University of Zurich^{UZH}

The Alps – A real Barrier for Bird Migration?

GEO 511 Master's Thesis

Author
Simon Hirschhofer
13-916-499

Supervised by
Dr. Peter Ranacher
Dr. Felix Liechti (felix.liechti@vogelwarte.ch)
Dr. Baptiste Schmid (baptiste.schmid@vogelwarte.ch)

Faculty representative
Prof. Dr. Robert Weibel

30.09.2021
Department of Geography, University of Zurich

GEO 511 Master's Thesis

The Alps – A Real Barrier for Bird Migration?

Author

Simon Jonathan Hirschhofer

13-916-499

Supervised by

Dr. Peter Ranacher	University of Zurich, Department of Geography
Prof. Dr. Robert Weibel	University of Zurich, Department of Geography
Dr. Felix Liechti	Swiss Ornithological Institute
Dr. Baptiste Schmid	Swiss Ornithological Institute

30.09.2021

Department of Geography, University of Zurich

Content

Abstract

Migratory birds are increasingly threatened by human influences. Efficient conservation measures require that we know how birds react to topography and how interactions of topography and meteorologic conditions influence broad front migration. I used radar data of birds from three sites to study how the Alps influence migratory birds. From the tree sites, one is in the Swiss lowlands in Sempach, the other two are in two Alpine valleys, the Urserental and the upper Inntal. My analysis suggests that birds strongly orient themselves on these Alpine valleys when crossing the mountains. This is indicated by a high degree or alignment of flight directions at the Alpine sites, while flight directions at the lowland site were much more dispersed and differed between night and day. I further found significant differences in the site-specific expected bird volumes over the course of the year. The Alpine sites showed high bird activity during spring migration compared to the lowland site. During autumn, bird volumes were similarly high at all three sites. This suggests that birds prefer different flyways in spring than in autumn and thus, adjust their routes to the topography of the Alps. Third, I found that the correlation of bird volumes between the sites is higher in spring that during autumn. Previous work on the correlation of bird volumes in the Swiss lowland found a higher connectivity during autumn migration. These differences highlight, that birds during autumn migration majorly fly towards the south-west, rather than crossing the Alps, but that in spring, many birds that approach the mountain chain from northern Italy cross the Alps using Alpine valleys as passages. These results highlight the importance of Alpine passes and Alpine valleys to migratory birds. The results of this study recommend a special consideration of these migratory bottlenecks in future planning of bird conservation.

1 Introduction

1.1 Why do Birds migrate?

Each year, millions of migratory birds travel from their European breeding grounds southwards to spend the winter months in a warmer and nutritionally richer environment (Hahn, Bauer and Liechti, 2009). Migration in birds is assumed to have developed as a result of competition over resources in highly seasonal habitats to increase an individual's probability of survival during the non-breeding season (Salewski and Bruderer, 2007). This is confirmed by a study which phylogenetically examined the way of life of some migratory bird species. As a result, species which increasingly eat fruits and berries are also more likely to be migratory birds, with an exclusively insect-based diet increasingly prevailing among long-distance migrants (Boyle and Conway, 2007). This means that the migratory behaviour has its origin in the resource dependence of the ancestors of today's migratory birds: the narrower the ecological niche that a species occupies, the higher the probability that it is also a migratory species (Brändle *et al.*, 2002).

1.2 Migratory Birds are Predictable

Rather than following specific routes, inland bird migration happens on a broad front. While most migrating bird species normally are diurnal, they become seasonally nocturnal (Martin, 1990; Åkesson and Helm, 2020) so that the largest proportion of bird migration happens by night (Harper, 1958). Migratory passerines have been found to be able to suddenly switch their activity pattern from diurnal to nocturnal, even during the breeding-season (Mukhin, Grinkevich and Helm, 2009). This sudden adaptation to a new biorhythm was also found in passerines departing to the first migratory flight stage (Zúñiga *et al.*, 2016).

Bird migration is principally driven by two groups of drivers. One is the intrinsic programming of a bird, the other one is its environment, especially the current weather. The intrinsic component is depending on the time of the year. In caged migratory birds, the phenomenon of nocturnal activity in otherwise diurnal species was defined as "Zugunruhe" and is likely influenced by the photoperiod (Yokoyama and Farner, 1978). First year migratory birds strongly depend on this intrinsic programming to initiate migration and find the way to their overwintering habitat (Åkesson and Helm, 2020). This initial genetic program that triggers migratory behaviour and serves as a guide for novice migrants gets completed by experience in older birds, thanks to remarkable cognitive abilities (Mettke-Hofmann and Gwinner, 2003). But the decision for departure, and during migration the choice for a route are not only dependent on endogenous programming and fixed routines. Besides static factors, the highly dynamic current meteorological situation has a strong influence on decision making before the departure during the first flight and also after stopover during migration (Åkesson and Hedenström, 2000).

Wind, rain, fog and clouds affect a bird's flight performance and orientation abilities. Tendentially, birds await situations with a high visibility, supportive winds and little or no rain. Reed Warblers, for example, a nocturnal passerine migrant, were found to have a strong dislike for clouds, most likely because they significantly hinder the visibility of the stars for orientation (Åkesson *et al.*, 2001). Several passerine species have shown to predominantly fly during nights where they experience tailwinds, which would allow them to save energy during slight stages (Åkesson and Hedenström, 2000). The energy expenditure because of wind even influences the survival rate of migrants (Erni, Liechti and Bruderer, 2005) and birds on a migratory stage adapt their flight altitude to exploit the best possible wind streams (Dokter *et al.*, 2013). The selection of profitable wind streams can also be responsible for extraordinarily high flight altitudes (Bruderer and Peter, 2017), especially, when long-distance flights lie ahead, or in front of an ecological barrier (Bruderer, Peter and Korner-Nievergelt, 2018). Rain is a third and very important factor: during rainfall, visibility and orientation is reduced, flying is more difficult and the energy costs of a bird's thermoregulation is increased due to the constant contact with cool or cold water (Erni et al., 2002).

In contrast, there was also evidence that the influence of these weather variables is not that strong, at least for some species (Richardson, 1978). The largest numbers of birds can be observed after a period of unfavourable weather that causes "Zugstau" – birds awaiting a better situation for migration which then turns into a favourable synoptic condition (Kestenholz *et al.*, 2009; Nilsson *et al.*, 2019). By using the European weather radar network during the autumn migration season, Nilsson et al. were able to observe how after a period of headwind, a sudden change in wind direction lured masses of birds into the air: a strong northeast wind moved like a wave over Europe and its arrival was congruent with very high migration intensities. While the tailwind situation was persistent for a longer period, bird volumes locally dropped just after two days, and places with high bird numbers shifted towards the south-west (Nilsson *et al.*, 2019). The same authors concluded that wind is the main influencing factor on birds, which prefer to sit out strong headwinds and will start migration with the arrival of a supportive airstream. After the birds passed a certain location, their numbers would be dropping because most birds left the area. So, birds seem to await such profitable conditions and then decide for departure. Having similar criteria for the decision, individual departures then result in mass movements.

For diurnal migrants, rainfall and fog were mentioned to have the largest negative influence on bird observations (Strandberg and Alerstam, 2007; Pastorino *et al.*, 2017). These authors highlighted the importance of thermals to diurnal migrants and thermals cannot develop under a thick layer of clouds or fog.

To migrate during daylight or at night-time is a question of species. Soaring birds necessarily migrate during daylight and strongly prefer clear sky conditions, as only then they can exploit thermal uplift to rise and use an energy-conservative gliding strategy for migration (Mellone *et al.*, 2015; Pastorino *et al.*, 2017). Diurnal migrants that use powered flight, however, were found to fly in high numbers shortly after sunrise and stop migration around midday with only a few birds continuing their flight into the afternoon hours (Hall and Bell, 1981). Most nocturnally migrating birds initiate their flight within the first two hours after civil dusk and land before dawn (Liechti *et al.*, 2018). In some nocturnal migrants, flight prolongation into the first hours of daylight is common (Åkesson *et al.*, 2001).

In spring, returning birds seem to prioritize an early arrival at their breeding grounds. This is indicated by several adjustments to the flight and rest phases. Returning birds reach higher airspeeds (Karlsson *et al.*, 2012; Nilsson, Klaassen and Alerstam, 2013), which is not only due to global wind zones that make Europe a continent dominated by south western winds (Kemp *et al.*, 2010). Furthermore, birds during spring migration use less time for resting (Strandberg and Alerstam, 2007; Nilsson, Klaassen and Alerstam, 2013), they have a higher tolerance towards unfavourable weather (Åkesson *et al.*, 2001) and have a tendency to prolong flights from night into daylight so that normally nocturnal migrants fly until late morning hours (Nilsson, Klaassen and Alerstam, 2013; Adamík *et al.*, 2016). In autumn instead, arriving safe at the wintering habitat is the priority (Hahn *et al.*, 2014).

1.3 The Influence of Topography

Besides the patterns of wind and rain, topography influences migration routes. In some species, landmarks even are used for orientation (Zehnder *et al.*, 2001; Tyagi and Bhardwaj, 2021). But topography can also provide major challenges to birds, namely then, when birds are confronted with an ecological barrier such as mountain ranges, oceans or deserts. Such an obstacle to the broad front migration is the central Alpine arc. It starts at the southern French coast goes through Switzerland, northern Italy, southern Germany and Slovenia and ends in the most eastern part of Austria.

During autumn migration, the Alps have been found to deflect the largest part of broad front migration that approaches the mountain range from the north (Bruderer and Jenni, 1990; Aurbach *et al.*, 2018). Most birds then adjusts their course to fly parallelly to the mountains towards Geneva, instead of maintaining a more direct, southwards direction that would require them to cross the Alps (Bruderer and Jenni, 1990). The number of autumn-migrants crossing the Alps can increase up to 30 %, when winds coming from the north promote a more southern flight course (Liechti, Peter and Lardelli, 1996). But even then, birds tend to follow mountain valleys to avoid higher climbs over the peaks (Aschwanden *et al.*, 2020).

We know less about Alpine spring migration, but there is evidence that birds on the return to their breeding grounds travel higher (Bruderer, Peter and Korner-Nievergelt, 2018), faster and make longer flight bouts (Adamík *et al.*, 2016) than during autumn migration. This would facilitate an Alpine passage during spring migration.

Almost all birds that migrate through Switzerland were also found to be able to overcome an Alpine pass (Jenni and Naef-Daenzer, 1986). However, White Storks (*Ciconia Ciconia*) for example, or waders in general seem to avoid crossing the Alps: Storks were observed to have returned to the lowlands after entering an Alpine valley during autumn migration (Jenni *et al.*, 1991) and waders have only rarely been captured at the bird ringing station of the Swiss Ornithological Institute on the Col de Bretolet (Thoma and Althaus, 2016). This suggests that the barrier effect of the Swiss Alps on migrating birds differs between species. Additionally, the migration patterns presented by Bruderer and Jenni highlight that for species which are frequently found on passes the tendency to cross the Alps strongly depends on the wind situation (Bruderer and Jenni, 1990).

1.4 How to Study Bird Migration

There are many ways to collect data on migrating birds. It depends on the study aim and research questions, which method is most appropriate because teach method has its strengths and weaknesses. Principally, we can collect information on individual birds, or we can monitor mass movements and bird densities.

Mass movements are monitored by using radar. The study of bird migration by radar goes back to 1941, when radar echoes on a military surveillance station were visually confirmed to originate from gannets (Lack and Varley, 1945). Generally, radar devices work by sending out an electromagnetic pulse which is reflected by an object. The returning echo is detected by an antenna. Multiple pulses echoed by a single object can increase the information from only the distance to an object's direction, its speed and specifically for birds, changes of its reflective shape that are caused by flapping wings (Bruderer, 1997).

Weather radar, especially the recent development of continent-wide meteorological surveillance networks enabled scientists in Northern America and in parts of Europe to launch a multitude on studies that investigated the large mass of migratory birds that moves through the aerosphere (Bruderer, 1997; Kelly *et al.*, 2012; Bauer *et al.*, 2019). These radar devices allow the surveillance of birds on a wide spatial extent, consistently and automatically over long time periods (Bauer *et al.*, 2019). As disadvantages, weather radar has a rather low resolution, has an increasingly low accuracy at altitudes below 400 m.a.g.l. and has blind spots in topographically complex terrain or near the ground (B Schmid 2021, personal communication, 13. September).

From the perspective of the individual bird, the options to gather data are much more diverse. Single birds can be tracked over long distances by capturing, ringing, releasing them again. A later re-capture can provide information on how much distance a single migrant covers within a certain time, how its physical condition develops over the course of migration, what flight route it follows, how fast it migrates overall, including time for resting and migration stages, and inform about survival rates (Newton, 2006; Karlsson *et al.*, 2012; Patchett and Cresswell, 2020). Newer methods of tracking single birds are done with geolocators that use either light intensity or GPS to estimate current positions, while simultaneously measuring air pressure, temperature and acceleration (Liechti *et al.*, 2018). Recent developments of these trackers keep on minimizing their size and weight, which makes these devices applicable for the study of increasingly smaller bird species (Tøttrup *et al.*, 2012). This kind of tracking allows us for example to retrieve detailed flight routes, stopover behaviour and reaction to changing weather for single birds. In other words, it helps us understanding the whole life cycle of migratory birds from the level of an individual (Vardanis *et al.*, 2011). On the other hand, it does not inform on the number of birds that is in the air or the influence of larger weather patterns on mass movements and accumulations of migratory birds. This is where simulations of many individual birds were already successful in creating a wider picture of the dynamic patterns that develop when many individual birds follow similar rules and are similarly affected by the environment (Aurbach *et al.*, 2018, 2020).

Another branch of using single bird information is to count migrants that pass by a certain location. Earlier, this was done by using the disk of the full moon during clear nights. This method is of course heavily limited by time and by the weather and requires the observer to be on spot (Bruderer, 1997). Today, vertically upwards pointing radar devices have overcome the limitation that the full moon provided and have replaced the necessity to be on spot. Such radar devices detect single birds that fly through the radar beam. These devices can collect time-series of birds including their flight speed, flight direction, flight altitude and even wing flapping patterns by which echoes can be classified into different groups of species (Bruderer, 1997; Zaugg *et al.*, 2008). As a disadvantage, these radar devices lack the information on the wider picture, as the data only covers a small spatial extent.

The Swiss Ornithological Institute was involved in the development of such a vertical radar, BirdScan MR1, specifically constructed for ornithology. I will describe it closer in Chapter 2.2 in the methods section.

1.5 Human Expansion: A Threat

During the last decades, humanity has dramatically increased its influence on the environment and of course also on the aerosphere. The part of the atmosphere inhabited and used by birds is changing, so birds must adapt to new situations and cope with new challenges. Some of those pressures are obvious to detect. Bird fatalities with aircrafts have been a topic since the beginning of aviation with airports being hot spots of problems, as there, aircrafts are low enough to collide with birds and as during take-off and landing, aircrafts are most vulnerable to damage (Shamoun-Barnes, van Gasteren and Ross-Smith, 2017; van Gasteren *et al.*, 2019).

A different collision risk comes from our effort to make energy production more sustainable. Wind power plants generate renewable, CO_2-neutral energy, but they are potentially dangerous obstacles to migrating birds. Especially under low-cloud or foggy circumstances, there is a substantial risk of birds colliding with the rotor blades of wind turbines (Erickson *et al.*, 2001; Aschwanden *et al.*, 2018). There is effort to confront the problem of bird collisions with man-made structures. In Switzerland, the Swiss Ornithological Institute published a risk map to provide information to stakeholders where wind turbines can be built so that the risk of bird collisions is minimal (Horch *et al.*, 2013). Additionally, experts suggest to temporally shut down wind turbines when high numbers of migratory birds are expected.

For nocturnally migrating birds, the artificial illumination of our cities (ALAN – artificial light at night) may impede birds from navigation, as it was observed that brightly illuminated objects attracted large numbers of birds which were seemingly disoriented (Evans Ogden, 2002; van Doren *et al.*, 2021).

In general, birds as other organisms may find it hard to adapt to changing land use and urban expansion and the associated risk of loss of ecologically valuable habitats threatens important stopover sites within migratory corridors (Tankersley and Orvis, 2003; Hardesty-Moore *et al.*, 2018). There is evidence that birds have clear preferences for their stopover sites in terms of land cover (Buler and Dawson, 2014). Furthermore, stopover sites must guarantee easy access to high energy food sources and conditions leading to food shortages significantly reduce the survival of migrants (Halupka *et al.*, 2017).

