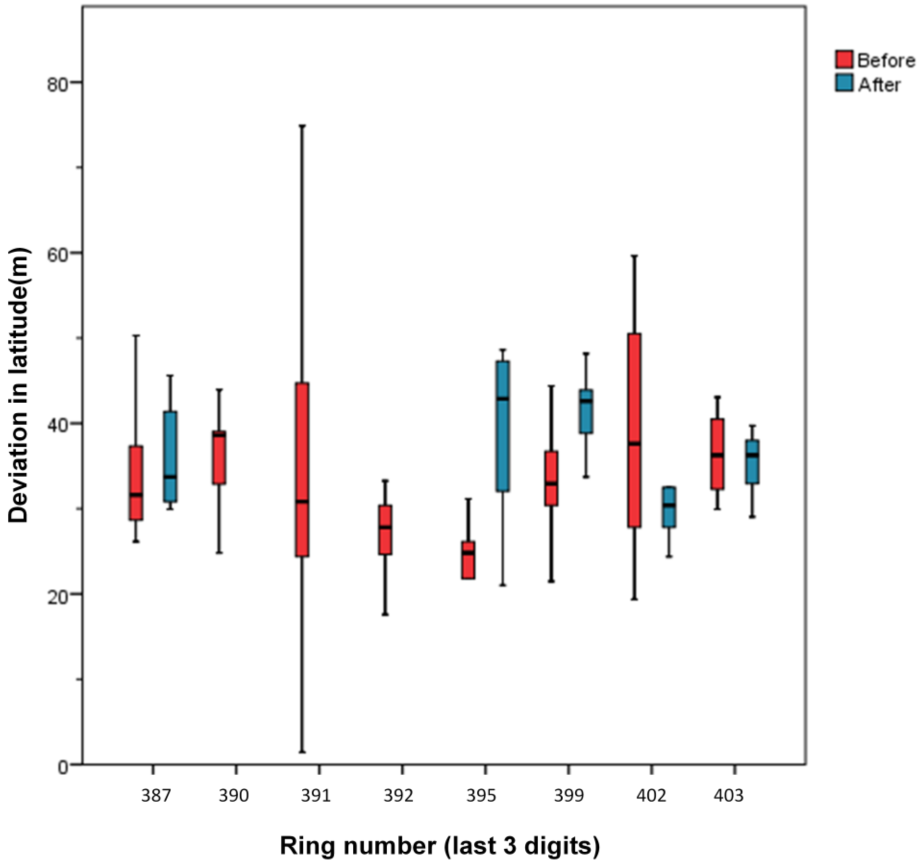


Figure 4. Deviation in latitude, before and after the flights, for each of the GPS rings, in meters relative to the RDW registration point.

Deviation in longitude

Longitude deviation from the RDW registration point was significantly higher in the before flight protocols test (x̅ =16 meters) compared to the after test (x̅ =12 meters) (Z=-2,393, p=0.017, Figure 5).

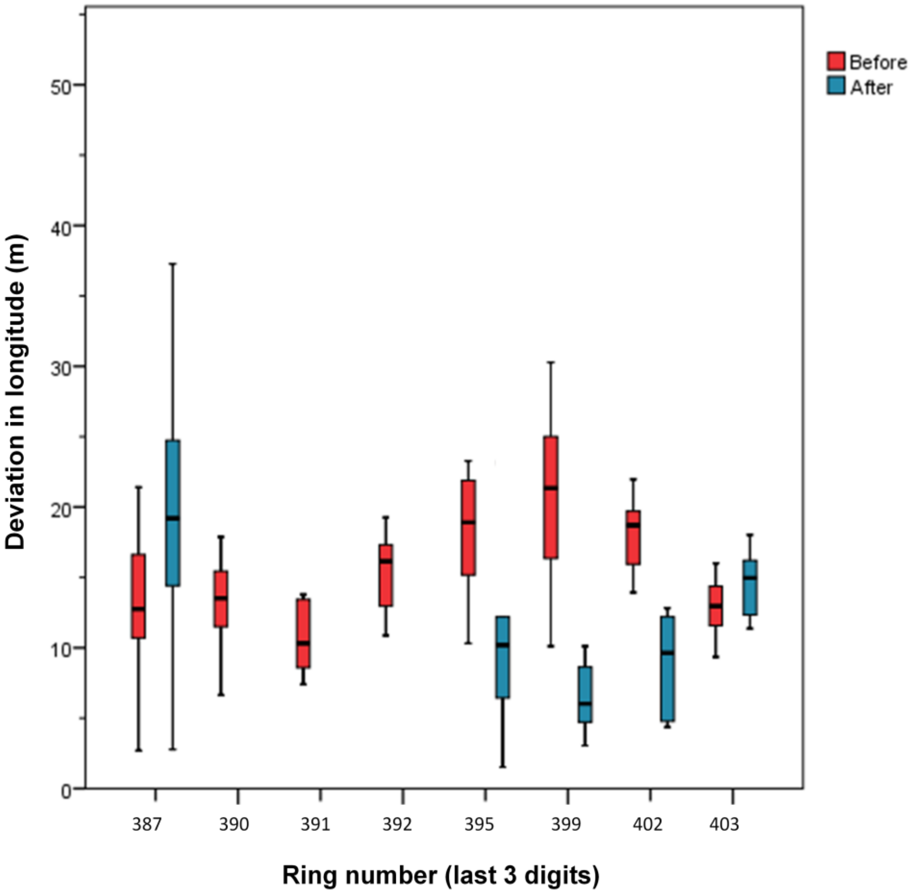


Figure 5. Deviation in longitude, before and after the flights, for each of the GPS rings, in meters relative to the RDW registration point.

The total deviation of the recorded locations did not differ that much between the before and after flight measurements, in the ‘before test’ (x̅ =37, SD=10 meters), 95% of the recordings had less than 50 meters deviation and in the ‘after test’ (x̅ =37, SD=11 meters), 95% of the recordings had less than 49 meters deviation.

Location recording – Exact device

Deviation in latitude

The deviation in latitude relative to the recordings of a exact GPS device, was varying between the different GPS rings. The GPS rings with the least variation were ring number 395 and 397 (Figure 6). The mean deviation in latitude was 13 meters.

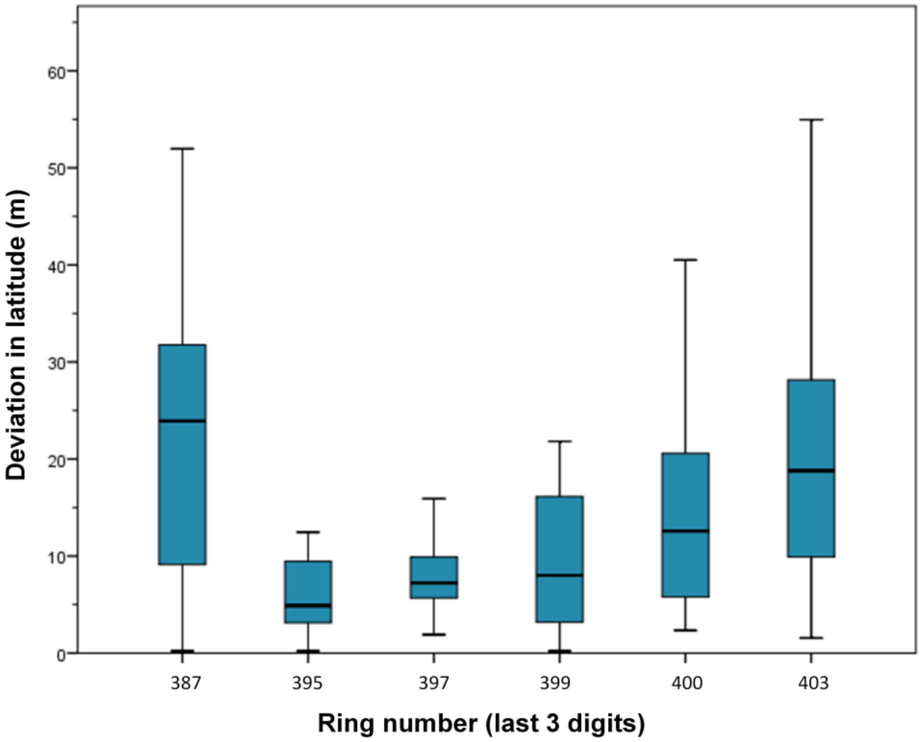


Figure 6. Deviation in latitude, after the flights, for each of the GPS rings, in meters relative to the recordings of an exact GPS device.

Deviation in longitude

In contrast to the deviation in latitude, the deviation in longitude relative to the recordings of an exact GPS device, did not differ that much between the different GPS rings (Figure 7). The mean deviation in longitude was 7 meters.

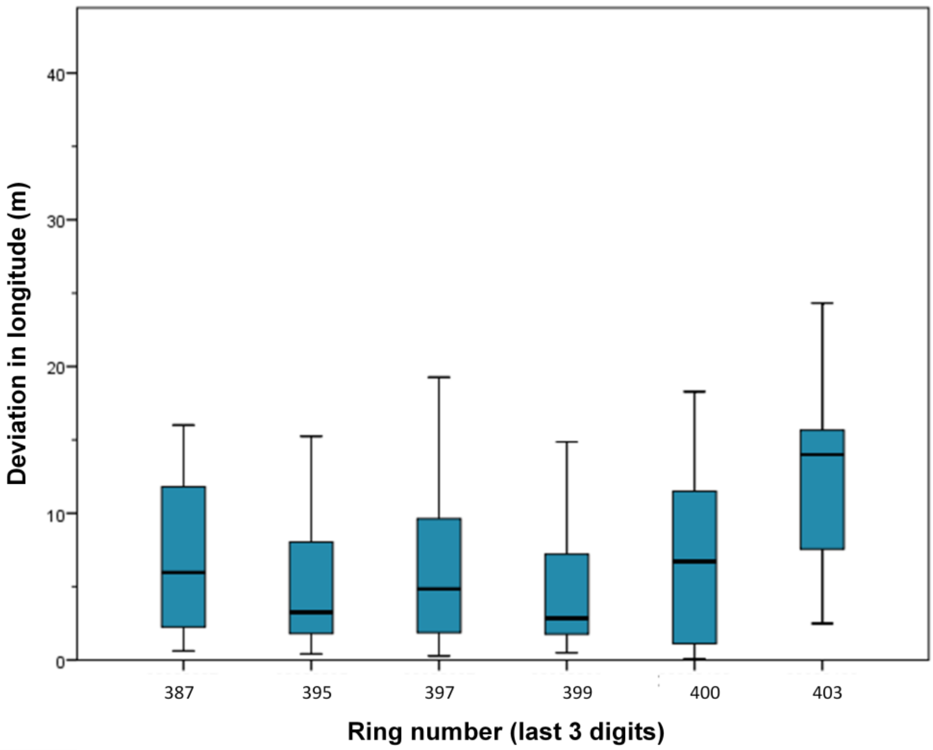


Figure 7. Deviation in longitude, after the flights, for each of the GPS rings in meters relative to the recordings of an exact GPS device.

95% of the recordings of the total deviation from the recorded location by the exact GPS device was within 40 meters ($\bar{x}$ =16, SD=12 meters).

Height – fixed location

There was quite some variation in the recorded heights between the GPS rings and over time (Figure 8). However, no significant differences were found between the before ($\bar{x}$ = 30 meter) and after ($\bar{x}$ = 25 meter) measurements of the height in comparison to the recordings of a GPS device (Z=-0.037, p=0.970, Figure 8).

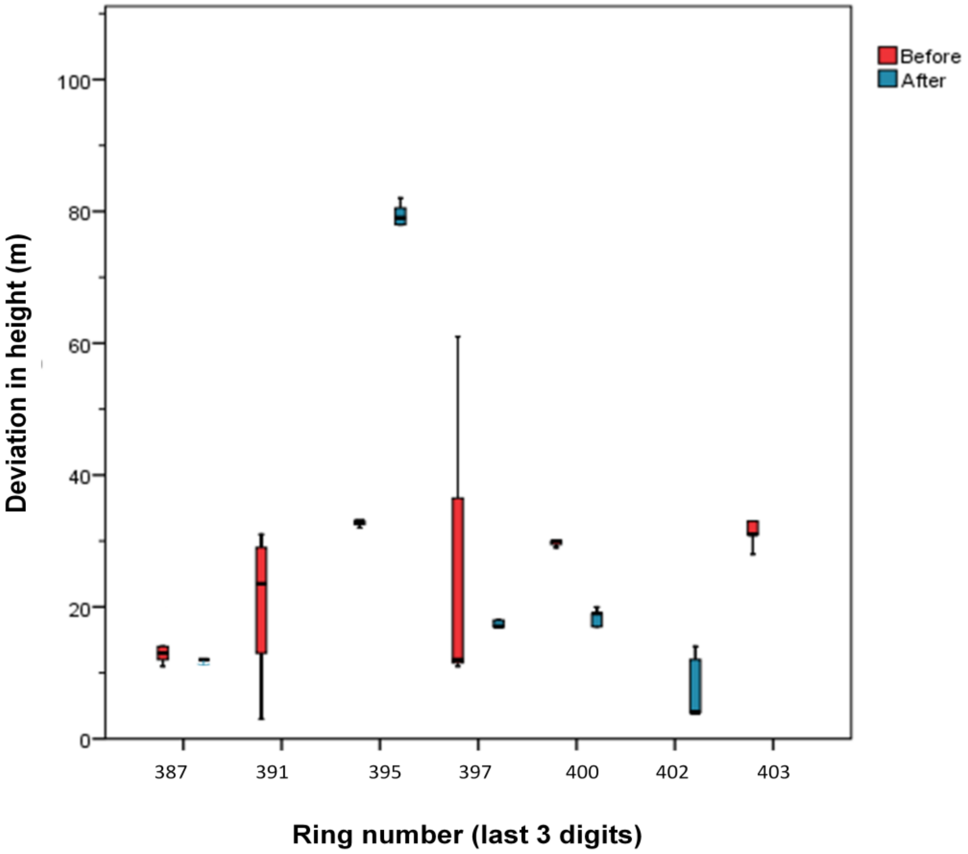


Figure 8. Deviation in height, before and after the flights, for each of the GPS rings, in meters relative to the recordings of a GPS device.

Height – Glider

Most of the GPS rings had quite some variation in the deviation in height recordings, except for three GPS rings (391, 395, 400), which had a very low variation in the deviation in height recordings and were quite exact in their height measurements (Figure 9). The mean deviation in height recordings for all GPS rings was 80 meters.