Finally, the ongoing agricultural intensification that began after the second world war is responsible for habitat loss and a massive reduction of insects which resulted in a global decline of many bird species (Johnson *et al.*, 2011). All these problems demonstrate that the threats on migratory birds are manifold and that there is no single solution to the problem of population declines. Many of these problems affect all bird species, but migratory species have special needs and are particularly endangered because global change processes affect their breeding- and wintering habitats as well as their migration routes and important stopover sites (Sanderson *et al.*, 2006; Hardesty-Moore *et al.*, 2018).

Besides these short-term dangers, climate change is an increasing long-term pressure on especially long-distance migrants (Sanderson *et al.*, 2006; Rubolini *et al.*, 2007; Tryjanowski *et al.*, 2013; Zurell *et al.*, 2018). Just recently, scientists reported on increasing migration distances because breeding habitats shift northwards while overwintering habitats move more towards the south. Furthermore, they claim that the risk to completely lose habitats is substantial and increases for birds that occupy only small ecological niches (Zurell *et al.*, 2018). The susceptibility to climate change is supported by the finding of ongoingly earlier spring arrival times in many avian populations (Tøttrup, Thorup and Rahbek, 2006).

1.6 Motivation

Migrating birds are an important part of the ecosystem and interlink habitats between continents (Bauer and Hoye, 2014). Like other seasonally wandering animals, migrating birds survive by exploiting excessive nutrients in highly seasonal habitats. During times of plenty, present migrants consume the excess of nutrients that the local fauna otherwise couldn't exploit (Drent, Fox and Stahl, 2006). Migratory birds being the regulatory element of seasonally exploding insect numbers are also of value for humanity. Insect herbivores that can develop into an agricultural plague are suppressed when migratory birds are present, so for us, migratory birds have a function as a natural crop pest control (Greenberg *et al.*, 2000). For plants, long-distance migrants are a valuable means of seed dispersal and thus, help to enhance the local genetic diversity of the vegetation (Sánchez, Green and Castellanos, 2006). These qualities make migratory birds a very important part of the ecosystem and underlines, why the protection of this animal group is directly linked to our own livelihoods (Bauer and Hoye, 2014).

Because of their importance and because of populations being on decline, we need to make progress in finding and implementing methods for effective conservation of migratory bird species. This includes their breeding habitat, stopover sites, critical passages during migration and their winter habitat. Such a critical passages can be ecological barriers like oceans or deserts, but also places where birds are concentrated because of the topography or because of interactions between topography and synoptic conditions. The Alps as a large structure with a major influence on winds create such places where migratory birds accumulate in higher numbers (Bruderer and Jenni, 1990). When confronted with unfavourable winds, birds arriving in the Swiss lowlands tend to enter Alpine valleys in higher numbers and get channelled between the mountain ridges (Peter, Trösch and Lücker, 1999). This phenomenon was also observed in another migratory system within a valley of the Appalachian Mountains (Williams *et al.*, 2001). The fact that with opposing winds, migratory birds can be found channelled in mountain valleys highlights that those valleys are important locations to consider for migratory bird protection. To better understand the dynamic interactions between birds, winds and topography, we need to collect and analyse more data for these special locations, especially nowadays, when such places are considered as potential construction sites for wind power plants.

1.7 Study Aim and Research Questions

In this master's thesis, I take up current research and try to answer the question if and how migratory birds adapt their behaviour when moving across the Alps. Previous researchers have demonstrated that bird volumes measured at different locations in the Swiss lowlands are very consistent, even over larger distances. This consistency though was highest for nocturnal autumn migration and relatively low in spring (Tschanz *et al.*, 2019), which raises the question why this is so. A topographic effect could be possible. A study on the barrier effect of the eastern part of the Alpine mountain chain concluded that topography largely had no effect on birds that crossed the mountains, but added that the central Alps are much higher and that there is a lack of comparable work to conclude on the barrier effect posed by other parts of Alps (Aschwanden *et al.*, 2020). So far, most research projects that studied bird migration across central Europe focused on autumn migration. The knowledge we gathered on spring migration is comparatively scarce.

I want to contribute to filling those gaps by analysing radar data from devices that continually recorded echoes over the course of two years on three different sites, two inside Alpine valleys and one in the Swiss lowlands, near to the northern foothills of the Alps. As a lowland reference site serves Sempach in the Canton Luzern. The two Alpine sites are Hospental in the Urserental (canton Uri) and Maloja at the pass height of the Inntal (canton Graubünden). All three sites will be better described in Chapter 2.1.

I want to investigate how the phenology of bird migration differs between the Alps and the lowlands. I expect that the topography has a major influence on the flyways birds take during autumn or spring and that because of the shape of the Alps, the preference for certain flyways differs between the seasons. It is necessary to quantify bird numbers that cross the Alps over the course of the whole year to be able to complete the image we have of where we can expect birds in what numbers. I will therefore show how the consistency of bird volumes across the Alps differs from what Tschanz et al. found for the lowlands.

Furthermore, I will investigate how birds that cross the Alps still conserve energy by using valleys as corridors. For the autumn season, high numbers of avian migrants inside Alpine valleys were observed, depending on the prevailing winds in the Swiss lowlands (Bruderer and Jenni, 1990). I will tie on these observations and try to quantify how many birds at what time of the year cross the Alps and what effects the weather has on those migrants in the lowlands compared to when they are inside the Alps. To demonstrate that valleys have a high importance as Alpine passages for birds, I will investigate their flight directions and flight altitudes in search of indices for a channelling effect by these valleys.

Ultimately, the increasingly clear understanding of bird migration dynamics allows us to focus our efforts for migratory bird conservation. The Alps as a major topographical structure have already been shown to deviate birds and lead to accumulations in some places. With this research project, I want to contribute to the completion of the image we have on where we can expect what volumes of migratory birds and how these dynamics depend on the meteorological situation. To guide my research, I ask three main questions.

1.7.1 Question 1: How does the seasonal and diurnal phenology of bird migration differ between Alpine and lowland sites?

The Alpine Mountain arc stands in the way of the palearctic broad front bird migration. In autumn, most birds circumvent the mountain range (Bruderer and Jenni, 1990). Birds that return for the breeding season however profit from an early arrival and thus, might be more willing to take up the challenge of crossing the Alps. Also, the arc-like shape of the Alps might have a stronger funnelling effect for birds that are arriving from the south, whereas when arriving from the north, the mountain chain appears more like a convex shape that invites flying south-west, parallel to the slopes.

Therefore, I expect more birds to cross the Alps in spring than in autumn, while the volume of birds in the lowlands would be more even between the two migration seasons.

For diurnal pattern differences between the sites, I expect that prolonged flights during barrier crossing extend the times of relatively high migration intensity into the early morning hours to go back again clearly after civil dawn. For the lowland site in Sempach, I assume that the main migration happens at night and that during the early morning hours, the volume of migrants is significantly lower than in the Alps. This would be in accordance with the theory on barrier crossing of migratory birds (Adamík *et al.*, 2016).

1.7.2 Question 2: To what extent are migratory birds crossing the Alps channelled in inner Alpine valleys?

Zehnder et al. suggested that migratory birds, rather than just flying over the Alps, avoid higher climbs by following mountain valleys (Zehnder *et al.*, 2001). High climbing is associated with greater energy costs and therefore, birds would prefer to fly at lower levels, even when conditions at higher altitudes would be slightly better (Liechti, Klaassen and Bruderer, 2000). Other case studies especially highlighted the role of the wind for birds entering valleys (Bruderer and Jenni, 1990; Williams *et al.*, 2001). That birds only fly over the Alps under certain circumstances and that when they do so, they use the valleys as passages, speaks against an unimpeded broad front migration over the Alps and thus for a barrier effect by the mountains.

I expect birds who follow an inner Alpine valley to have a low variance of flight directions. Their flight directions will be more aligned and point to the same direction when channelled in a valley. I further expect that the flight altitudes measured inside valleys have a lower variance because low flying birds are driven upwards to overcome the pass heights, while high-flying birds preserve their flight level.

1.7.3 Question 3: What is the effect of the local weather on bird migration intensity, and does it differ between Alpine and lowland sites?

Besides topography, wind and rain influence bird migration (Erni *et al.*, 2002). Birds prefer not to migrate during rain events. (Schaub, Liechti and Jenni, 2004; Haest *et al.*, 2019). Tschanz et al. specify that birds are not strongly affected by short rain events, even if they are rather strong, but avoid flying during long-lasting rainfall (Tschanz *et al.*, 2019). How birds react to winds is rather complicated. Migrants clearly prefer tailwinds (Erni *et al.*, 2002) and supporting winds can be responsible for birds flying at extreme altitudes (Liechti, Klaassen and Bruderer, 2000; Bruderer and Peter, 2017). Haest et al. (2019) report that wind speed was the most important predictor for bird migration intensity. Therefore, also with tailwind conditions, birds tend to stay on the ground, if the winds are too strong (Aurbach *et al.*, 2018). While the wind component blowing parallel to the bird's preferred flight direction can either increase the amount of energy needed to overcome a certain distance, or be supportive to the bird, cross winds, the component blowing perpendicular to the flight direction results in wind drift. Cross winds deviate birds from their projected flyway and must be compensated to stay on target. Compensation however is energetically expensive and requires different strategies, depending on how strong and how constant the winds are (Alerstam, 1979). Researchers found that birds have to tolerate an additional 25 % of energy costs for wind drift compensation to minimize migration time (McLaren, Shamoun-Baranes and Bouten, 2012). In a case study in Scandinavia, scientists found the effect of wind direction to be close to zero, while birds clearly preferred low wind speeds (Karlsson *et al.*, 2011).

A special situation occurs with birds that find themselves in front of a large ecological barrier. In a case study situated in the North Sea, scientists used tracking radar to reveal how migratory birds adapted their flight routes to maximally benefit from the prevailing westerly winds at these latitudes (Bradarić *et al.*, 2020). During spring, migrants usually experience wind support and consequently, there was no effect of wind on departure decisions before crossing the Sea. During autumn instead, when birds usually face headwinds, a strong tendency towards weaker winds was found. Furthermore, around one third of the recorded birds awaited tailwinds before they decided to take-off (Bradarić *et al.*, 2020). The selection of tailwind support before barrier crossing is a commonly found feature in studies that investigate departure behaviour in migratory birds (Dossman *et al.*, 2016). The adaptation of flight routes to prevailing winds has also been observed in other regions besides the Northern Sea (Patchett and Cresswell, 2020). For the Alpine region, Zehnder et al. described how birds were found entering valleys during strong westerly winds in the lowlands, while inside the valleys, birds found supporting airstreams (Zehnder *et al.*, 2001). Aurbach et al. confirmed that wind patterns differ between lowlands and Alps and concluded that topography deviates the predominant wind direction.

Topography and wind alter broad front migration and they do interact with each other making the barrier effect posed by the Swiss Alps dependent on wind patterns (Aurbach *et al.*, 2020). Birds that would have to fly against the wind in the lowland find relatively calm conditions within the Alps, making the crossing of the mountain chain energetically attractive. After this, the effect that the Alps have on broad front bird migration can best be explained by the effect that the mountains have on wind patterns and birds seeking out the most stable and energy-conservative wind situations select flight altitude and direction to optimize their energy costs (Aurbach *et al.*, 2018).

I therefore hypothesize that birds chose the southern Alpine route preferably when the costs of flying around the Alps are large, or, when the meteorological situation benefits birds that cross the Alps, for example when a strong tail wind makes maintaining the north-south direction attractive. I further assume that in the Alps the effects of rain, wind clouds and fog are smaller than in the lowlands, because during barrier crossing, making progress is of higher importance than awaiting perfect conditions.

2 Methods

2.1 Study Site

The data were collected with three radar devices, one in Sempach, while the two others are observing birds in two different Alpine valleys, one in the Urserental, the other one in the Inntal.

The device in Sempach (47°7'38.63"N / 8°11'32.47"E) is at 505 m.a.s.l. and serves as a lowland reference station. The site is near the northern foothills of the Alps but has a relatively flat surrounding.

The second radar was installed in Maloja (46°24'19.71"N / 9°42'8.51"E) at 1804 m.a.s.l., next to the highest elevated point of the Inntal (1815 m.a.s.l.). From northeast to southwest, the Inntal can be described as a quite straight channel through the Alps. After reaching the pass height, the channel continues through the Val Maroz to Italy. On each side, these two valleys are flanked by high mountain chains.

The third location is in the Urserental. The radar device was first installed in Andermatt (46°38'30.26"N / 8°35'26.16"E) at 1430 m.a.s.l. but was moved to Hospental (46°37'16.28"N / 8°34'10.66"E) at 1454 m.a.s.l. on the 21st of July in 2019. Theoretically, birds that passed by Sempach during autumn migration and decided to enter the Alps could follow the Reusstal to the Urserental and would then be recorded by the radar station in Hospental. Other than the upper Inntal, birds would have two possibilities to continue after having reached Andermatt from the north: the first being the Gotthard Pass (2106m.a.s.l.) in the south and the second being the Furka Pass (2429 m.a.s.l.) in the southwest. Towards the north, there is again a clear channel through the Reusstal.

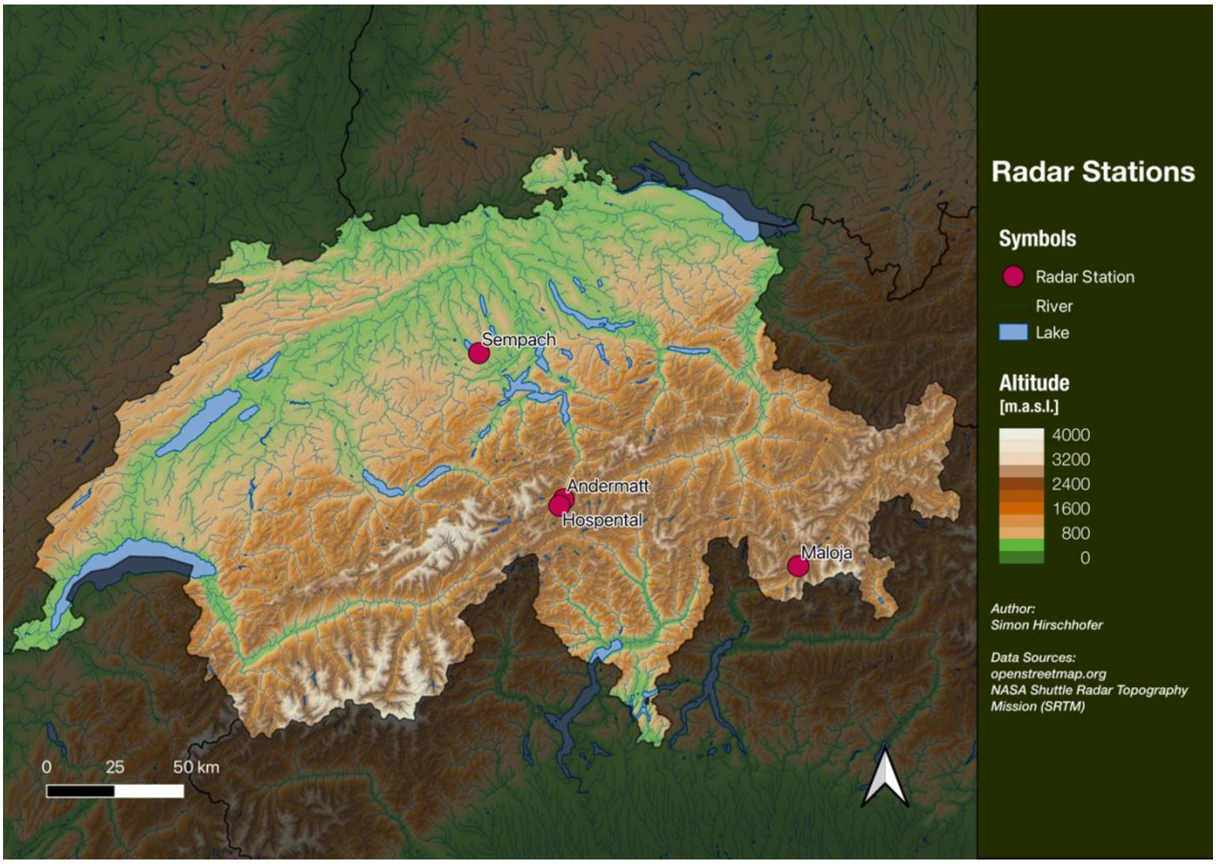

Figure 1: Topographic map of Switzerland showing the four locations of the radar devices as red dots.

2.2 Ornithological Radar: BirdScan MR1

The radar devices with which the data was gathered are specialist systems for ornithology. While weather radar collects information over large areas, BirdScan was developed to gather information on local bird movements with high accuracy, also at lower altitudes (Nilsson *et al.*, 2018). BirdScan is a collaborative project of the Swiss Ornithological Institute and the Zürcher Hochschule für Angewandte Wissenschaften ZHAW. Each device combines a rotating horn antenna with a server that digitizes, processes and hosts the data. BirdScan uses a rotating x-band antenna with 0.8 rotations per second and a pulse frequency of 1800 Hz. The signal frequency is around 9.4 GHz (F Liechti 2021, personal communication, 6. September). The radar can be operated in different modes, using different pulse lengths. During each hour, the radars recorded 20 minutes using short pulse and 40 minutes using long pulse. This switching of the pulse modes improves the overall accuracy of the bird quantification. Short pulse is best suited to scan lower altitudes, but its maximum range is limited to approximately 800 m.a.g.l. long pulse instead is blind at low altitudes, but can detect even small birds at higher altitudes (Nilsson *et al.*, 2018). Additionally, the radar switched between a static and a rotating mode. Only during the rotating mode can flight direction and flight speed be collected. The radar beam has an opening angle of 30° and has a 2° deviation from the vertical axis (ZHAW, 2021). The radar device is illustrated in Figure 2.

The amount of time that passed between sending the signal and receiving the echo gives the distance of an object from the antenna, while the intensity of the returning echo gives information on the size of the surface that reflected the signal. From the distinct fluctuations in the signal's intensity, the wing flapping frequency can be retrieved, which allows an automated classification of the recorded object in different categories of birds, insects and bats (Zaugg *et al.*, 2008; Schmid *et al.*, 2019). The rotation of the antenna allows to retrieve an object's speed and heading (Steuri, 2012).

The number of birds passing by a site usually is given as migration traffic rate (MTR). It is an estimate to quantify how many birds cross an imaginary perpendicular transect of 1 km during one hour (Lowery, 1951) and is the recommended unit to communicate the volume of migrating birds (Nilsson *et al.*, 2018). Figure 3 illustrates how single echoes contribute to the MTR of an hour on the example of a bird that is crossing the radar beam. Depending on the flight altitude, a bird is given a score (MTR factor) which is later used to calculate the MTR estimate. The score depends on the diameter of the area that is covered by the radar beam at the altitude of the object. This area is larger with increasing distance to the antenna. Exemplary, the score for a very high-flying bird will be lower than for one flying closer to the device because one bird detected within a large area theoretically represents a smaller volume of birds than one bird detected within a small area.

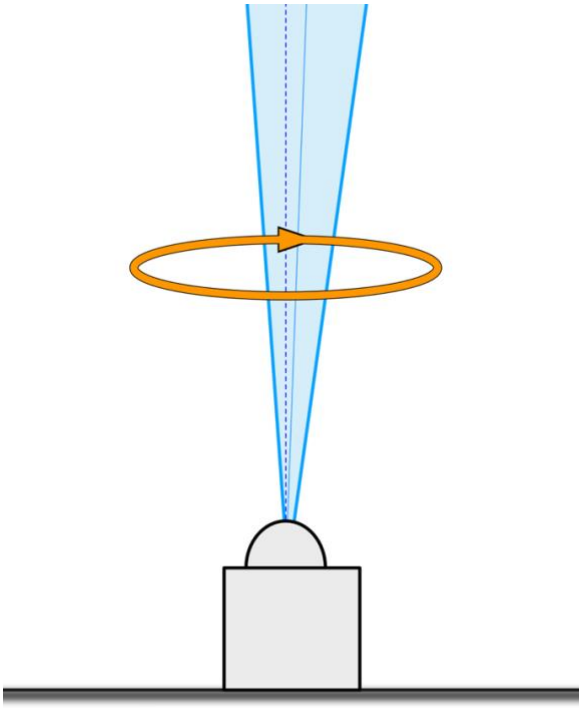

Figure 2: Illustration of the Swiss BirdScan MR1. The blue triangle describes the radar beam, with a 2° tilt from the vertical axis. The vertical axis is shown with the dashed black line, the NADIR of the radar is shown with the thin blue line. The orange arrow shows the antenna's rotation.

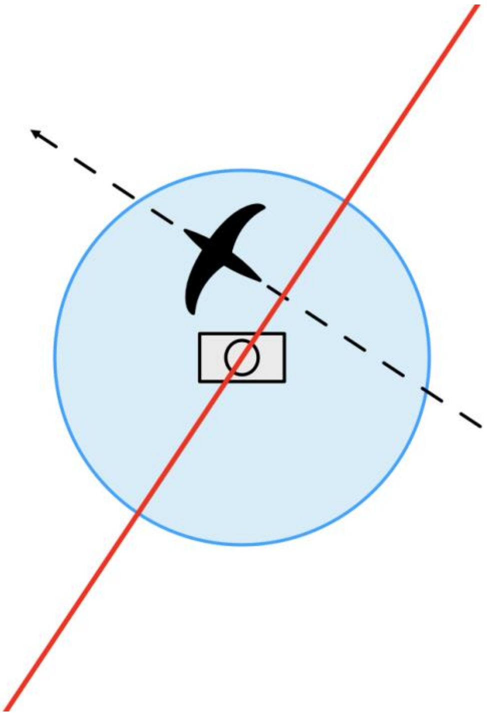

Figure 3: Illustration of the radar beam from above showing a bird flying through. The red line indicates an imaginary transect of 1 km length, perpendicular to the bird's flight heading. The blue circle represents the radar beam from above, which is sent out by the radar device, illustrated as grey rectangle with the antenna coverage as grey circle inside the rectangle.

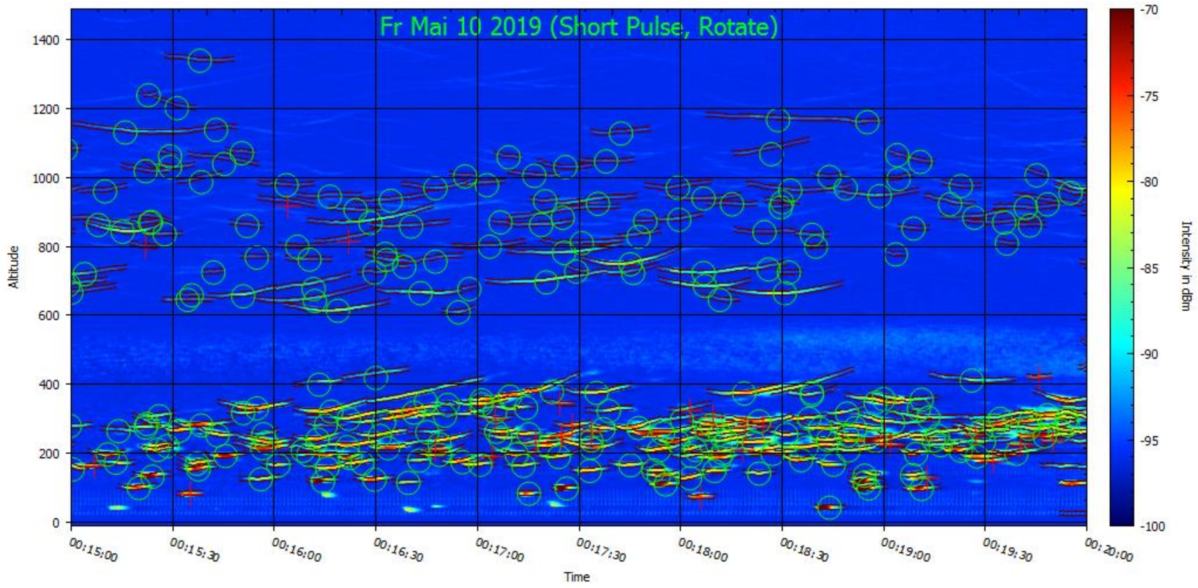

Figure 4: Screenshot showing bird and insect signals between 00:15 and 00:20 on Mai 10th in 2019 in Andermatt. The x-axis shows the time, on the y-axis is the altitude above ground. Green circled echoes were classified as bird, red crosses belong to insect echoes. A horizontally moving object that enters the radar beam reduces its distance to the antenna while moving closer towards the most central point of its secant and again increases the distance while leaving the beam. This results in the concave shape of the echoes in the diagram. In the image, there are two layers with relatively high bird densities, separated by a layer of no birds. The empty layer still shows a pattern of echoes which was eventually caused by water droplets of the size between fog and rain.

Figure 4 shows a screenshot of the visualization of the radar recording during a night of high migration intensity. This was during spring migration in the Urserental, shortly after midnight.

Each of the green circles marks an object that was classified as bird and was given an MTR score. To get the MTR for this example, the scores of all objects detected between 00:00 and 01:00 o'clock were summed up.

Figure 4 shows a recorded time interval of five minutes during night with no rain. Because X-band radar signals are sensitive to rain and during rain events, there frequently are false positive bird classifications (rain that was classified as bird) (Bruderer, 2003). To prevent that, the radar automatically sets itself blind during rainfall, so that no echoes recorded during rain events are evaluated. To make the radar switch to this blind state, the rain must reach the ground. This is not always the case. Before the rain reaches the ground, or when water drops are too small to trigger the blind switch, or when they don't reach the ground at all, false positive bird classifications can still happen. Therefore, the data must be pre-processed manually to check if there were any rain events where the radar did not switch to the blind mode and misclassified rain as birds. If this is the case, the blind times are adjusted to exclude false positive bird echoes. For the year of 2019, this has already been done. For 2020, the adjustment of radar blind times was done by using a pre-defined workflow provided by the Swiss Ornithological Institute. By the help of images like the one shown in Figure 4, time intervals with rain are identified and it is checked, if the radar did the switch to blind mode. If not, the time interval is manually entered in a table. With this table, the blind times are adjusted so that all bird echoes recorded during rain events are excluded from a further analysis.

2.3 Data and Data Preparation

The whole data processing, analysis and visualization was performed in R studio version 1.4.1106 for mac, running R version 4.1.

The bird data covers the years of 2019 and 2020. It was provided by the Swiss Ornithological Institute in two formats. The first format lists the individual echoes that were recorded at a radar station. The second format contains the hourly aggregation of echoes as MTR values distributed on altitude intervals of 50 m from 50 to 1950 m.a.g.l.

To investigate the effect of the weather on bird migration, I needed meteorological data with the same temporal, spatial and altitudinal coverage to match the bird data. The meteorological data was delivered by the Federal Office of Meteorology and Climatology MeteoSwiss. The data was calculated by the COSMO-1 weather model which used local measurements to estimate the exact variables at the locations of the radar stations. For the weather data, I had again to formats available. One contained variables that depend on altitude. The second format contains variables that are independent from altitude.

The meteorologic data was merged with the bird data. The structure of the final data is shown in Table 1 and Table 2.

I will now provide a more detailed description of the data and how I processed it to prepare the analysis.

2.3.1 Weather Data: Atmosphere

Atmospheric parameters were extracted from the COSMO-1 weather model for each of the locations investigated in this study. For any study site, the data was extracted at the nearest possible grid point of the COSMO-1 model on 50 m height intervals from 50 to 1950 m.a.g.l. so that the values can be matched with the bird data. The atmospheric weather data contains wind speed, wind direction, vertical wind speed, air temperature, dew point temperature, relative humidity and air pressure (see the grey entries in Table 2). To estimate if there was fog at any of the altitude intervals, I used the dew point temperature and air temperature (dew point > air temperature). An exact estimation of the occurrence of fog is much more complicated than just comparing the dew point temperature with the measured air temperature (Shim and Lee, 2017). As a rough simplification though, I assumed that all the water that exceeds the capacity of the air fell out as fog. This simplification does not consider water droplets that form clouds or that accumulate as dew, but as a simplification this is valid (Federal Office of Meteorology and Climatology 2021, personal communication, 24. August)

2.3.2 Weather Data: Visibility

MeteoSwiss has prepared a second data frame for each site that contains variables for which the above-described altitudinal resolution was not applicable. This second format includes the total precipitation and the cloud area fraction. I merged this data with the atmospheric weather data and then joined this joint data frame to the bird data containing the MTR values (see Chapter 2.3.4).

2.3.3 Bird Data: Echo

The echo data tables, one for each site, are an extract of what the radar devices recorded during the data gathering period. Other signals than birds were already filtered out. This happened via an automated algorithm that classifies incoming echoes based on the signal intensity and the wing flapping pattern into birds, bats and insects (Zaugg *et al.*, 2008; Schmid *et al.*, 2019). In the data, each observation relates to one bird echo. Each of these recordings has at least a timestamp, a unique identifier, the flight altitude, the MTR factor and a variable indicating if the radar was running in short- or long-pulse mode. If the radar was in the rotating mode at the time when the bird was recorded, the observation additionally has a variable for the bird's ground speed and flight direction.

To each location's echo data, I added an identifier for the site and the latitude and longitude coordinates. The coordinates were necessary to calculate the exact time of civil dusk and civil dawn for each day at each site. These sunlight times were added by using the *suncalc* R package. By comparing civil dusk and dawn with the time stamp of the echo, I created a variable that groups the echoes into diurnal and nocturnal migrants. An echo recorded between civil dawn and civil dusk of the same date was classified as diurnal, all other echoes were classified as nocturnal.

Finally, I added a variable that groups the observations into three different migration seasons, spring- and autumn migration and a third group, off-season for times of the year when majorly undirected, resident bird movements were registered. The process by which the migration phases spring, autumn and off-season were determined is described in Chapter 2.4.

Table 1 gives an overview of the final structure of the echo data frames.

Variable	Format	Meaning
TimeStamp	POSIXct	Time string with year, month, day, hour, minute and second
Datum_Ymd	POSIXct	Time string with year, month and day
DayOfYear	Numeric	Day number within one year from 1 to 365
MTR_Factr	Numeric	MTR factor
FlightDir	Numeric	Flight direction from 0.00 to 359.99°
FlightAlt	Numeric	Flight altitude from 10.0 to 3000.0 m.a.g.l.
IsNightCT	Logical	Classification into day- or night-time using civil twilight
Stat_Name	Factor	Classification into the three different sites
SunLength	Numeric	Time interval from civil dusk to civil dawn
Mig_Phase	Factor	Classification into spring, autumn, or off-season

Table 1: Overview of the final variables in the echo data tables. Variable names match the column names I used in R. Yellow shaded rows were calculated based on other variables or else added.

2.3.4 Bird Data: MTR

While the echo tables have individual birds as observations, the observations in the MTR tables are aggregated on hours and altitude intervals. So, for each hour there are height intervals from 50 to 1950 m.a.g.l. The MTR value for each observation is calculated by taking the sum of the MTR factors of all echoes recorded during one hour within one 50 m height interval.

For each of the unique combinations of time stamp and height interval there were two entries, one for each type of pulse that was used (short and long). These needed to be combined in a first step. Short pulse works best for low altitudes, while long pulse performs better than short pulse at mid altitudes. Based on this fact, only short pulse MTR values were used for altitudes below 300 m.a.g.l. Between 300 and 800 m.a.g.l., the mean MTR value of short and long pulse was calculated and for all altitudes above 800 m.a.g.l., only long pulse MTR values were taken.

The MTR tables originally included an ID, time stamp, height interval, MTR, the number of echoes contributing to that MTR, the direction of mean vector of the birds, the length of the mean vector, the median ground speed, a variable for categorization between day and night, the recording time of the radar in seconds, the radar blind time in seconds and the used pulse type.

The processed MTR tables were merged with the meteorological data described in 2.3.1 and 2.3.2 by using the common variables TimeStamp (date and time), HeightInt (altitude interval) and Stat_Name (location). Table 2 gives an overview on the variable names and types of the final data frames.

I calculated the values for cross wind, head wind and wind profit out of wind direction and wind speed by using the R package *circular*. WindDirec was first transformed into a circular variable. This tells R that the values in the direction variable go from 0 to 359 and that after 359, the next value is again 0 – in other words, that the values of the direction variable are arranged on a circle with 0 as minimum and 359 as maximum value. The calculation for cross- and head wind was done with formulae based on simple trigonometry.

$$CrossWind = \sin\left((WindDirec - HDG_{bird}) \cdot \frac{\pi}{180}\right) \cdot WindSpeed$$

$$HeadWind = \cos\left((WindDirec - HDG_{bird}) \cdot \frac{\pi}{180}\right) \cdot WindSpeed$$

Cross- and headwind were calculated by using the site-specific mean heading of all birds during spring- or autumn season (HDG_{bird}).

In contrast to cross- and head wind, the formula for wind profit additionally considers the flight speed of a bird (v_{bird}) which was estimated to be 12 m/s (Erni *et al.*, 2002).

$$Wind\_Prof = v_{bird} - \sqrt{{v_{bird}}^2 + WindSpeed^2 - 2 \cdot v_{bird} \cdot WindSpeed \cdot \cos\left((WindDirec - HDG_{bird}) \cdot \frac{\pi}{180}\right)}$$

Unlike cross- and head wind, wind profit describes how the wind feels from a bird's point of view, by considering the movement of the bird and the moving air around the bird. It therefore combines the wind component that blows parallel to the bird's trajectory and accelerates or decelerates the bird (head wind) with the perpendicularly blowing wind component which is responsible for sidewards drift from the targeted route (cross wind). For the bird, it describes how much effort it costs to fly from one point above the ground to another under the current wind situation.