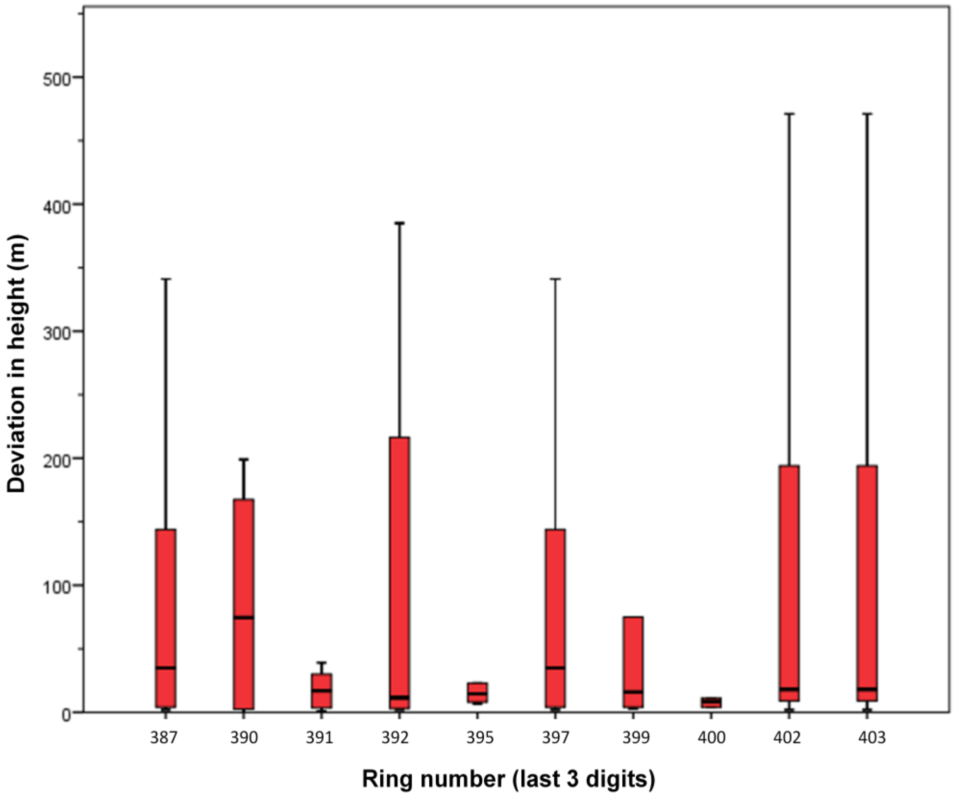


Figure 9. Deviation in height, before the flights, for each of the GPS rings, in meters relative to the recordings of a glider.

Speed

All GPS rings performed similar in the speed accuracy test (Figure 10). The mean deviation in speed recordings relative to that of navigation device was 16 m/s.

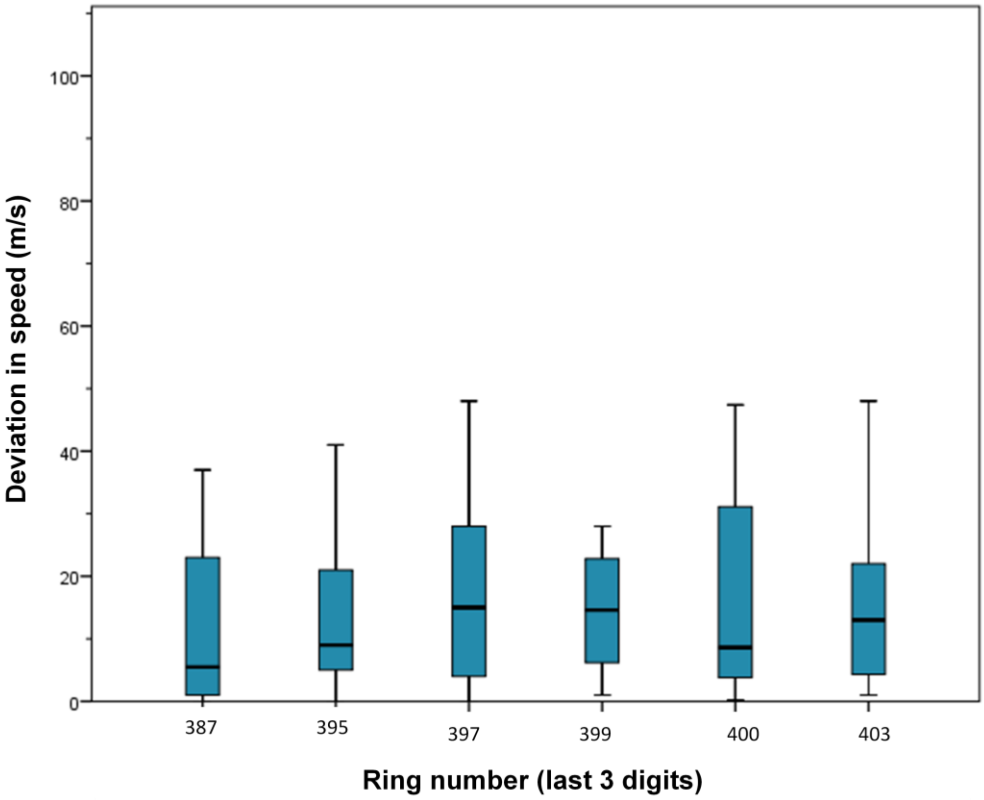


Figure 10. Deviation in speed, after the flights, for each of the GPS rings, in m/s relative to the recordings of a navigation device.

Discussion/conclusion

The GPS specifications of the de manufacturer of the GPS rings was indicating that the lifespan of the battery should be 12 hours. However, the test on data recording time was showing that the GPS rings were recording data for an average of 10 hours before the flights and an average of 8,5 hours after the flights. The decrease in recording time and the thereby lifespan of the battery, observed in most of the GPS rings, could be due to a degradation in the battery or other materials. However, over all rings, no significant difference was found between the before and after flight protocols measurements. The manufacturer did not made any claims on the accuracy of the GPS rings. When analysing the accuracy test results, it was noticed that in the fixed location test, the recordings of the ''Before'' test was significantly less accurate than the ''After'' test. This was not expected, but can be due to several factors, including blockage of the signal by buildings, the atmospheric conditions and the quality of the materials. The ''fixed location'' tests were executed in neighbourhoods, therefore the environment included several buildings. Both tests were performed on different locations. It could be that in the ''Before'' test, there was more blockage of the signal by buildings compared to after. In the test of the RDW registered location, also a less accurate before measurement was observed, this time only for the longitude. No clear cause for this could be found. In contrast, for the height recordings, no difference between before and after the flight protocols was found. The recorded accuracies of our GPS rings were in line with some other studies, except for the recordings in the first measurement on the fixed location. In all other tests, 95% of the recordings were within the range of 38-50 meters deviation. In comparison, Rose, Nagel, & Haag-Wackernagel (2005) found deviations of 25 meters for 81.8% of their recordings, and 100 meters deviation for 96.3% of the total recordings. Dussault, Courtois, Ouellet, Huot, & Courtois, (2001) found an accuracy of 75 meters for 95% of the recordings, after some corrections for bad satellite geometry. In contrast, Steiner et al. (2000) found a higher accuracy, 95% of their recordings were within 12 meters deviation of the real location. The devices in these studies are all designed for scientific use. In contrast, there is much less published on the accuracy of commercial GPS devices (Scullion, 2016). Testing this for the Photomate 887 Lite (TranSystem Inc., Taiwan), Scullion (2016) found an accuracy of 100% of their recordings within 10 meters of deviation. In contrast, the height measurements were less accurate. In my accuracy test, also the height measurements were in some cases less accurate (30-80 meters of deviation on average) and more variable. Scullion (2016) suggested that this is not unusual for GPS devices and is caused by the geometry of the satellite constellations and the shape of the earth. The weight of the device, tested by Scullion (2016) was 18 grams, in contrast to the 4 grams of our GPS rings. The development of GPS devices is often a compromise between weight and the amount and quality of data that can be recorded by the device. Lighter devices are more useful for tracking smaller birds. As a consequence their accuracy is often somewhat poorer in accuracy and temporal resolution compared to some heavier devices (Bouten, Baaij, Shamoun-Baranes, & Camphuysen, 2013). Therefore, when comparing the accuracy of the measurements by our GPS rings to what is commonly observed, the deviation is in the range that could be expected. Although the number of repeated measurements was low, the accuracy of our GPS rings seems to be good for the type device, except for some extreme deviations, likely due to an error in signal receiving. In flight, the pigeons will be mostly in open area, and so less blocking of the signal by buildings is expected. However, the possibility of an error through bad signal receiving needs to be taken into account when analysing the tracking data. Also the lifespan of the battery should be taken into account when using the GPS rings for experiments. For shorter flights, the battery expenditure is long enough. However, on longer flights, this would be insufficient.