Variable	**Format**	**Meaning**
TimeStamp	POSIXct	Time string with year, month, day, hour, minute and second
Datum_Ymd	POSIXct	Time string with year, month and day
DayOfYear	Numeric	Day number within one year from 1 to 365
DayTime_H	Numeric	Hour number within one day from 0 to 23
HeightInt	Numeric	Height interval margin from 50 to 1950 m.a.g.l in 50 m steps.
MTR	Numeric	MTR value
IsNightCT	Logical	Classification into day- or night-time using civil twilight
Stat_Name	Factor	Classification into the three different sites
Mig_Phase	Factor	Classification into spring, autumn, or off-season
WindSpeed	Numeric	Wind speed in m/s
WindDirec	Numeric	Direction from which the wind is blowing in degrees
VertVeloG	Numeric	Vertical wind speed in meters per second
AirTemp_K	Numeric	Air temperature in Kelvin
DewPointT	Numeric	Dew point temperature
RelHumPct	Numeric	Relative humidity in percent
AirPresPa	Numeric	Air pressure in pascal
FogSitEst	Logical	Estimate if there is fog or not
Cloud_Tot	Numeric	Total percentage of cloud coverage

Precip_Tot	Numeric	Total hourly precipitation in mm
Precip_TF	Logical	Categorization if precipitation was more than 0.5 mm per hour.
Cloud80TF	Logical	Categorization if there was more than 80% cloud coverage
CrossWind	Numeric	Wind component blowing perpendicular to the mean flight direction of birds in meters per second
Head_Wind	Numeric	Wind component blowing parallelly to the mean flight direction of birds in meters per second
Wind_Prof	Numeric	Variable indicating how birds experience the wind in meters per second
D_ATempMean	Numeric	Change in air temperature from the previous hour in Kelvin
D_AirPresPa	Numeric	Change in air pressure from the previous hour in pascal
D_CWindMean	Numeric	Change in cross wind from the previous hour in meters per second
D_HWindMean	Numeric	Change in head wind from the previous hour in meters per second
D_WindProf	Numeric	Change in wind profit from the previous hour in meters per second

Table 2: Overview of the final variables in the MTR data tables. Variable names match the column names I used in R. Grey shaded rows originally belonged to the meteorological data tables from MeteoSwiss. Yellow shaded rows were calculated based on other variables ore have been added in some other way.

2.4 Definition of the Migration Periods

To differ between time periods of mainly residential bird movements and mainly migratory, directed bird movements, I defined start and end points of spring and autumn migration. For each day, I calculated the alignment of all bird movements and the mean normalized MTR with each of both measures having values between 0 and 1. The grade of directional alignment of the birds I used all observations of the echo data tables that included information on the bird's flight direction. The flight direction can be seen as a unit vector for each bird. By using the R function circular::rho.circular() I calculated the length of the mean directional vector of all birds during each day. By multiplying the mean resultant vector length with the normalized mean MTR value of each day I calculated a bird migration index (BI). The BI therefore considers the degree of alignment in all the birds flight headings: for residential, undirected movement, this is expected to be relatively low, while during peak migration, many birds fly in the same direction and the vector length should be near 1. By including the normalized MTR I weighted the grade of alignment. This prevents that if only one bird was detected during a day, that day is classified as a spring or autumn migration, because all birds have flown in the same direction. It also accounts for the assumption that during migratory phases, a lot of birds should pass by the radar. The formula used to calculate BI can be seen below.

$$BI = \overline{R}_{\iota} \cdot MTR_{norm\ i}$$

Where R_i is the mean resultant vector length of day i and $MTR_{norm\ i}$ is the normalized MTR value for day i.

$$MTR_{norm\,i} = \frac{MTR_i - \min(MTR)}{\max(MTR) - \min(MTR)}$$

With MTR$_i$ being the MTR value for a specific day, min(MTR) being the minimum of all daily MTR values and max(MTR) being the maximum of all daily MTR values.

$$\bar{R_\imath} = \frac{R_i}{N_i}$$

$$R_i = \sqrt{\sum_{n=1}^{N_i} \cos(\theta) + \sum_{n=1}^{N_i} \sin(\theta)}$$

Where N$_i$ is the number of echoes of day i and θ is the polar angle of an echo's trajectory. Mean resultant vector length can range from 0 (no alignment) to 1 (total alignment, all vectors point to the same direction). The final BI ranges between 0 and 1.

BI (in the code below called "Phase_Ind") was then smoothed with a loess model. The loess model smooths the BI over the course of the year (see Figure 5).

```
model <- loess(Phase_Ind ~ DayOfYear, data=data, span=3/12,
method="loess", degree=2, family="gaussian")
```

The smoothing of BI over the course of one year is thought to cancel daily fluctuations that can occur because of larger rain events when residential flights exceed migratory flights so that a day that belonged into the migration phase got classified as off-season. From all daily BI values, I calculated the mean to use as a threshold. If a day had a value below the threshold it was classified as off-season. BI-values equal or above to the threshold were classified as days during one of the two migration phases. I used day number 180 as a separator for the two semesters of the year. Days in the first half of the year with a BI greater than the threshold were classified as "Spr" for spring migration season, days in the second half of the year with a BI greater than the threshold were classified as "Aut" for autumn migration season.

For 2019, the spring season began on day number 56 and ended on day number 123. The autumn season lasted from day number 217 to day number 315. In 2020, the spring season began on day number 60 and ended on day number 119. The autumn migration season lasted from day number 222 to day number 315. The classification is visualized in Figure 5 and Figure 6.

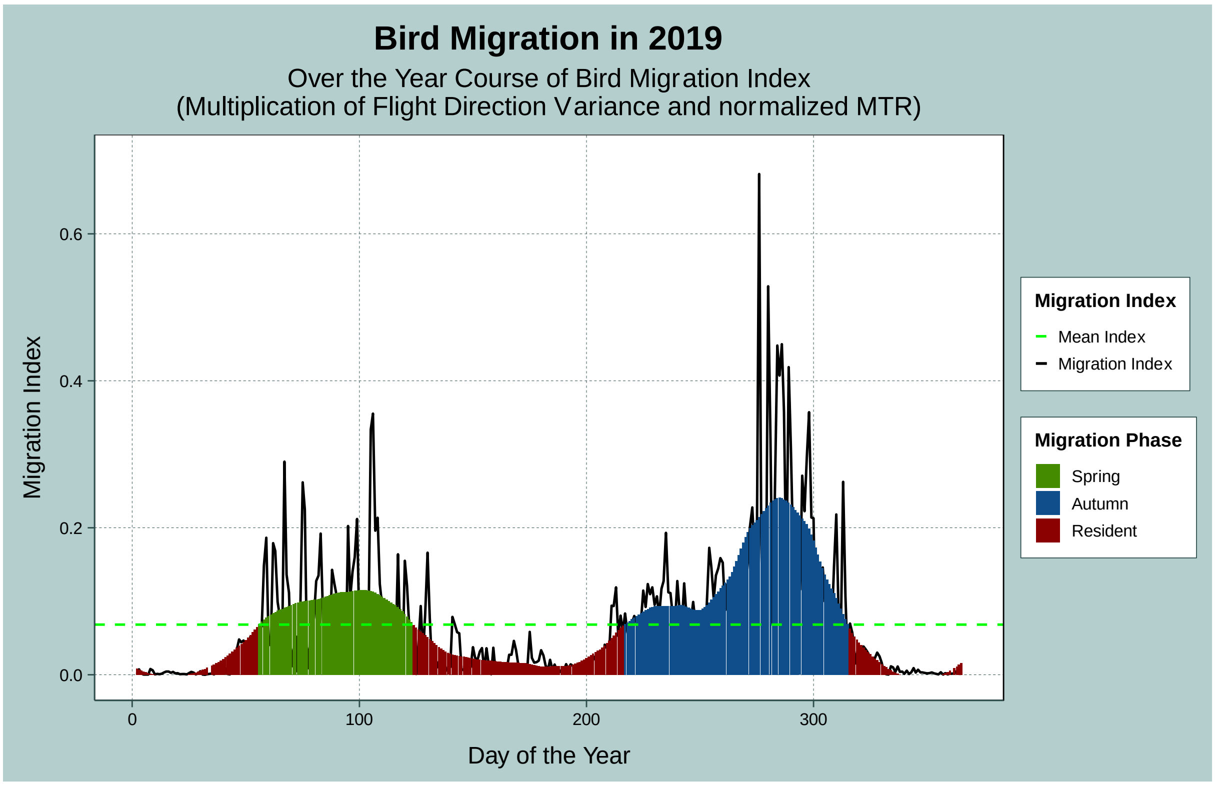

Figure 5: Migration phase classification for the year 2019. Visualized classification of the data into migration phases. The black line indicates the calculated bird migration index BI, which has a lot of variability. Therefore, it was smoothed. Smoothed values are displayed as red (off-season), green (spring migration phase) and red (autumn migration phase) bars.

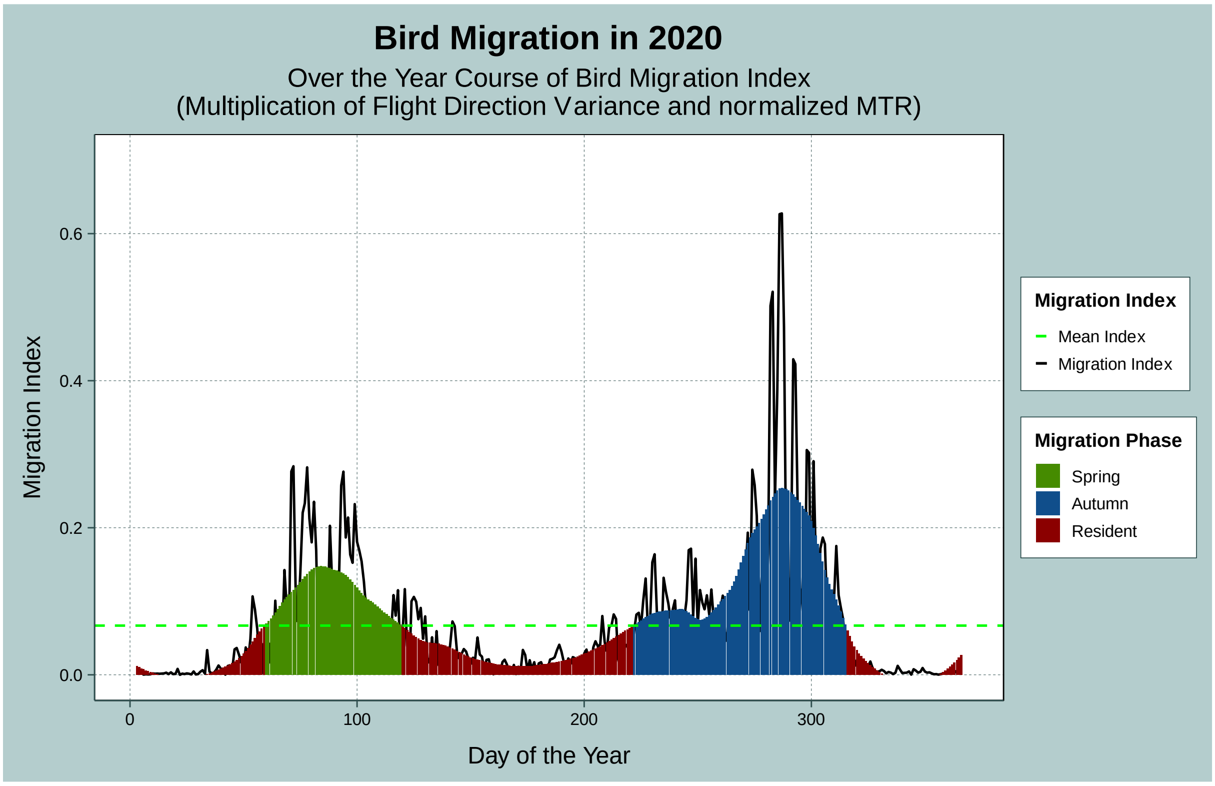

Figure 6: Migration phase classification for the year 2020. See Figure 5 for a closer description.

Differing between residential and migratory movements is important because of the modelling. I expected that residential flights with the goal of foraging, building nests, etc. follow different rules than migratory flights. Doing such a classification based on the index allowed to separate the data based on observed features and not by manually defining beginnings and endings of the migratory phases. This classification was then used for filtering of the data during the analysis in R.

2.5 Site-specific Directional Variance

I investigated the channelling effect of Alpine valleys on birds by plotting the flight trajectories of individual echoes for each site and each migration season.

Site-specific data for each of the two migration seasons was grouped by diurnal and nocturnal daytimes. The flight directions of all recorded birds during a day or night of one day were aggregated into one-degree segments of the circle. I then calculated the mean number of birds per hour moving in each direction over the whole season. For the calculation of the mean I used the aggregated data of both years, 2019 and 2020, to increase the amount of data and because I assumed that by including a wider time span, temporal variations in the directional preference of birds as they are caused by persistent synoptic conditions should decrease. As I wanted only the effect of the topography to reveal itself in the result, reducing the effect of changing weather conditions is justified.

In R, I plotted the result as density graphs on a circular axis and used them as overlay on six maps (one for each site and migration season) generated in QGIS. The overlay was done in Affinity Designer for Mac.

2.6 Site-specific Vertical Distribution

Like the flight directions, I analysed the distribution of flight altitudes over the course of the day visually. Again, I combined the echo data from 2019 and 2020 to increase the amount of data and because I wanted to investigate if the topography was causing any differences in the patterns between the stations. The data was grouped by hour of the day to allow a display of flight altitudes for each hour. I then made bar plots to display the flight altitude of birds for each hour of the day. Additionally, I marked the mean time of civil dusk and dawn of the spring or autumn season.

2.7 Modelling of Expected Bird Volume

As I have described in the Chapter 1.2, bird migration is driven by a seasonal and an environmental component. To be able to model how the environmental component depends on different factors of the current weather, the seasonal component must first be extracted. The estimation of an expected volume of birds for each day or hour over the course of the year allows such a separation into these two components with the expected MTR values being the seasonal part. After modelling the seasonal component, the residuals of the MTR measurements from the expected value should contain the information on the effects of extrinsic, environmental factors on the birds' flight behaviour.

For the extraction of the seasonal component out of a time series, generalized additive models have been suggested and presented multiple times (Pedersen *et al.*, 2019; Shi *et al.*, 2021). I did this in R by using the gam() function in the *mgcv* package (Wood, 2021). I made two models, one with a daily, the second with an hourly resolution. Generalized additive models in R use smooth terms to link the explanatory variables with the response. These models are very useful for the decomposition of a time series into several components because the smooth terms estimate the trend of each of the defined components (Liu, 2008). These smooth terms differ, depending on the assumptions that are made and depending on the number of independent variables. I will explain the smooth terms below in the presentation of the daily and hourly models. For both models I used a quasipoisson distribution because MTR values are, strictly speaking, a count of birds. I did not use a poisson distribution because therefore, the MTR values were overdispersed.

```
model <- gam(MTR ~ s(DayOfYear, k=60, bs="cr"), data=data,
family=quasipoisson(link="log"), method="REML")
```

The code above shows the model for daily expected bird volumes. It uses the standard smooth term s(…) which is required in a gam() model. k=60 specifies that the smoothed function is allowed to use 60 knots (Wood, 2021). k can also be described as the maximum allowed degree of freedom for a term in the model. bs="cr" tells the function to use a cubic regression spline. The "REML" method includes a penalty for increased wigglyness in the modelled function – in other words, it increases the smoothness of the resulting curve.

```
model <- gam(MTR ~ t2(DayTime_H, DayOfYear, bs=c("ps","cc"),
k=c(24,12), full=TRUE) + Mig_Phase + IsNightCT, data=data,
family=quasipoisson(link="log"), method="REML")
```

In contrast to the daily model, the hourly model uses a different type of smooth term within the model function. Alternatively, I could have done the model with two simple smooth terms, but this would have assumed that the bird numbers over the course of the day were similar for the whole year. Using the interaction term t2(…) tells the model that for each day, the course of MTR values from early morning to late night can vary between the days over the course of a year. Mathematically, it models a tensor product smooth for the main effects of DayTime_H and DayOfYear and additionally includes an interaction of the two. Again, the bs command defines the base functions used for both explanatory variables. Here I specified a cyclic cubic spline for DayOfYear to link the first day of the year with the last. For DayTime_H I used a p-spline. For k, the number of knots for the smooth I used 24 for the hour term and 12 for the day term. I have chosen 24 for the hour part to match the number of hours during the day. I iteratively have chosen 12 for the daily part of the model to reduce the computational effort for the calculation, but still get a good fit, as indicated by the function mgcv::gam.check(), which returns model diagnostics of a gam object and includes an assessment of the chosen parameter for k.

Besides the hour and day components inside the t2() smooth term, I included two factorial variables, Mig_Phase and IsNightCT, which allow the model to calculate different smooths for every possible combination of the two factors. This makes sense because birds seem to have different priorities during spring than during autumn migration and because it can be assumed that there is a major difference in the bird species composition between day and night.

The data used for the calculation of the expected MTR (MTRExpVal) was a continuous record of five years (2016 to 2020) from the lowland station in Sempach. Figure 7 shows the model diagnostics for the hourly model, which do not show patterns that would have required attention. Temporal autocorrelation in the data was inspected using the acf() and pafc() function from the R *stats* package on the residuals of the model. The output of these two functions is shown in Figure 8. The autocorrelation analysis with acf() and pacf() justified the inclusion of the factors Mig_Phase and IsNightCT in the hourly model, because it led to a major reduction of autocorrelation in the error term.

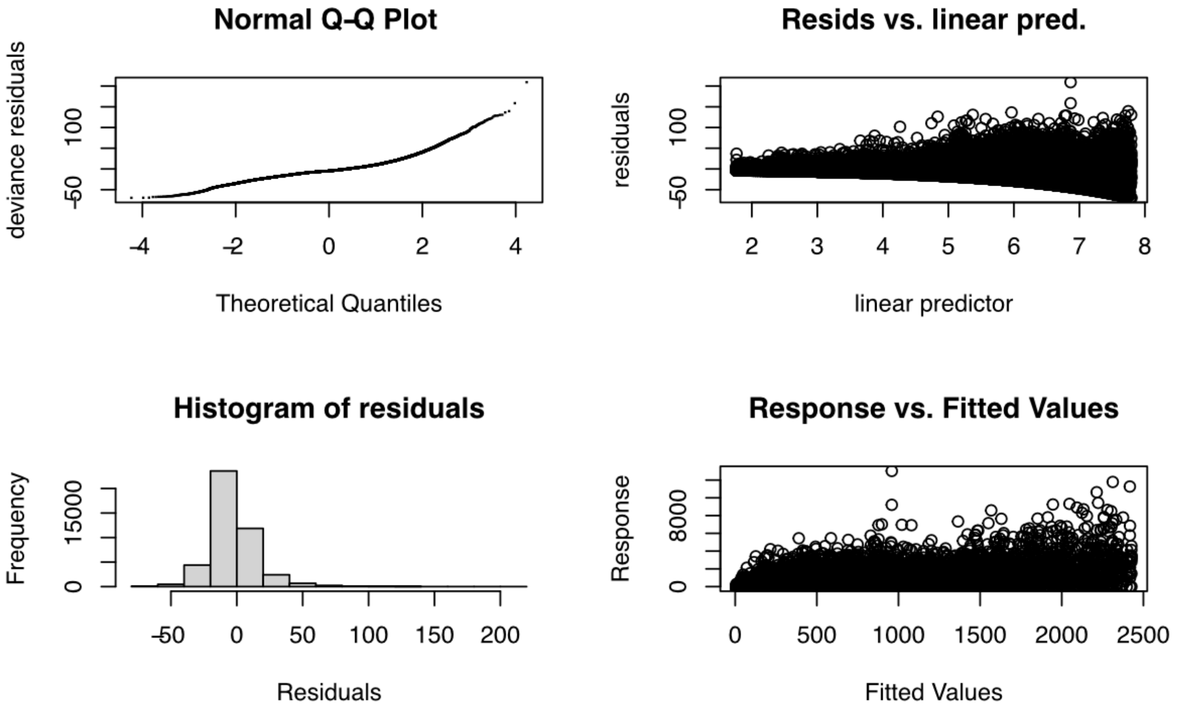

Figure 7: Diagnostics for the model to estimate expected MTR values in Sempach.

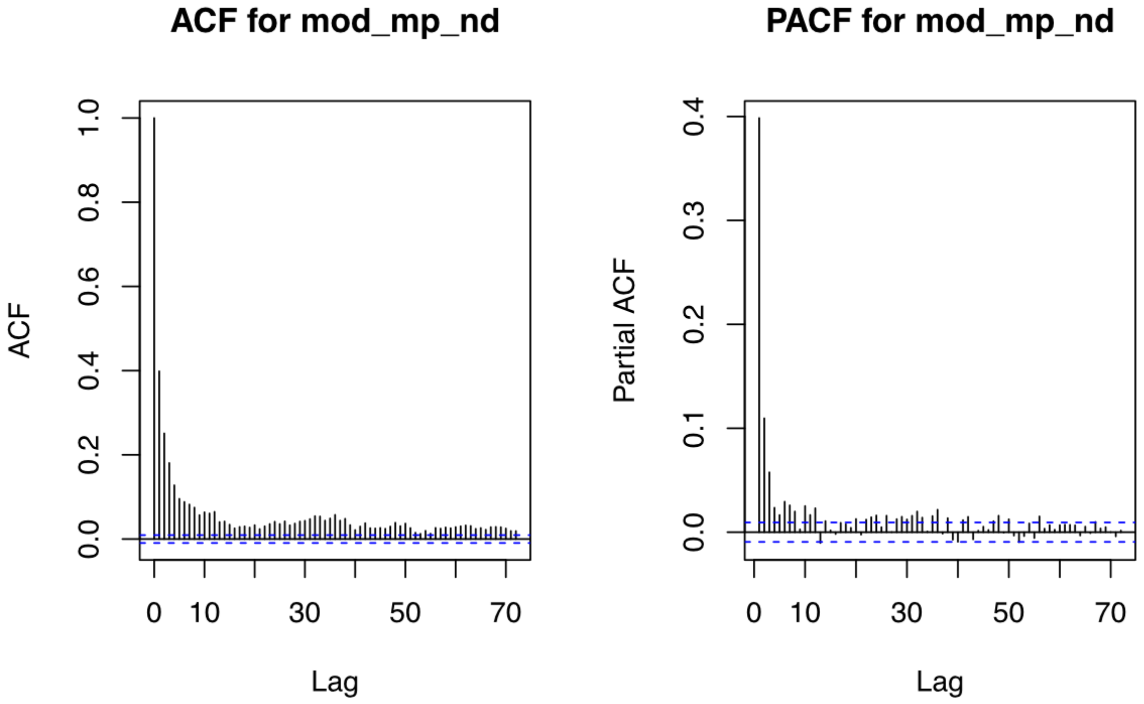

Figure 8: Autocorrelation function (left) and partial autocorrelation function (right) for the expected MTR model.

The expected MTR values were joined to the daily or hourly MTR tables for 2019 and 2020 as MTRExpVal. Finally, MTRExpVal was subtracted from the measured MTR values to get the residuals (Resid_MTR).

2.8 Explaining Residuals with Wind and Rain

Before, I have described how I have separated the two components that contribute to the MTR values and have stored them in the variables MTRExpVar for the seasonal trend and Resid_MTR for the influence of the environment on migratory bird volumes. Wind, rain, fog and clouds should have a major influence on Resid_MTR, as these are expected to be the reason why there is deviation of the measured MTR values from the seasonally expected migration volume. To model the effects of the environment, I used linear mixed effects models from the *lme4* package.

I have selected environmental variables for the modelling by drawing correlation matrices and by considering the variance inflation factors of the draft model's terms. Finally, I have selected WiDir_Std, Wind_Prof, AirPresPa, ATemp_Mea and the change of these from one time interval to the next as continuous predictors. Furthermore, I included the factorial variables Precip_TF, FogSit_TF and Clouds_TF. The year (2019 or 2020) was included as a random variable. During the model calculation, I used the scale() function on all numeric terms. scale() centralizes and scales a vector so that vectors with very different ranges of values become comparable to each other. For such scaled vectors, the relation between the predictors and the response is interpreted in standard deviations: one standard deviation change in an independent variable results in one standard deviation change of the response. The code snippet below shows how such a model (both types, daily and hourly resolution) looks like.

```
model <- lmer(formula=scale(MTR_Resid) ~ scale(WiDir_Std) +
scale(Wind_Prof) + scale(AirPresPa) + scale(ATemp_Mea) +
scale(D_ATempMean) + scale(D_AirPresPa) + scale(D_Wind_Prof) +
Precip_TF + FogSit_TF + Clouds_TF + (1|Year), data=data)
```

For each possible combination of site, migration season and daytime (day or night), an individual model was calculated.

As for the calculation of the expected bird volume, I did the models for the environmental effects on bird volumes on a daily and hourly scale. For the daily scale I grouped the data by DayOfYear and used daily mean values of the explanatory variables and the response. For the hourly models I grouped the data by DayOfYear and DayTime_H with hourly mean values of the predictors and the response. For each resolution, daily and hourly, and each season, spring and autumn, I calculated six models, one for each unique combination of site and daytime (day or night).

2.9 Site-specific Migration Phenology

So far, I have used the expected volume of birds as calculated from data of only the reference station. For each site, I have used this reference in the calculation of Resid_MTR, which makes the deviations of measured MTR values at each site a deviation from what would be an expected bird volume at the lowland site in Sempach. I wanted to analyse how the result changed, when Resid_MTR was calculated with local expected migration intensities. By using the procedure that I have described in Chapter 2.4, I modelled MTRExpVal again by calculating generalized additive models with site-specific MTR values from Maloja and the Urserental of the two available years 2019 and 2020.

With the new values for MTRExpVal I followed the process described in Chapter 2.8 to make a second version of the assessment of the environmental factors.

2.10 Consistency Between the Sites

After Tschanz et al. (2019) I calculated the Spearman's rank correlation coefficient between the MTR values of each site. This correlation was estimated on daily mean values to follow the procedure used by Tschanz et al. and allow a comparison between the results. Just as described in their research article, my calculation was also done separately for diurnal and nocturnal migration, for the spring and autumn season and the two years.

3 Results

3.1 Site-specific Directional Variance

Figure 9 illustrates patterns for flight trajectories for all three sites. In general, all panels reveal that during the migration season in spring and autumn, recorded birds tendentially move towards a common direction. The alignment of flight trajectories seems to be stronger for nocturnal observations. This difference is most obvious for the panel that shows spring migration in the Urserental, where diurnal flight directions appear to be random. However, in the Alps, the variability in the birds' flight directions seems to be lower than at the lowland site in Sempach. Especially the observations in Maloja show a very clear common direction. Another phenomenon can be seen in Sempach. Here, the birds seem to prefer having different headings between day and night: in spring, diurnal migration appears to be a little more northwards oriented, while in autumn, the orientation of diurnal birds appears to be more southwards. In contrast, at the Alpine sites, diurnal and nocturnal observations overlap better.

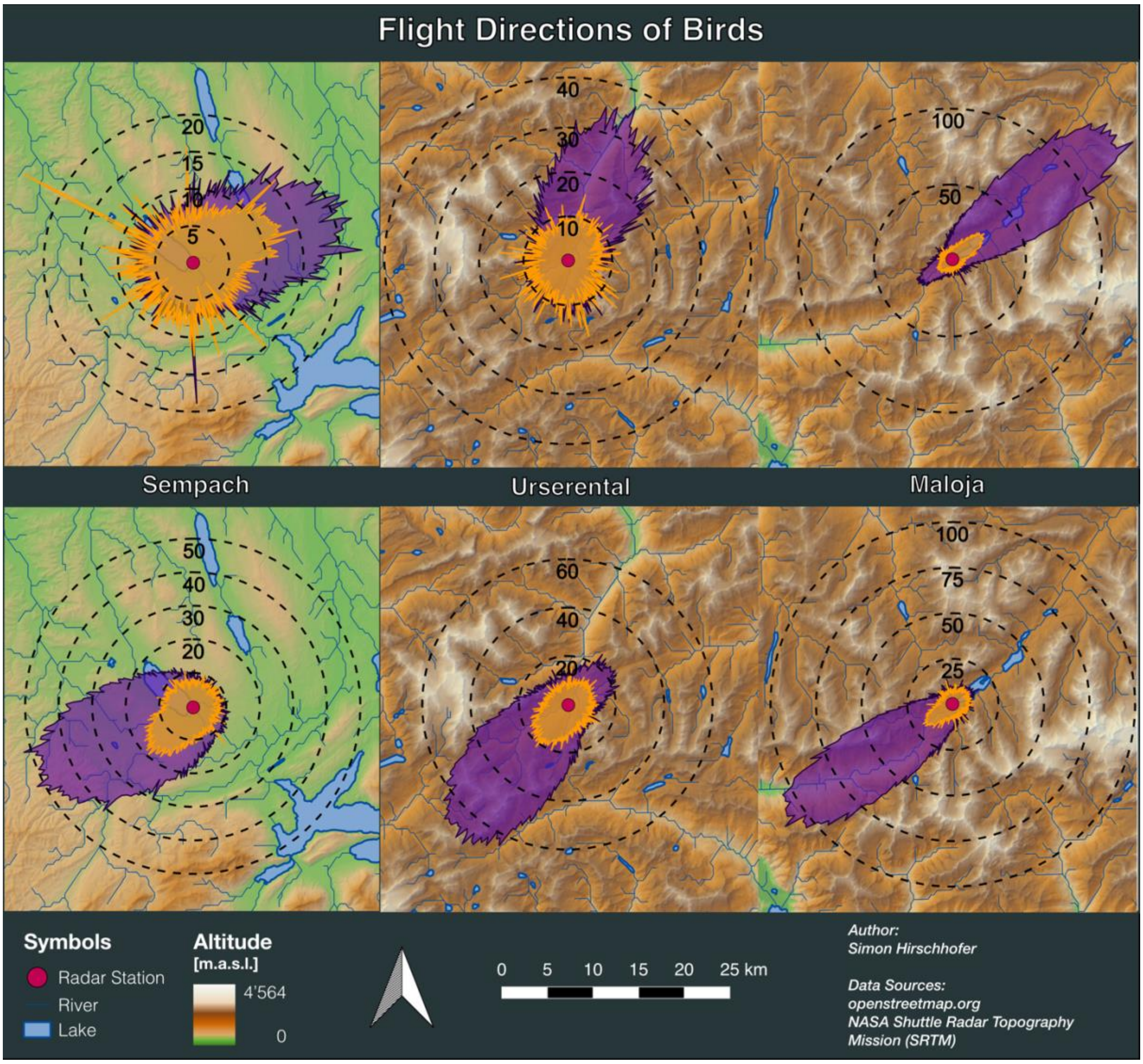

Figure 9: These maps and graphs show the site-specific distribution of flight directions of birds. The upper three panels display flight directions during the spring migration season, while the lower three panels show the situation during the autumn season. From left to right, the panels show maps of the lowland site in Sempach, and the alpine sites in the Urserental and in Maloja. Each panel shows the flight direction distribution of diurnal (orange) and nocturnal (purple) migration. For each graph, the full circle is split in one-degree segments (described in Chapter 2.5) by which the flight directions are grouped. The graphs show the seasonal mean hourly number of birds that

move in a certain direction. Dashed circles indicate the distance from the radar station. The underlying data covers the years 2019 and 2020.

3.2 Site-specific Vertical Distribution

From a stopover site, birds initiate their departure at very different times: depending on species, latitude, season, weather and arrival time at the stopover site departures from shortly after sunset until late in the night were observed (Åkesson, Alerstam and Hedenstrom, 1996). There is even a large intraspecific range of departure times (Åkesson *et al.*, 2001). But after initiation, migrating birds prioritize climbing to their preferred cruise altitude, even tolerating major drift by winds (Sjöberg and Moore, 2015).