Appendix 11. Normal distribution tests of the dummy arrival data

1. Test for equal variances

Levene's Test of Equality of Error Variances[a]

Dependent Variable: LogLog_arrival_time

F	df1	df2	Sig.
1.235	2	108	0.295

Tests the null hypothesis that the error variance of the dependent variable is equal across groups.

a. Design: Intercept + Flight_no

<u>H0: equality of variances, can not be rejected.</u>

2. Test if the residuals follow a normal distribution

Tests of Normality

	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	df	Sig.	Statistic	df	Sig.
Residual for log_logflight3	0.152	34	0.044	0.898	34	0.004
Residual for log_logflight2	0.183	34	0.005	0.914	34	0.011
Residual for log_logflight1	0.207	34	0.001	0.869	34	0.001

a. Lilliefors Significance Correction

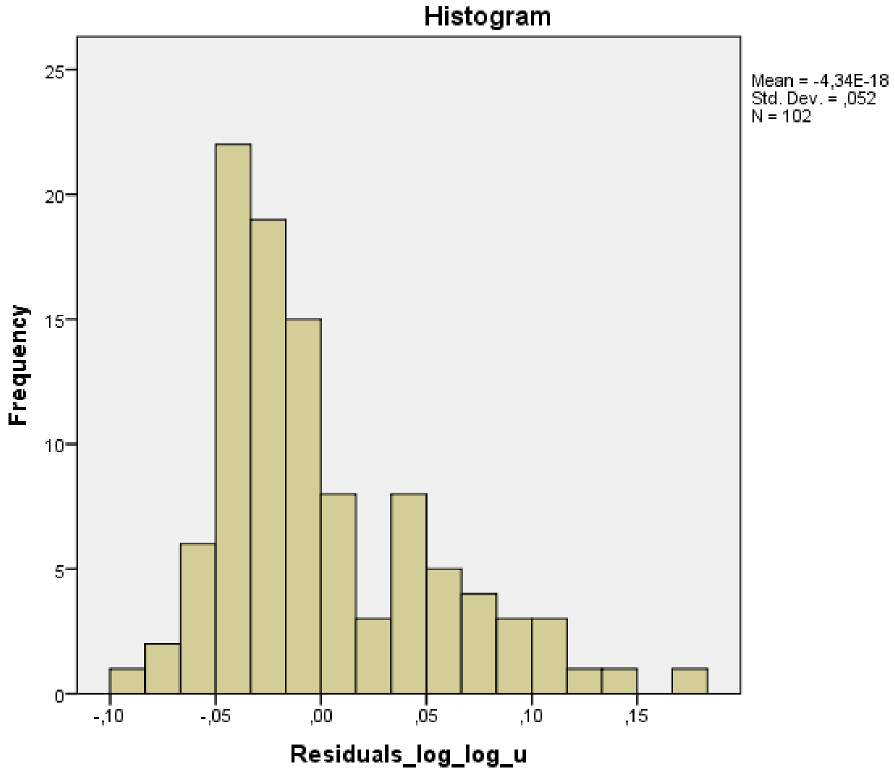
Tests of Normality

	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	df	Sig.	Statistic	df	Sig.
Residuals_u_log_log	0.152	102	0.000	0.915	102	0.000

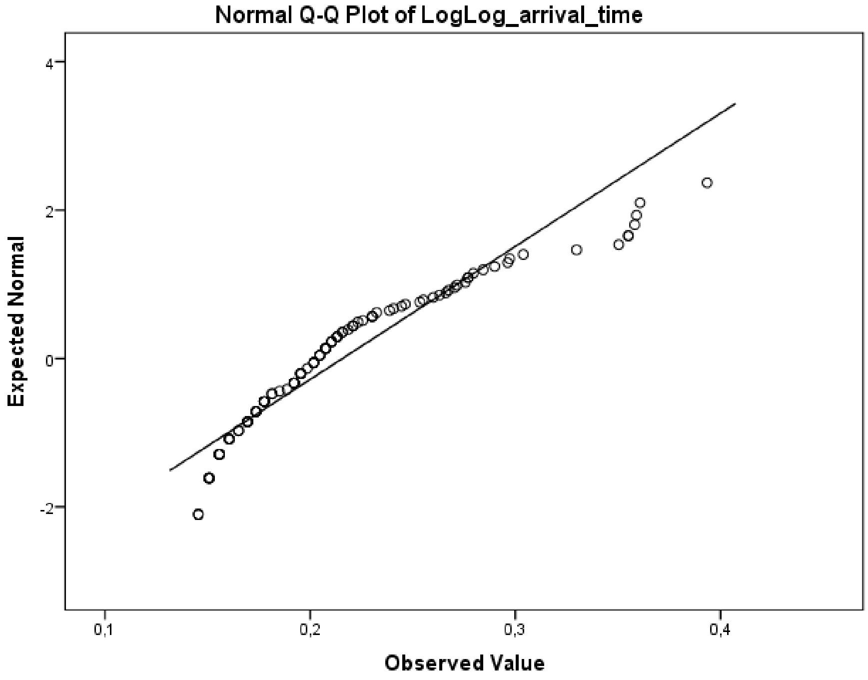
a. Lilliefors Significance Correction

<u>H0: residuals are normally distributed, is rejected.</u>

3. Plot of the residuals_log log transformed data



4. Q-Q Plot _log log transformed data



Conclusion: the arrival times in the dummy flights are not completely normally distributed, as the residuals are not. Moreover, there are some extreme tails in the data. Transformation did not resolve this.

Appendix 12. Normal distribution tests of the GPS arrival data

1. Test for equal variances

Levene's Test of Equality of Error Variances[a]

Dependent Variable: LogLog_arrival_time

F	df1	df2	Sig.
4.332	4	55	0.004

Tests the null hypothesis that the error variance of the dependent variable is equal across groups.

a. Design: Intercept + Flight_no

H0: equality of variances, is rejected.

2. Test if the residuals follow a normal distribution

Tests of Normality

		Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Flight_no	Statistic	df	Sig.	Statistic	df	Sig.
Residual for LogLog_arrival_time	1	0.293	14	0.002	0.800	14	0.005
	2	0.261	11	0.035	0.802	11	0.010
	3	0.218	11	0.152	0.927	11	0.383
	4	0.261	12	0.023	0.805	12	0.011
	5	0.289	12	0.007	0.745	12	0.002

a. Lilliefors Significance Correction

Tests of Normality

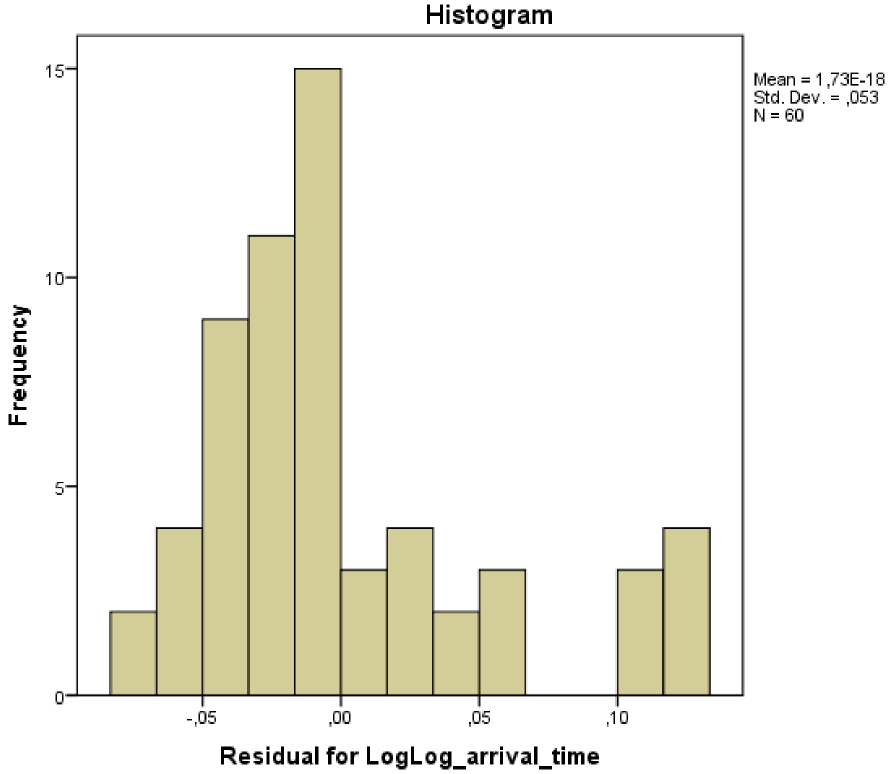
	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	df	Sig.	Statistic	df	Sig.
Residual for log_log_arrivalTime	0.096	60	0.200*	0.915	60	0.000

*. This is a lower bound of the true significance.