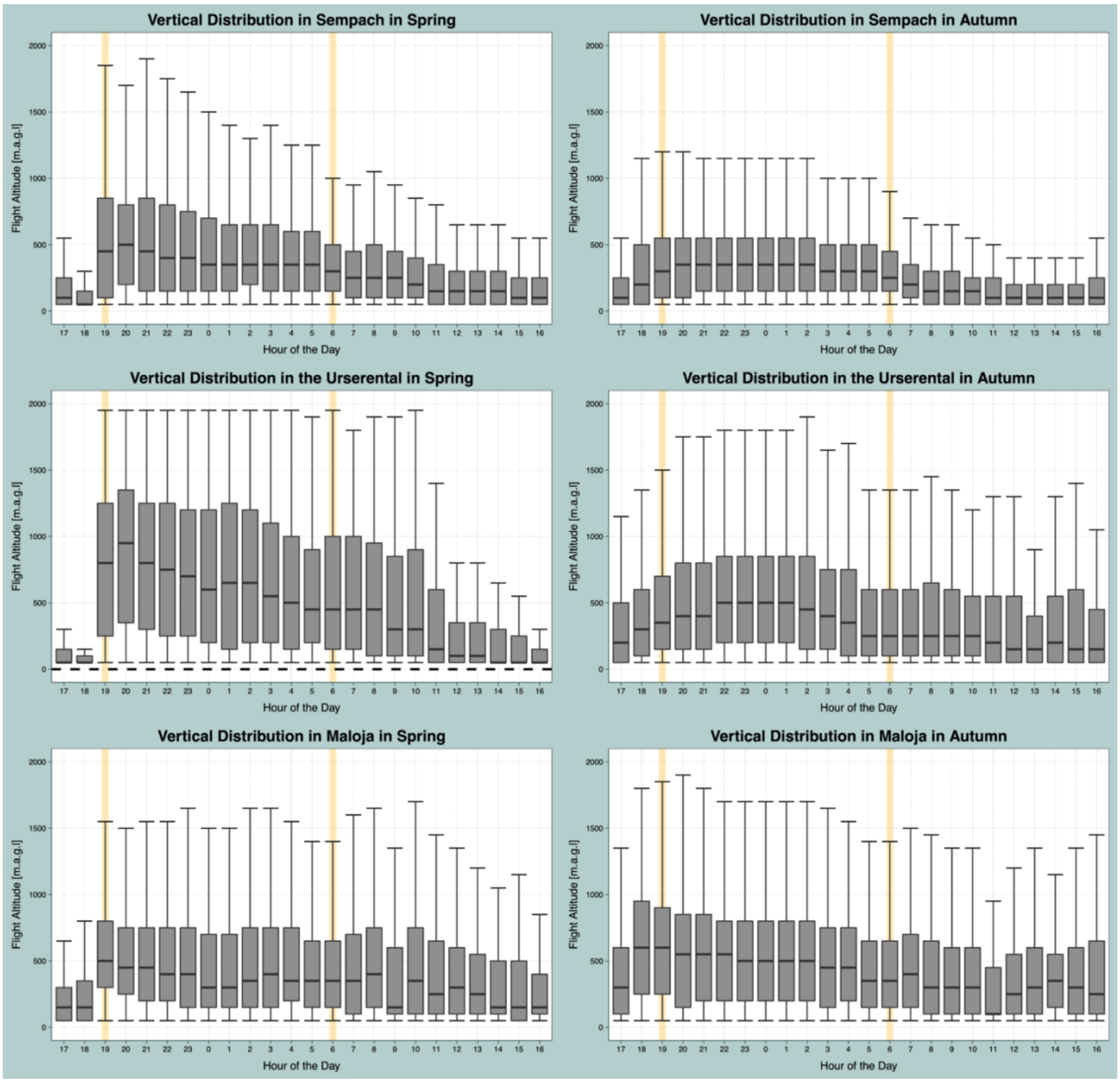

Figure 10: Hourly vertical distribution of birds for Sempach (top), the Urserental (middle) and Maloja (bottom). For each site there is a panel for the spring (left) and the autumn (right) migration season. Each panel shows daytime from 0 to 23 on the x-axis, starting with hour 17. On the y-axis is the flight altitude in meters above ground level. The seasonal mean times of civil dusk and civil dawn are marked with a vertical yellow band. The graphs show boxplots of the distribution of flight altitudes for each hour of the day. Grey boxes represent the interquartile range, the thick black line inside each box marks the median and whiskers mark the highest and lowest recorded echo. The maximum length of the whiskers is 1.5 times the interquartile range. If there were echoes outside this range, they are not included in the graph.

As Figure 10 shows, during night-time, birds generally move at higher altitudes than during the day. This can be seen very clearly after civil dusk, when almost all the panels show a leap from low to high altitudes. The exception is found in the graph displaying the Urserental during autumn: in comparison to the leap after civil dusk, flight altitudes decrease only slowly after civil dawn. In Sempach, birds usually moved at lower altitudes with a relatively small interquartile range (IQR). On the other hand, observations in the Urserental reveal a lot of relatively high-flying birds, especially during the spring migration season.

In Sempach during the spring season, diurnal activity happens mainly between 0 and 300 m.a.g.l., while after dawn, the IQR rises to approximately 100-900 m.a.g.l. Right after civil dusk there is a sharp increase of flight altitudes. During autumn, nocturnal observations are lower than during spring with an IQR between approximately 100 and 500 m.a.g.l.

The highest daily variance in IQR over the course of the day was found during the spring migration season in the Urserental. From noon to civil dawn, the IQR was very low, between 0 and 300 m.a.g.l. But after civil dawn, there was a large leap and the IQRs of flight altitudes suddenly shift to higher altitudes. During night-time, spring migration in the Urserental had the widest IQR from all three sites, reaching from approximately 200 to 1300 m.a.g.l. After dawn the IQRs decrease only slowly. During autumn, the distribution of flight altitudes is more constant, especially the leap-like altitude increase of the IQR at civil dawn is lacking. The IQRs during the day are at around 0 to 600 m.a.g.l. and rise to approximately 100 to 900 m.a.g.l. during the night.

In Maloja during the spring season, flight altitudes are quite regularly distributed over the day. The IQRs of nocturnal observations are between 100 and 800 m.a.g.l. and, like in the Urserental, decrease only slowly during daylight. Solely the two hours before civil dawn have clearly lower IQRs followed by a leap increase after dawn. During autumn, the IQRs are slightly higher than during spring and the leap increase at civil dawn is weaker.

3.3 Site-specific Migration Phenology

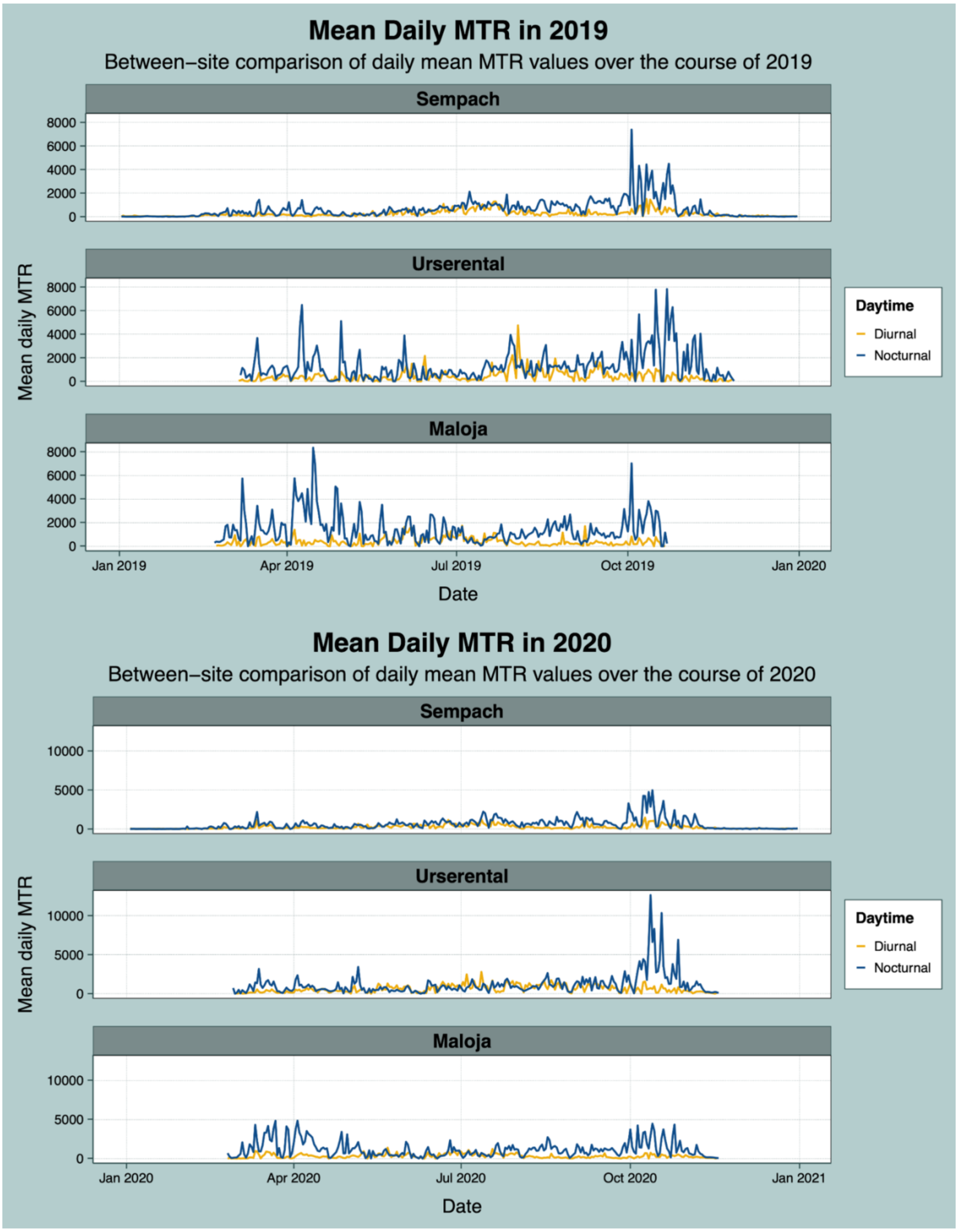

Figure 11: Site-specific daily mean MTR for the years 2019 (top) and 2020 (bottom). The y-axis shows the daily mean MTR in birds per hour per km (see Chapter 2.2), with the same intervals for the three sites within the same year. The x-axis depicts the date. The daily MTR values are split into diurnal (yellow) and nocturnal (blue).

3.3.1 Measured MTR

Figure 11 shows how the three sites differ in regard of the number of birds that were measured by the radar device. For both years, the site in Sempach shows the lowest overall numbers. Over the year, diurnal MTR values are rather constant with an exceptional rise in numbers during summertime in the Urserental. Nocturnal MTR values instead can be clearly separated in times of relatively high bird numbers during spring and autumn and very low numbers during summer and winter.

Spring migration did not produce significantly higher numbers of birds in Sempach. For the Alpine sites instead, there were very high MTR values measured, especially in the year 2019 when in the Urserental more than 6000 birds per hour per km passed by the radar station. The maximum spring migration intensity measured in Maloja still exceeded this with over 8000 birds per hour per km in April. In Maloja, bird volumes measured during spring were even higher than during autumn, which was not so with the other two sites. As suggested by these measurements, the spring migration season lasts longer than the autumn migration season.

During autumn, the radar located in Sempach measured clear peaks of high migration intensities with numbers of almost 8000 birds per hour per km. But again, there were more birds detected at the Alpine sites. The absolute maximum of all recordings was at 12th October 2020 at 7 pm with 24685 birds per hour per km in the Urserental. The highest daily mean MTR therefore too can be found in October 2020 in the Urserental with an MTR of 12345 birds per hour per km. In Maloja, the MTR values during the autumn migration season are like the values measured in Sempach with almost 5000 birds per hour per km in 2020 and around 7500 birds per hour per km in 2019.

These graphs that display the measured daily mean MTR values show days of very high migration intensities followed by days of very little birds in the air. Especially during the migration seasons, the difference from one day to another can be extremely large. This variability is most likely due to environmental influences.

3.3.2 Modelled expected MTR

Figure 12 shows the result of the modelling procedure described in Chapter 2.7. The illustration shows how the expected bird activity in the air varies over the course of the year and over the course of each day during the year and allows a comparison of this phenology between the sites. Like the measured MTR values plotted in Figure 11, the model output suggests that the highest bird volumes are to be expected during autumn, shortly after civil dusk. Only in Maloja, peak MTR during spring exceeds the maximal values modelled for autumn migration. Relatively high values were also predicted for the early morning hours during the migration seasons. In summer, off-season, there are also local maximum during the day.

During spring, the highest volume of birds in Sempach was modelled to be at 1 am with 579 birds per hour per km. This is the lowest value for the maximum spring migration intensity for all three sites. In the Urserental, the highest MTR during spring was 1593 birds per hour per second at midnight. After the model, the absolute maximum MTR during spring can be expected in Maloja at 9 pm with 3692 birds per hour per km.

In autumn, Sempach clearly has higher migration intensities than during spring. The maximum can be found in October at 8 pm with 2429 birds per hour per km. In the Urserental, the model suggests the highest global MTR with 5482 birds per hour per km at 8 pm. For autumn migration, the model calculated the lowest maximum MTR for Maloja at 11 pm with 2803 birds per hour per km.

For all three sites and for both seasons, relatively high MTR can be expected until the early morning hours. In spring, this is most clear for Maloja. During autumn, Sempach has relatively high MTR values of around 600 until 10 am.

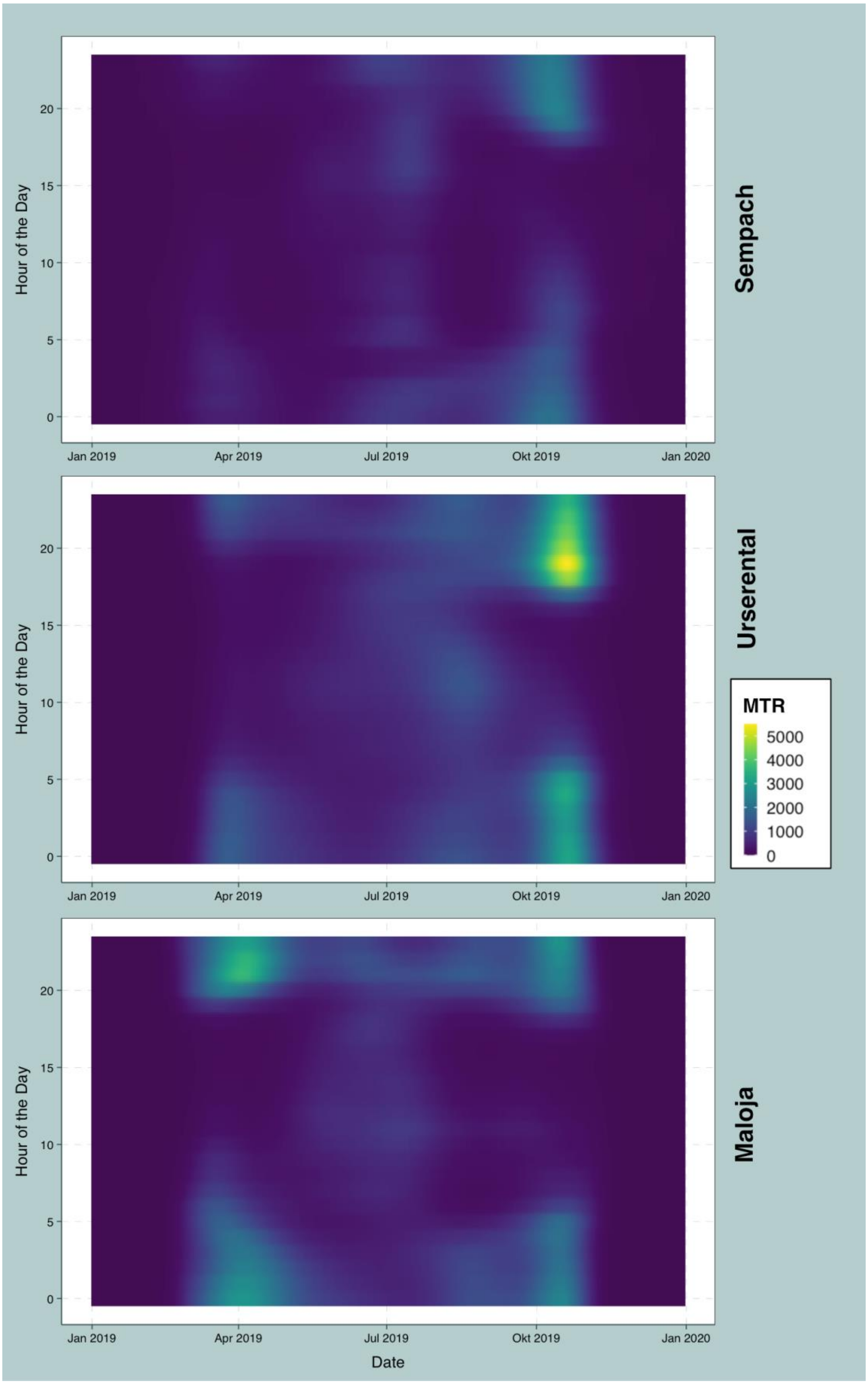

Figure 12: Migration phenology for Sempach (top), the Urserental (middle) and Maloja (bottom). Each panel shows the course over the year as date on the x-axis and the hour of the day on the y-axis. The three graphs show tiles,

one for each hour for each day of the year. The tiles are filled with colour to represent the expected number of birds with purple for 0 and a bright yellow for 5482 birds per hour per km.