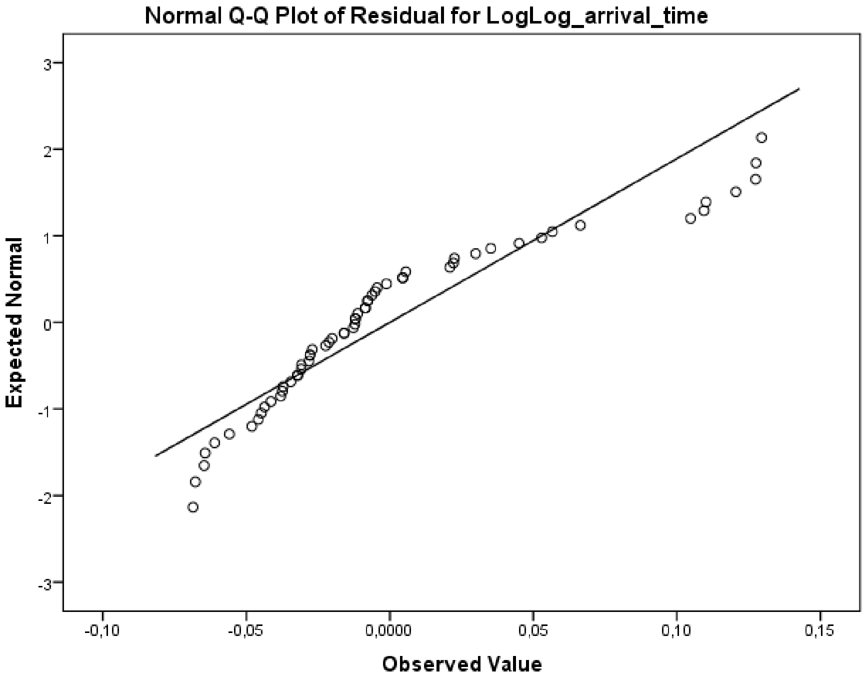
a. Lilliefors Significance Correction

H0: residuals are normally distributed, is rejected.

3. Plot of the residuals_log log transformed



4. QQ-Plot _log log transformed data



Conclusion: the arrival times in the GPS flights are not completely normally distributed, as the residuals are not, and the Levene test was rejected. Moreover, there are some extreme tails in the data. Transformation did not resolve this.

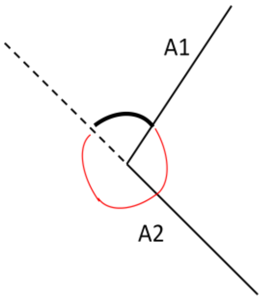
Appendix 13. Calculation turning angles

The angles of the line segments between the fixes were calculated using the python code in the field calculator in ArcGis (v. 10.5.1). The following script was used for this:

```
# Pre-Loci Script Code
import math
def GetGeographicalDegrees(shape):
  radian = math.atan2(shape.lastpoint.y - shape.firstpoint.y,
                    shape.lastpoint.x - shape.firstpoint.x)
  radian = radian - (math.pi /2 ) # turn minus 90°
  if (radian > 0):
    degrees = 360 - ( radian  *  360) / ( 2 * math.pi  )
  else:
    degrees = 360 - ((2* math.pi + radian  ) * 360) / ( 2 * math.pi  )
  return degrees

# angle =
GetGeographicalDegrees( !SHAPE! )
```

Next, the angles were transformed from a 0 – 360 degrees range to -180 – 0 – 180 range with the following formula in Excel (2007):
=IF(ANGLE>180;ANGLE-360;ANGLE)

Then, the turning angles were calculated by subtracting the angle of one line from the previous one. As the previous calculation can yield the wrong difference (red circle in figure underneath), thereby result in higher turning angles than 180 degrees or lower than -180 degrees, another if function was needed:
=IF(ANGLE<-180;ANGLE+360;IF(ANGLE>180;ANGLE-360;IF(AND(ANGLE>-180;ANGLE<180);ANGLE)))



Thereafter, the turning angles were transformed in absolute values.

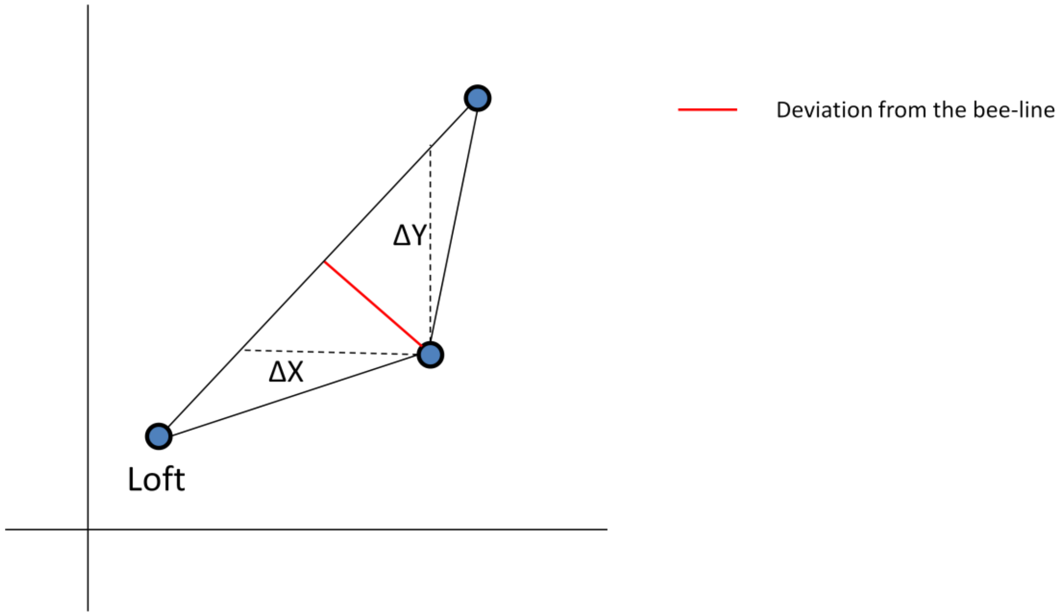
Appendix 14. Calculation deviation bee-line

The deviation from the moving bee-line was calculated by use of angle addition formulas (described underneath) in R statitiscs (v. 3.4.1).

```
#  Calculate UTC xy of loft
loft_xy = LonLatToUTM(lon = 4.732278, lat = 51.557139, zone = 31)

# Calculate UTC xy of all coordinates
xy = LonLatToUTM(lon = latlon$Longitude, lat = latlon$Latitude, zone = 31)
allcoordinates = cbind(latlon,xy)

# Calculate distance to loft
allcoordinates$distance_loft = sqrt((allcoordinates$x - loft_xy$x)^2 + (allcoordinates$y - loft_xy$y)^2)

# Determine line function
allcoordinates$deltax_loft = loft_xy$x - allcoordinates$x
allcoordinates$deltay_loft = loft_xy$y - allcoordinates$y
allcoordinates$a = allcoordinates$deltay_loft / allcoordinates$deltax_loft
allcoordinates$b = loft_xy$y - (loft_xy$x * allcoordinates$a)
allcoordinates$a_shift = c(NA,allcoordinates$a[1:(nrow(allcoordinates)-1)])
allcoordinates$b_shift = c(NA,allcoordinates$b[1:(nrow(allcoordinates)-1)])
```

(additionally the first row of each individual of each flight is deleted, as first fix has no deviation value).

```
# Calculate deviation from the bee-line
allcoordinates$deltax_moving_beeline =
  ((allcoordinates$y - allcoordinates$b_shift)/allcoordinates$a_shift) - allcoordinates$x
allcoordinates$distance_moving_beeline = sin(atan(allcoordinates$a)) *
allcoordinates$deltax_moving_beeline
```



Appendix 15. Landscape types of the worldwide land cover dataset

For the landscape analysis landscape data were used of the worldwide land cover dataset (Climate Change Initiative, 2015). To facilitate the analysis of the data, the land cover types were reclassified as indicated in the table underneath.