3.4 Influence of the Environment by Day

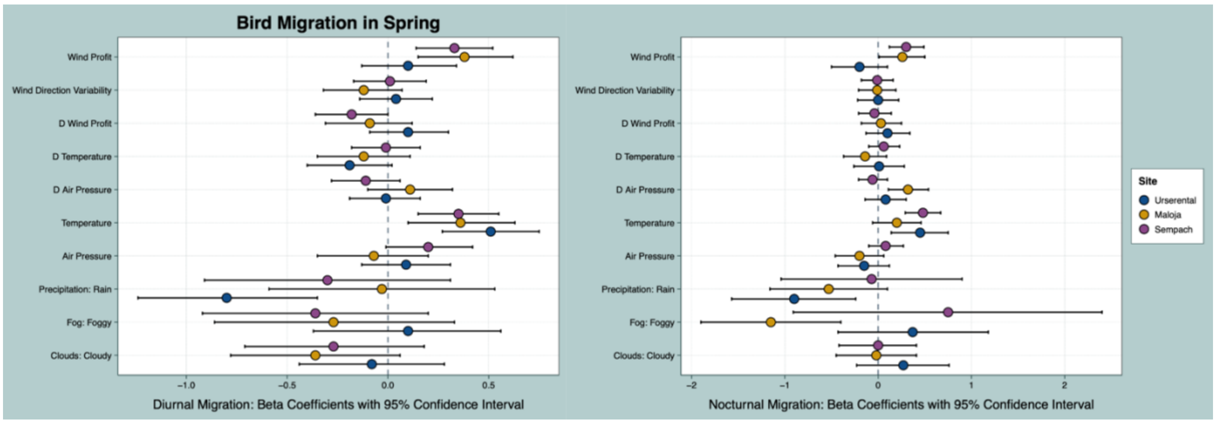

Figure 13: Influence of environmental predictors on daily Resid_MTR during spring.

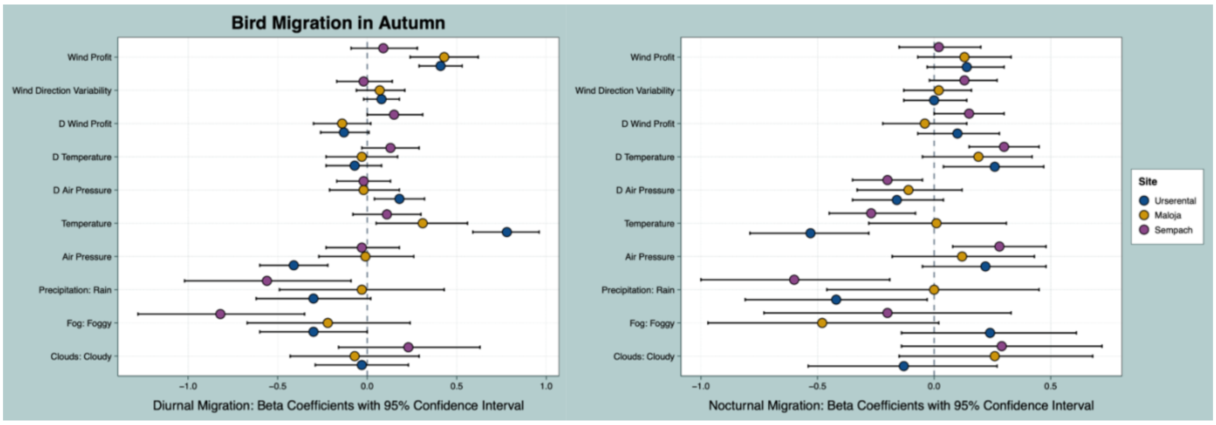

Figure 14: Influence of environmental predictors on daily Resid_MTR during autumn.

Figure 13 and Figure 14 show the effect sizes of environmental factors on MTR. The modelling process is described in Chapter 2.8. Numeric R summary table outputs can be found in the Appendix (I).

It comes clear that the effect sized were estimated with large confidence intervals that often overlap zero. This indicates the low significance of these effects. On the other hand, there are also variables with a clear effect on Resid_MTR, which is also revealed in the summary tables in the Appendix. Wind profit has a significant positive effect on MTR residuals, while rain and fog generally have a negative effect. It is interesting that for nocturnal spring migration the error intervals are relatively small, but in the other cases, large errors are responsible for the low significance.

The highest overall significance was found in Sempach, while the model for Maloja had the lowest significance.

It is difficult to find common differences between Alpine and lowland sites when regarding the effects of meteorologic variables. But there are quite clear differences in how wind profit influences MTR residuals during autumn. While wind profit has an effect around zero in Sempach, there is a very clear positive effect at the two Alpine sites.

3.5 Influence of the Environment by Hour

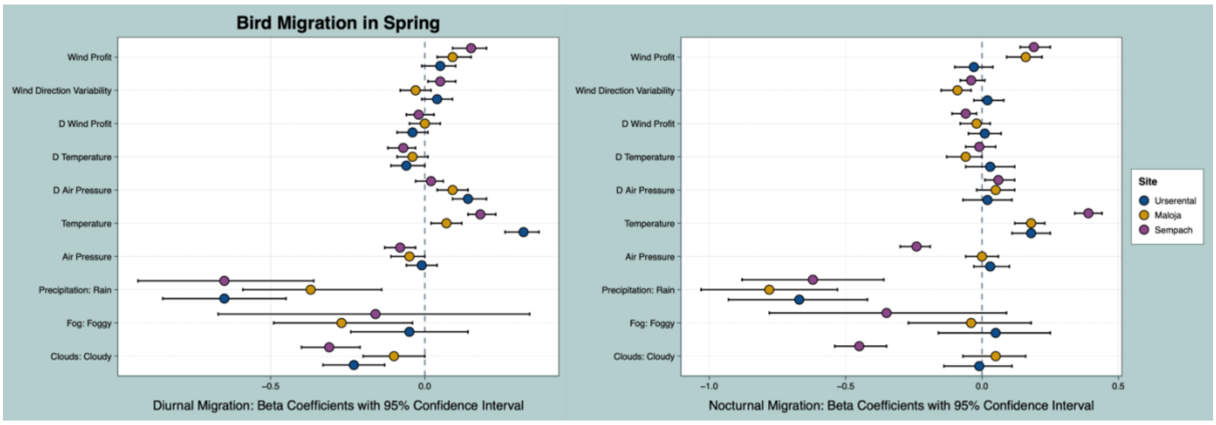

Figure 15: Influence of environmental predictors on hourly Resid_MTR during spring.

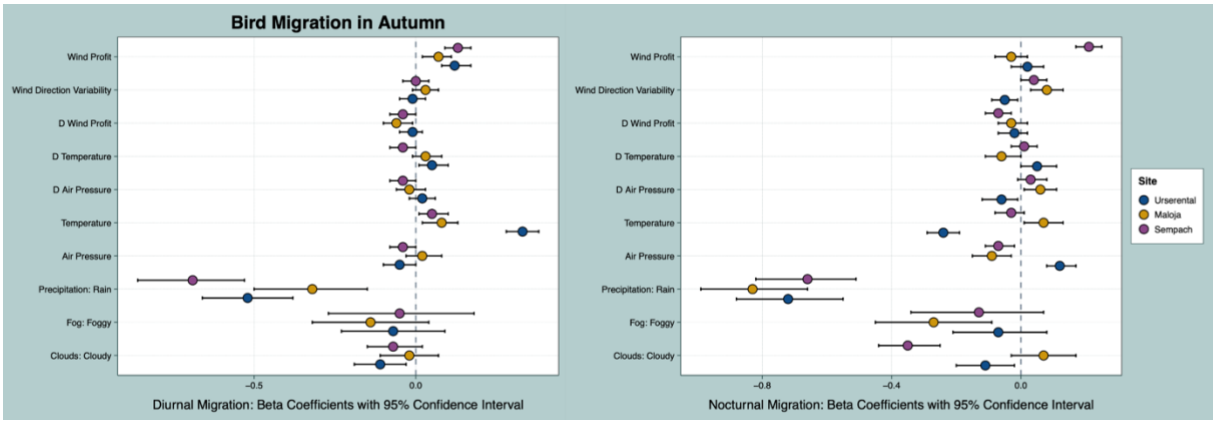

Figure 16: Influence of environmental predictors on hourly Resid_MTR during autumn.

Calculating the same model based on hourly values resulted in higher significance of the environmental predictors (see Appendix II). In Figure 15 and Figure 16 this is expressed through much narrower error bars. Rain, fog and clouds generally cause a negative deviance of measured bird volumes from the seasonally expected MTR while wind profit is positively related to MTR residuals.

Because the least significance was found in the change variables (D_Wind_Prof, D_ATempMean and D_AirPresPa) and the wind direction variability (WiDirStd) I fitted another model without including these four variables. The result can be seen in Figure 17 and Figure 18.

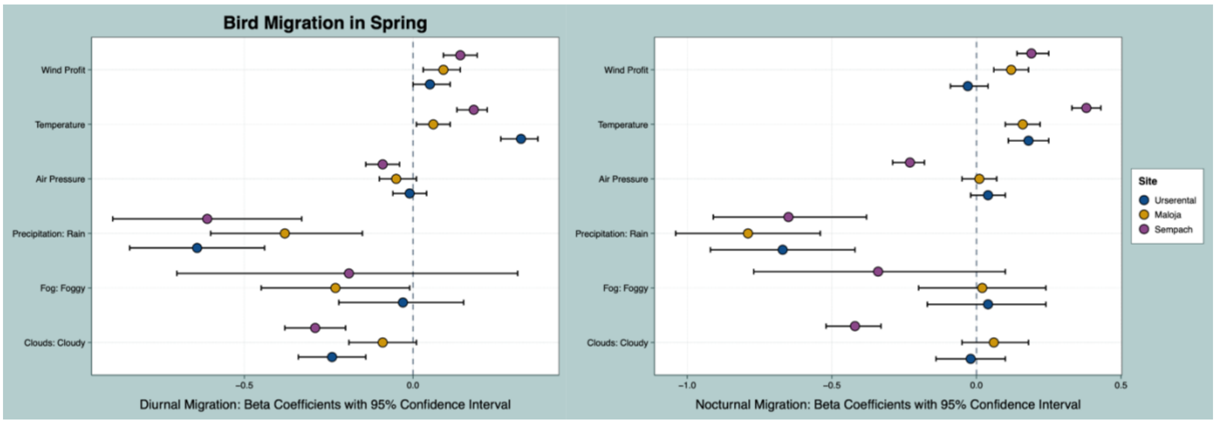

Figure 17: Influence of a limited set of environmental predictors on hourly Resid_MTR during spring.

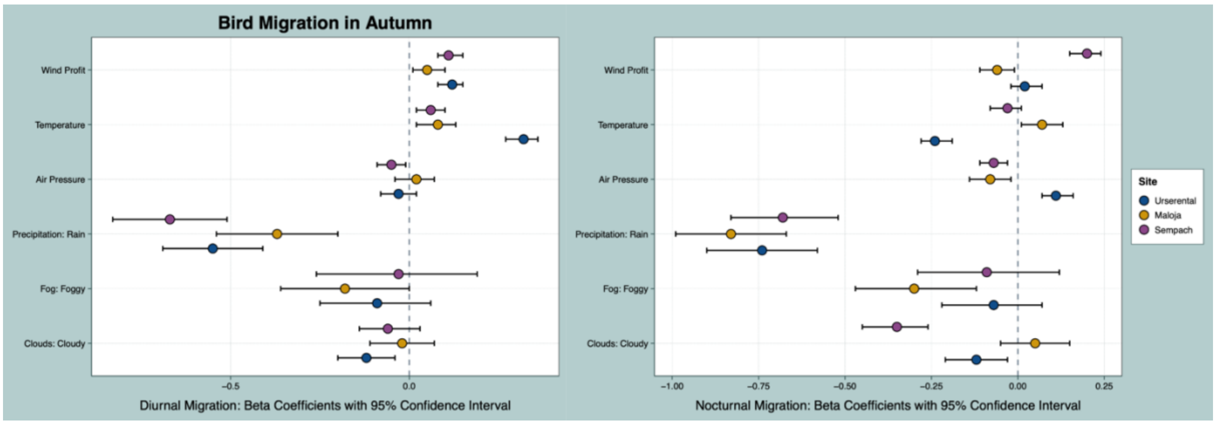

Figure 18: Influence of a limited set of environmental predictors on hourly Resid_MTR during autumn.

Now it becomes apparent that for spring migration, the confidence intervals are wider than for autumn migration, making the effect estimates less significant. Wind profit clearly has a positive effect when regarding Sempach, but the effect is less significant for the Alpine sites. Temperature has a positive effect at all sites, except for nocturnal autumn migration, while for Sempach and the Urserental the effect is negative. The effect of air pressure generally is significant, suggesting that lower air pressure is in favour of migrating birds. For air pressure, the effect is strongest for the lowland site in Sempach. Rain has a very strong negative effect for all three sites. Similarly, for fog, the effect is negative, but has a larger uncertainty for the lowland site. In spring, fog seems to negatively influence Resid_MTR in Sempach, while having no effect at Alpine locations. Clouds also have a negative effect in general, but again, except for diurnal autumn migration, the strength appears to be highest in the lowlands.

In addition to the models that were calculated based on the expected MTR values for only the reference station, I have created a second data frame for the expected migration intensities by using local measurements. The result was a local expected migration intensity over the course of the year for all three sites separately. On this, I once again modelled the effect of the environment, using the limited set of explanatory variables. The result can be seen in the plots contained in Figure 19 and Figure 20.

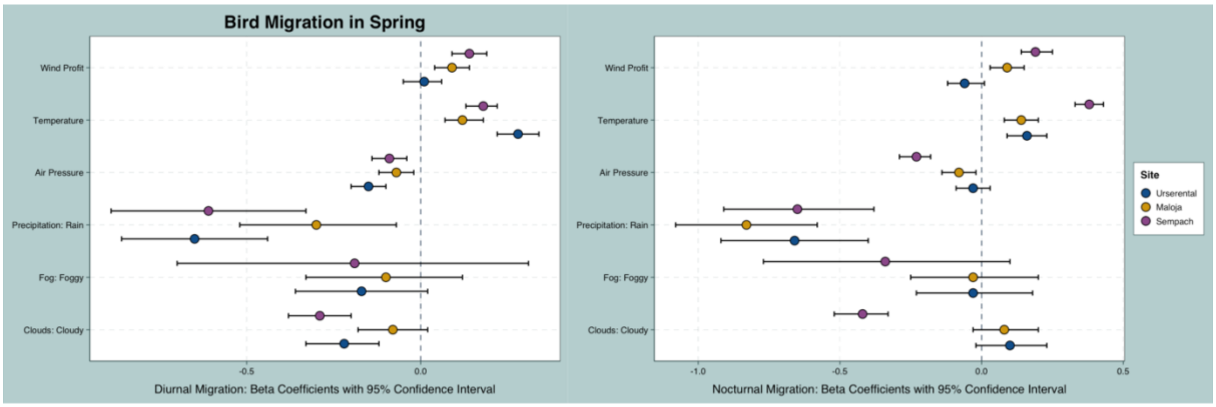

Figure 19: Influence of a limited set of environmental predictors on local hourly Resid_MTR during spring.

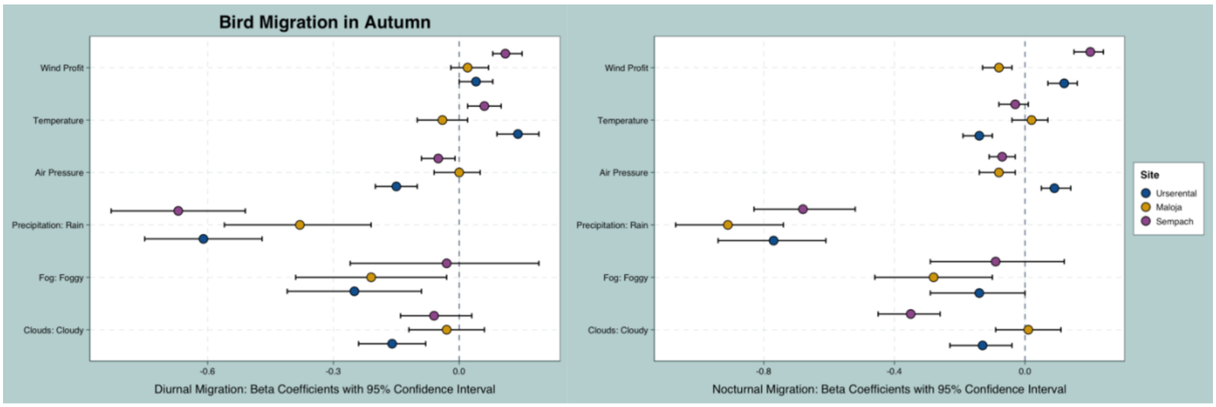

Figure 20: Influence of a limited set of environmental predictors on local hourly Resid_MTR during autumn.