Number	Description landscape type	Reclassified - type
10	Cropland, rainfed	1
11	Herbaceous cover	1
12	Tree or shrub cover	1
20	Cropland, irrigated or post-flooding	1
30	Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	2
40	Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)	2
50	Tree cover, broadleaved, evergreen, closed to open (>15%)	3
60	Tree cover, broadleaved, deciduous, closed to open (>15%)	3
61	Tree cover, broadleaved, deciduous, closed (>40%)	3
62	Tree cover, broadleaved, deciduous, open (15-40%)	3
70	Tree cover, needleleaved, evergreen, closed to open (>15%)	3
71	Tree cover, needleleaved, evergreen, closed (>40%)	3
72	Tree cover, needleleaved, evergreen, open (15-40%)	3
80	Tree cover, needleleaved, deciduous, closed to open (>15%)	3
81	Tree cover, needleleaved, deciduous, closed (>40%)	3
82	Tree cover, needleleaved, deciduous, open (15-40%)	3
90	Tree cover, mixed leaf type (broadleaved and needleleaved)	3
100	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	2
110	Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	2
120	Shrubland	1
121	Shrubland evergreen	1
122	Shrubland deciduous	1
130	Grassland	1
140	Lichens and mosses	1
150	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	4
151	Sparse tree (<15%)	4
152	Sparse shrub (<15%)	4
153	Sparse herbaceous cover (<15%)	4
160	Tree cover, flooded, fresh or brakish water	3
170	Tree cover, flooded, saline water	3
180	Shrub or herbaceous cover, flooded, fresh/saline/brakish water	1
190	Urban areas	5
200	Bare areas	4
201	Consolidated bare areas	4
202	Unconsolidated bare areas	4

Number	Description landscape type	Reclassified - type
210	Water bodies	6
220	Permanent snow and ice	Not included anymore as this type is not occurring in our trajectories.

Appendix 16. Number of recorded stops in the GPS flights

The analyses of the recorded tracks of the GPS flights were performed without the stops. Stops were defined as the fixes at which a speed lower than 3 m/s was recorded. In figure 1 of this appendix the number of stops per flight is presented.

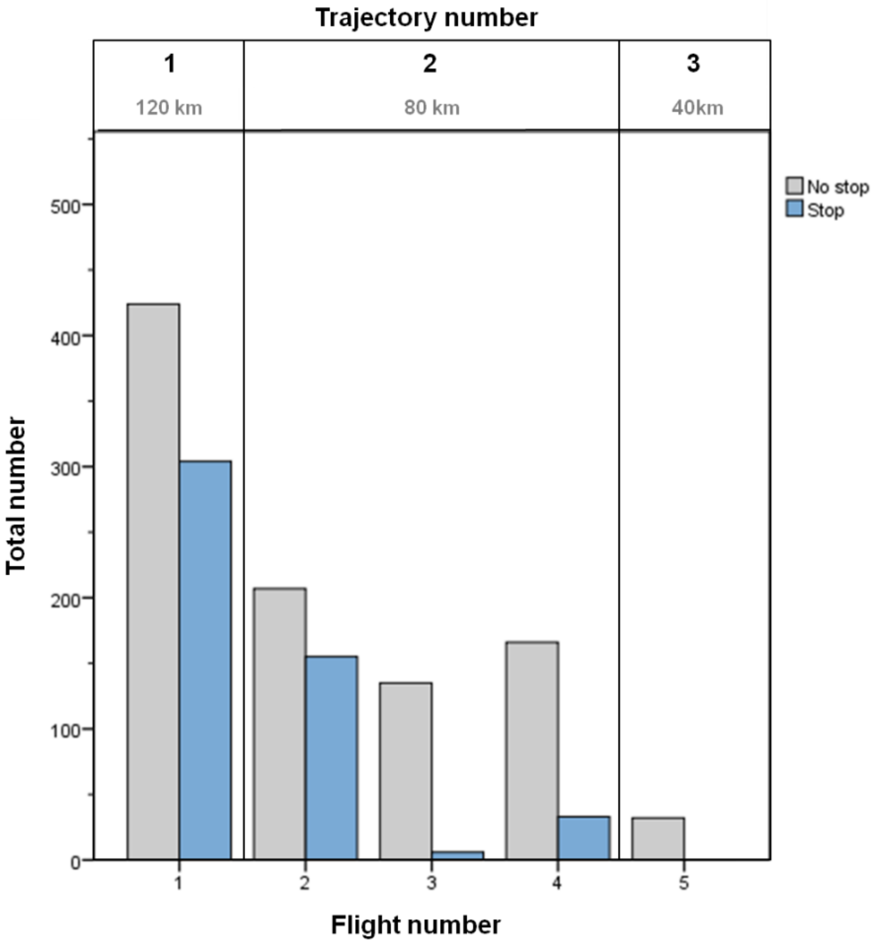


Figure 1. The number of fixes defined as stops (blue bars) and no stops (grey bars) per flight on the three trajectories.

Appendix 17. Excluded fixes from the statistical models

Flight number	Individual number	Fix number
1	**2**	*No records*
	4	**1,2,72-74,76-141**
	6	**1,2,37-40,46-51,58,59,61-82,84-143**
	8	**1-5,16,17,22,23,25,26,30,35,36,38-40,44,45,62,63,87,89-99**
	10	**1,2,70-152**
	12	*No records*
	14	*No records*
	16	**1-8,57,58,86-126**
	18	**1-9**
	20	**1-6,53,54**
2	**2**	*No records*
	4	
	10	**1-3,6,38-43,55-59,61,62-142**
	16	**1-11,35**
	18	**1-4,56-72,77-121**
	20	**1-2,55**
3	**2**	**1-3,14-19,42-44**
	4	*No records*
	10	**1-3,4**
	16	**1-4,31**
	18	**1-5,32,33**
	20	**1-6,31,32**
4	**2**	**1-6,10-20,22,29,32-38,42,43-48,87,88**
	4	**1-10, 31,32**
	10	**1-3, 23**
	16	**1-9,35**
	18	**1-3, 19,27,38-41,44,59,60**
	20	*No records*
5	**2**	**1-6,17,18**
	4	**1,8-10**
	10	**1,2,12,13**
	16	*All records excluded*
	18	**1-3,11,12**
	20	*No records*

Unrealistic speed or height measurement
Release site
Loft site
Stop

Incorrect measurements of flight speed and height sometimes coincided with the stops. In that case the reason of exclusion is indicated as stop in the table above.