The locally modelled effects highlight the difference of the influence of wind profit between Alpine and lowland site.

3.6 Consistency between Sites

Table 3: Between-site correlations for the year 2019 (top) and 2020 (bottom). The values show correlations between the daily mean MTR values at each site with differentiation between diurnal (left) and nocturnal (right) migration.

2019					
Spring Day			Spring Night		
	rho	p-value		rho	p-value
SEM-MAL	0.3374836	0.008949602	SEM-MAL	0.3051184	0.01878095
SEM-URS	0.5339061	1.332054e-05	SEM-URS	0.5751359	1.893182e-06
MAL-URS	0.4275526	0.0007312985	MAL-URS	0.6098049	2.949859e-07
Autumn Day			Autumn Night		
	rho	p-value		rho	p-value
SEM-MAL	0.2338992	0.02252889	SEM-MAL	0.3597115	0.000343274
SEM-URS	0.2990459	0.003241751	SEM-URS	0.5288708	3.600439e-08
MAL-URS	0.5654355	2.371165e-09	MAL-URS	0.2561929	0.01221138
2020					
Spring Day			Spring Night		
	rho	p-value		rho	p-value
SEM-MAL	0.6522996	1.637348e-08	SEM-MAL	0.5995332	4.156142e-07
SEM-URS	0.5255977	1.615955e-05	SEM-URS	0.7226452	0
MAL-URS	0.6346899	5.157634e-08	MAL-URS	0.765922	1.006557e-12
Autumn Day			Autumn Night		
	rho	p-value		rho	p-value
SEM-MAL:	0.4350749	1.175319e-05	SEM-MAL	0.4399017	1.133217e-05
SEM-URS:	0.1531003	0.1406965	SEM-URS	0.3906961	9.893871e-05
MAL-URS:	0.2836324	0.005601191	MAL-URS	0.5373787	2.34507e-08

I calculated the Spearman's rho of the MTR values between each of the sites for spring and autumn migration. Values for *rho* and the associated p values are listed in Table 3.

As documented in in Table 3, generally, I found higher correlations during spring than during autumn migration. Within one of the two seasons, the values for rho suggest a higher correlation during the night than for diurnal migration.

For nocturnal migration, Spearman's *r* usually was smaller between Sempach and Maloja than between Sempach and the Urserental. However, the highest values during spring were estimated between the two Alpine sites. It is much more difficult to retrieve general trends for autumn migration. In 2019, the highest values were also estimated between Sempach and the

Urserental. However, the correlation was lower than during the spring season. In 2020, the correlation between Sempach and the Urserental was estimated as the lowest. The correlation between the two Alpine sites was very low in 2019 relatively high in 2020.

For diurnal migration, values above 0.5 for *r* are comparatively rare. Such high values were estimated between Sempach and the Urserental in spring 2019, between the two Alpine sites in autumn 2019 and between all sites during spring 2020.

The p-values highlight a low significance of the estimated correlation between Sempach and Maloja for 2019 and for diurnal between-sites correlations in general.

4 Discussion

4.1 Flight Directions

During this study I have uncovered several signs that the Alps have an influence on central European broad front bird migration. After these presented results, the alternative, an unhindered, topography-independent crossing of the mountain ridges is unlikely. This is in contrast to findings from the Austrian Alpine foothills, where it was concluded that birds overcome the lower eastern end of the Alpine mountain chain on a broad front (Aschwanden *et al.*, 2020).

The comparison of flight directions between the lowland site in Sempach and the two Alpine sites shows that birds who decide to cross the Alps are funnelled much more by topography and follow the course of valleys through the mountain chain. The maps in Figure 9 make it clear that the flight directions of most birds that pass by one of the radar stations at the Alpine sites match the local orientation of the Urserental or the Inntal. Likewise, Zehnder et al. who investigated the flight directions of birds at the Julier Pass and in Bivio presented a similar result, that birds follow the lowest elevation through valleys and only fly above the mountain peaks under the best environmental conditions with a strong support by the wind (Zehnder *et al.*, 2001).

The influence of the topography on migratory birds can also be found in the comparison between Maloja and the Urserental. While the upper Inntal leaves only little choice for the pursuit of a route with minimal climbs, the Urserental bifurcates at Hospental. During autumn migration, birds approach the branching through the upper Reusstal from the north. After passing by Hospental, they have the choice to fly over the Gotthard Pass towards the south, or to further follow the Urserental and fly over the Furka Pass towards the southwest. However, the plots in Figure 9 indicate that birds mainly follow the river Reuss to the southwest and fly over the Furka Pass, even though this requires them to climb to 2429 m.a.s.l. instead of only 2106 m.a.s.l. for the Gotthard Pass. A possible explanation could be that following the Urserental looks like the easier way because the valley is quite flat until the birds reach Rehalp. A second explanation could be that birds prefer to follow a southwestern direction, instead of going too far south. During spring, it is not clear from which pass the birds are coming. Either is possible, the Furka or the Gotthard, because when passing by Hospental they would probably follow a similar flight path, no matter from what mountain pass they were coming, and then follow the Reuss towards the lowlands.

A further interesting difference between Alpine and lowland flight directions is that in Sempach, diurnal and nocturnal patterns differ from each other for both, spring and autumn migration. While during spring, birds fly more northwards during the day than at night, in autumn, birds at daylight are heading more southwards. Because in the Alps, steep slopes guide the birds on a relatively narrow flyway through the valleys, diurnal and nocturnal flight directions do not differ significantly. The open space in Sempach does not require birds to follow such a narrow flyway. Diurnal and nocturnal migrants may follow different courses, owing to of the usage of different navigation cues. The phenomenon of clearly differing directional patterns between diurnal and nocturnal bird migration in Sempach has already been shown by Tschanz et al. in 2019, who studied data from the year 2017. They too have found these differing flight directions between diurnal and nocturnal migrants in Sempach, but not at their other two study sites in Winterthur and Geneva. Despite showing this phenomenon, they have not further described it or discussed the reason behind it. Although it is not known yet why in Sempach, diurnal and nocturnal migration directions differ from each other, there are two hypotheses which I was discussing with Felix Liechti from the Swiss Ornithological Institute. The first is that nocturnal migrants tend follow the artificial light of the Swiss plateau in the west and avoid the dark Napf region in the southwest of Sempach. It has been immensely discussed that nocturnal migrants are attracted or disoriented by ALAN (Martin, 1990; Evans Ogden, 2002; Van Doren *et al.*, 2017; van Doren *et al.*, 2021) and so, the pull of the brightly illuminated Swiss plateau is plausible. The second hypothesis has to do with the fact that nocturnal migrants fly at higher altitudes than diurnal migrants (see Figure 10). Because of this, they can see the larger picture of the Alps as an obstacle and spaciously fly around the northern foothills of the mountain chain. Diurnal migrants instead fly at lower altitudes and thus do not recognize the Alps as such an obstacle that needs to be circumvented. Instead, they would follow the valleys of the pre-Alps, which would guide them from Sempach to the southwest through the Entlebuch. Both hypotheses are possible and do not exclude each other.

The channelling of birds in the Swiss Alpine valleys that I have observed in the data and that I have illustrated in Figure 9 does not exclude that there still are birds that cross the Alps at much higher altitudes and just fly across the mountain chain, uninfluenced by topography. This is because the radar recording did not record birds that have passed by the sites at altitudes of more than 2000 m.a.g.l. Yet, we know that birds are capable of flying at much higher flight levels of 5000 meters and more above sea level (Bruderer and Peter, 2017; Bruderer, Peter and Korner-Nievergelt, 2018)

4.2 Flight Altitudes

I hypothesized that at higher elevations, flight altitudes would be more compressed than in the lowlands. As shown in Figure 10, I did not find any evidence for this. Instead, the widest IQRs were measured in the Urserental during spring migration. But also, during autumn migration, IQRs at both Alpine sites were wider than those for Sempach. It is therefore not the case that birds who decide to follow Alpine valleys through the mountains avoid high climbs to a level that would significantly increase bird densities at very low flight levels. It seems much more likely that birds adjust their flight levels to the rising ground or that other factors are responsible for the birds to climb to higher altitudes than would be required. It is well possible that also within Alpine valleys, birds seek out flight levels to maximize wind support (Liechti and Schmaljohann, 2007).

The overall general pattern showed higher IQRs during nocturnal migration with a sharp increase shortly after civil dusk. This is in accordance with previous observations, who reported that birds after their evening departure quickly climb to their preferred flight altitude (Dokter *et al.*, 2011; Bruderer, Peter and Korner-Nievergelt, 2018).

During migratory stages, the highest bird densities within a vertical profile typically correlate with altitude where the most supporting winds can be found and birds accept climbing to higher altitudes when the excess amount of energy spent is compensated by wind support at the optimal flight level (Able, 1970; Gauthreaux, 1991). Some of the wider IQRs during autumn migration at the Alpine sites could be explained by local wind systems that are a part of what makes the weather inside Alpine valleys special. The wind system in a valley is highly influenced by local thermal effects: in the morning, the air usually flows upwards the valley, driven by the faster heating of air above the mountain slopes. After sunset, the faster cool down of air masses at higher elevations causes a downwards airflow. The radar's location in the Urserental still lies around 1000 meters below the pass height and so, during the early night hours, birds that come from the lowlands would face this downwards flowing airstream at lower altitudes. Maybe this phenomenon is responsible for the birds to quickly rise above the air that is influenced by the mountain breeze. In Maloja, which is located at the pass height of the Inntal, this weather effect could have some influence on low-flying birds too because the surrounding mountain peaks still are considerably higher and make the emergence of such winds possible.

However, winds probably can't explain the additional increase of IQRs during spring migration in the Urserental. But during spring, birds who pass by Hospental already climbed over the Furka Pass or the Gotthard. From a bird's perspective, it is reasonable to preserve the flight altitude that was required to overcome the Furka Pass at 2429 m.a.s.l or the Gotthard at 2106 m.a.s.l. and descend slowly while exploiting the potential energy accumulated during the high climb. Birds that took off before nightfall and then flew over the top of the pass would explain the extremely rapid increase of the IQRs after civil dusk. The fact that during autumn, the vertical patterns of the Urserental and Maloja do not differ significantly from each other supports this explanation.

4.3 Migration Phenology

Migration patterns between the sites differed significantly. Figure 11 shows the raw bird migration volumes for each site and reveals that there are seasonal, as well as spatial differences in the data. Just recently, scientists modelled year-round bird migration with a fluid dynamics model based on weather radar data and found that the relative number of birds arriving in spring is less than half the relative number of birds that leave in autumn (Nussbaumer *et al.*, 2021). During spring migration, less birds return than have flown away during autumn migration. Challenges faced during migratory flights can cause mortalities up to 90 % (Newton, 2006). It is therefore not surprising that the estimates for year-round bird numbers as plotted in Figure 12 show significantly weaker migration during the spring season than in autumn. This feature is especially strong in the Urserental, where the estimates during autumn exceed the maximum numbers in spring more than 8 times. The effect is much weaker in Sempach (~ 2 times) and Maloja, where in fact spring migration was stronger than autumn migration during 2019 and about equal during 2020. However, Figure 11 also shows that in the Urserental, the number of birds is strongly depending on the year, so that during 2019, spring migration included some massive events with more than 6000 birds per hour per km, while during 2020, only smaller events with numbers below 4000 birds per hour per km were recorded.

These findings indicate that birds chose different routes, depending on the season and year. The effect of large-scale wind patterns could be responsible for differences between years. When during autumn migration, dominating winds support flying through the Swiss plateau towards France, only few birds are expected to cross the Alps (Aurbach *et al.*, 2020). In consideration of energy efficiency, obstacle avoidance by flying around or climbing over a large object like a mountain did not have an effect as high as changing wind streams (Aurbach *et al.*, 2018). In other words, the theory that the crossing of the Alps is mainly dependent on prevailing winds is supported by simulations and energy models. Explicitly, the Alpine crossing is attractive when there are beneficial wind streams supporting it or when the wind situation for flying around the Alps is highly inconvenient (Bruderer, 1996).

As an example, Liechti et al. (1996) have observed how during autumn migration, the emergence of foehn winds led to the con centration of birds along the northern foothills of the Alps, where they moved towards southwest in the wind shade of the mountain chain. It would be unlikely that under such unfavourable wind conditions, birds chose to cross the Alps. Instead, prevailing northern to north-eastern winds would be supportive for an Alpine crossing and also led to a very low concentration along the northern Alpine boarder (Liechti, Peter and Lardelli, 1996).

Besides differences between years, there are significant differences between the seasons and sites. To understand why during the spring season, the two Alpine sites show much clearer signs of migration, in the case of Maloja in 2019 even the highest measured MTR of that year it is necessary to understand bird migration from the perspective of the birds. Birds have different priorities during spring than during autumn migration. Migration likely has evolved so that birds can exploit the seasonal abundance of resources within a habitat, which is especially beneficial during the breeding time when large quantities of food needs to be collected to feed their offspring and ensure a fast growth (Salewski and Bruderer, 2007; Somveille, Rodrigues and Manica, 2015). In autumn, birds leave their breeding habitat to spend the winter in the south. This allows them to avoid the extremely cold winter weather and associated food shortages (Boyle and Conway, 2007). So, in autumn, birds follow the food with the goal to survive the non-breeding season. The goal is to ensure their survival and therefore, migration is all about a safe arrival in the wintering habitat. In spring, besides exploiting the time of plenty, birds prioritize to maximize reproductive success. It is not just their own survival, but the passing on of their genes. Reproductive success is entangled with the amount of time available for breeding, including the possibility to replace a lost clutch (Morrison *et al.*, 2019). Successful occupation of a high-quality territory and an optimal nesting site is probably of similar importance, especially for male birds (Forstmeier, 2002). Male competition over ideal nesting sites is suspected to be a key driver for fast spring migration in male birds, which usually arrive earlier than the females (Kokko, 1999). So, while in autumn, flying safely is preferred because the goal is their own survival. Therefore, birds accept making detours from the shortest flyway, which is different during spring migration, where it is all about a fast arrival (Hahn *et al.*, 2014).

The urge to arrive early in spring could be responsible for different route choices between the seasons with the result that more birds cross the Alps during spring than in autumn. Differences between the seasons can though have another reason. In these latitudes, westerly winds prevail and the Bergell, which is the Alpine valley that leads to Maloja from the south, together with the Inntal forms a corridor from southwest to northeast. So, birds that would fly along this route can probably benefit from wind support more often, because the Alpine valleys would also channel the wind. Both explanations make sense and could also work together.

Because the years 2019 and 2020 differ from each other in terms of spring migration intensities in the Alps, a major effect of the weather is obvious and in accordance with previous studies. So far, other case studies highlighted the role of the wind for the crossing of the Alps during autumn and the spring migration season has not been studies so much yet. This is evidence that there are major differences between different years that might be caused by large-scale weather patterns.

4.4 Influence of the Environment

It is well established that wind and rain are the main environmental impacts on bird migration. Migrants schedule their departure in dependence of beneficial weather. On their way, birds are at the mercy of the wind which can easily double the effort necessary to overcome a certain distance, or half it (Liechti, 2006). Fog and low-altitude clouds make navigation difficult and were found to be responsible for birds to interrupt a flight, make a detour or return from the attempt to cross an ecological barrier (Martin, 1990; Saino *et al.*, 2010; Panuccio *et al.*, 2019). Heavy rainfall can quickly kill thousands of birds in flight (Newton, 2007). To cope with such meteorological challenges, migratory birds adjust their flight altitude to maximize wind profit (Liechti *et al.*, 2018) or they sit out poor weather situations on the ground (Schaub, Liechti and Jenni, 2004).

The findings from my own analysis are consistent with these prior results. Wind profit, rain, fog and clouds were the environmental effects that I found to have the strongest and most significant effects on MTR residuals from the expected bird migration volume for a given time on a given day. In addition, air temperature and air pressure had surprisingly strong influence on the number of birds recorded. While the effect of air pressure was negative in most cases, temperature was positively correlated with Resid_MTR for diurnal, and negatively correlated for nocturnal migration. The reason for this could be that under a clear sky, diurnal temperatures increase fast under the light of the sun, while during the night, a clear sky leads to a faster cooling of the atmosphere. As for air pressure, only a handful of studies venture a statement on how birds react to it. Panuccio et al. found that higher air pressure correlates with larger numbers of birds (Panuccio *et al.*, 2019), or, in other words, during nocturnal spring migration, most birds were recorded after the passage of a warm front just before the arrival of a cold front (Bagg *et al.*, 1950), which is also when barometric pressure is increased. Inexplicably, I found air pressure to have a negative effect on Resid_MTR in most cases, as Figure 15 and Figure 16 show. But the p-values of the models did not support a significant effect of air pressure on bird volumes (see Appendix I).

Wind profit