Appendix 18. Results of efficiency index

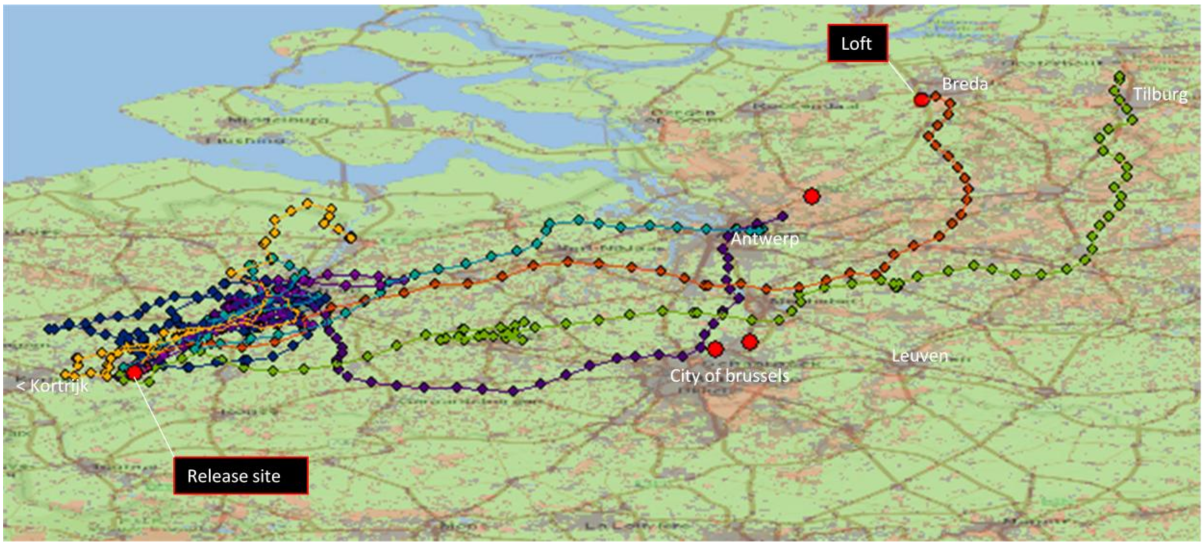
The efficiency index was analysed descriptively. Mean and standard deviation values for each of the GPS flights and for each of the trajectories, were calculated. The results of these calculations are presented in the graphs underneath.

Flight_number	Mean	N	Std. Deviation
1	0.72668	1	.
2	0.67014	2	0.285238
3	0.82443	3	0.030332
4	0.77925	5	0.167736
5	0.95902	3	0.025368
Total	0.80811	14	0.155667

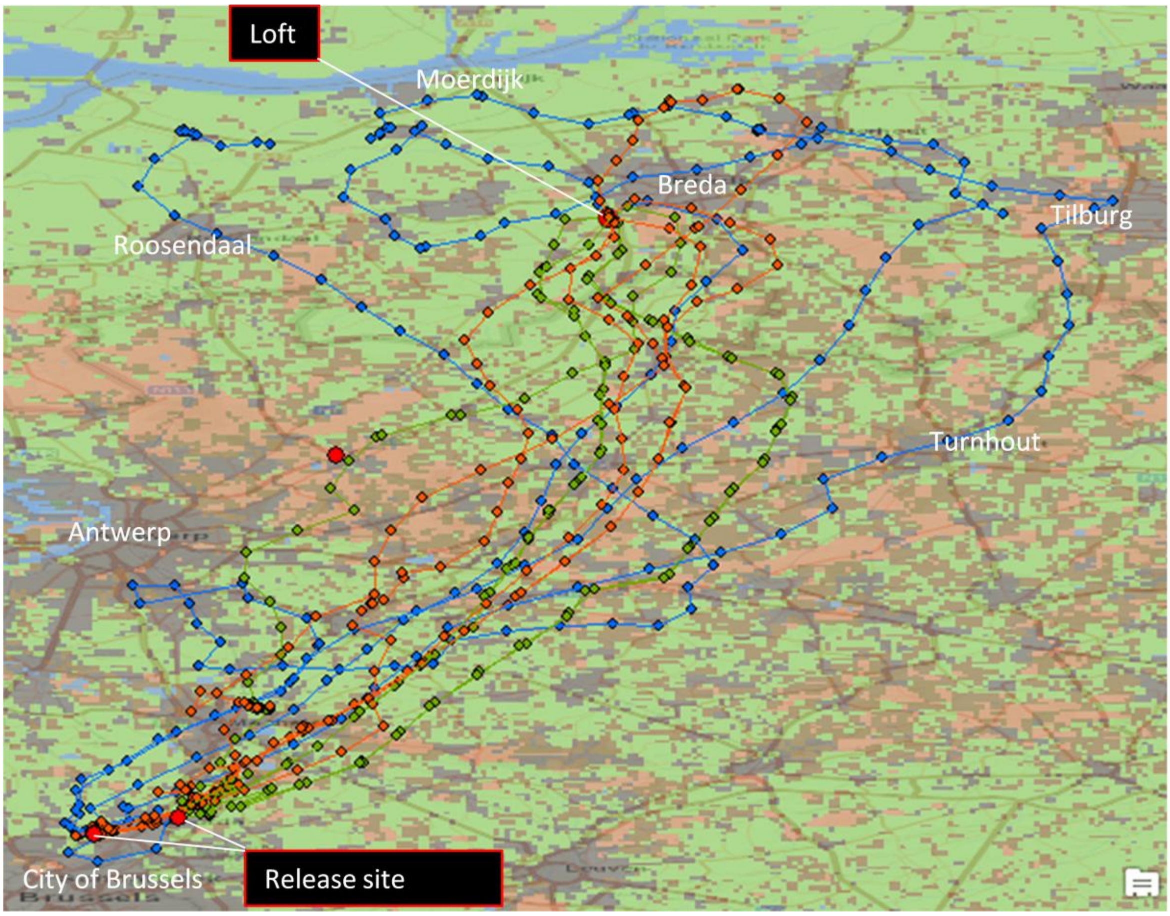
Trajectory	Mean	N	Std. Deviation
1	0.72668	1	.
2	0.77098	10	0.158112
3	0.95902	3	0.025368
Total	0.80811	14	0.155667

Appendix 19. Tracked flight paths in the GPS flights

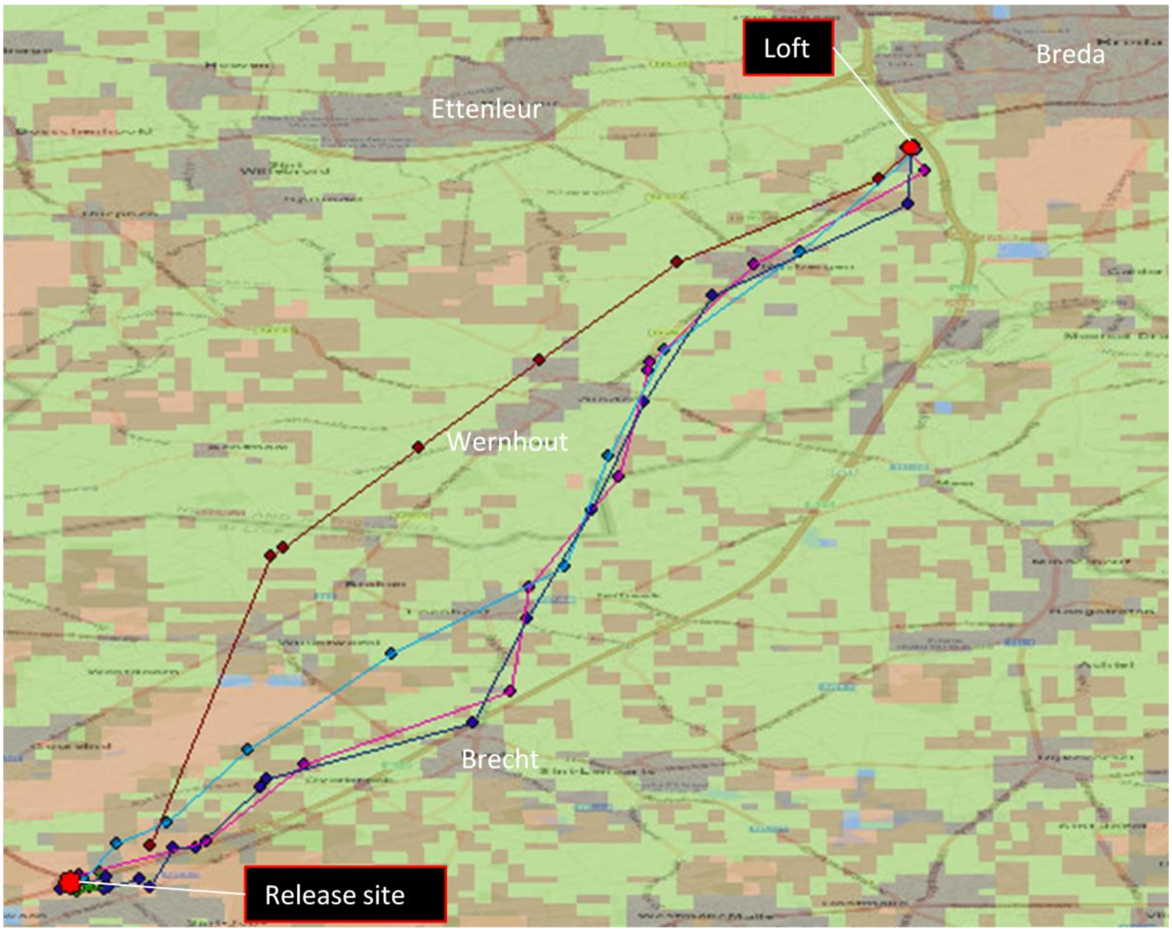
Traject 1



Traject 2:

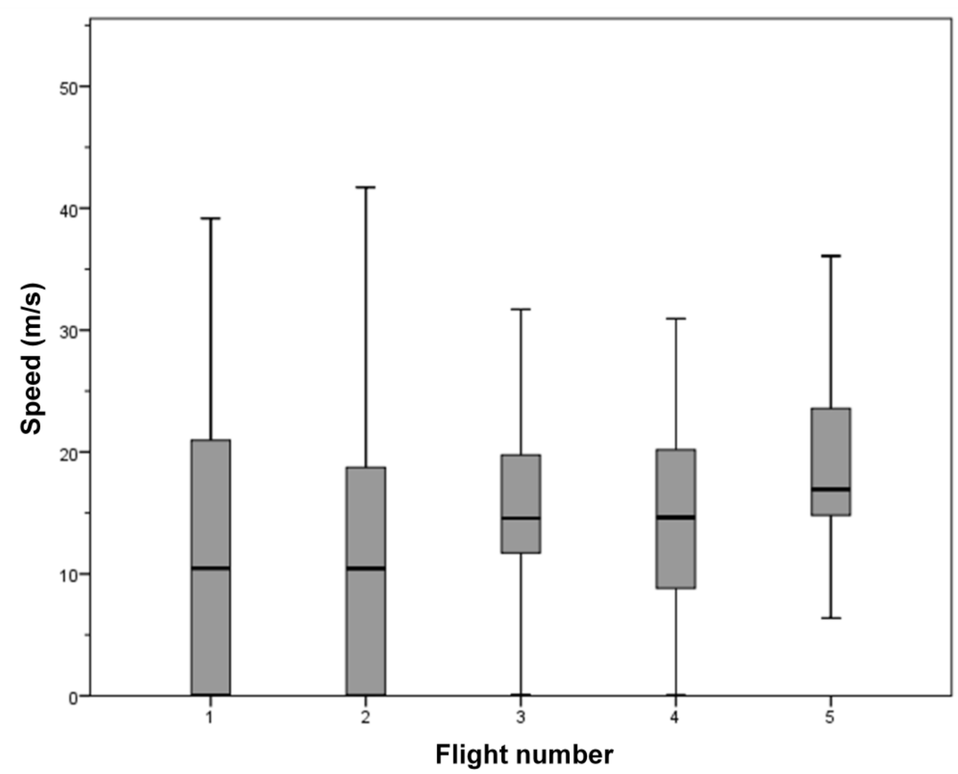


Traject 3:

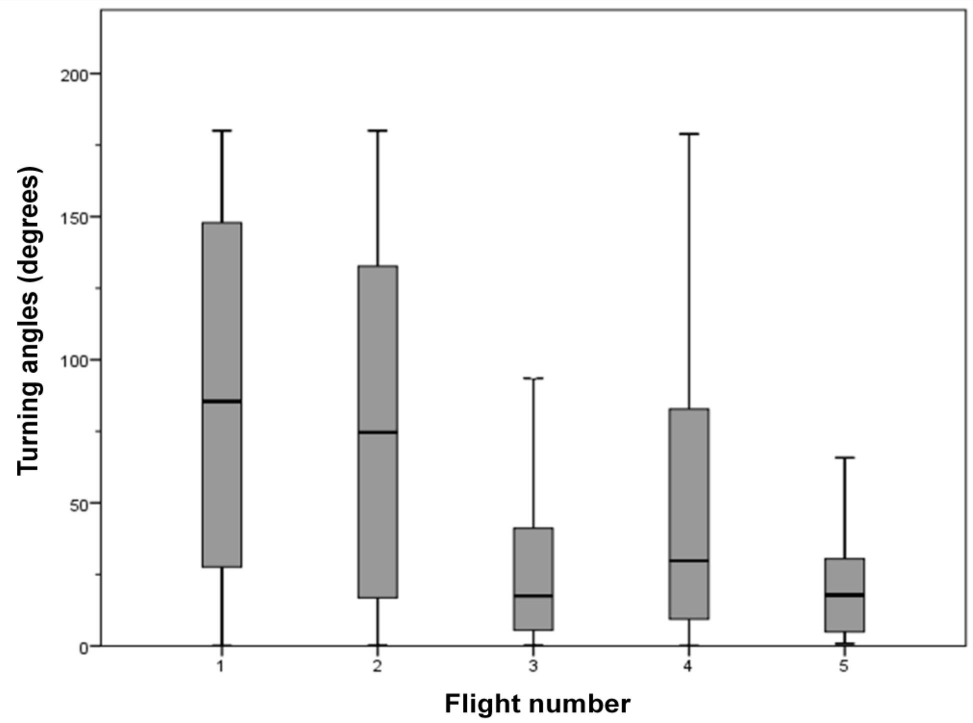


Appendix 20. Step characteristics per GPS flight

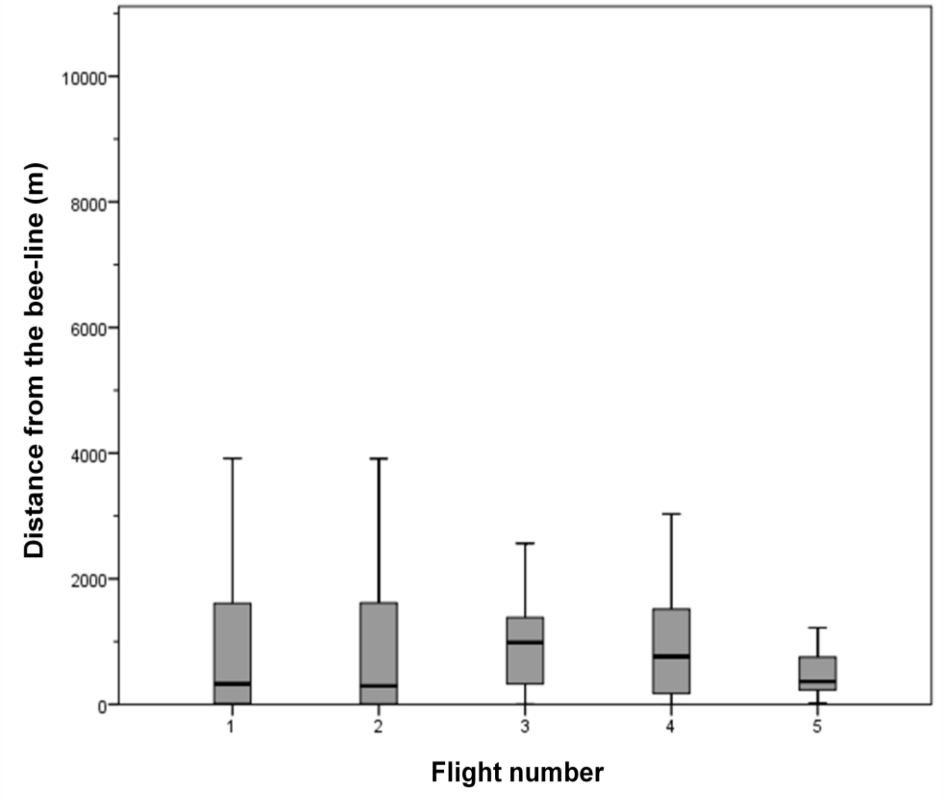
Speed:



Turning angle:



Deviation from the bee-line:



Height: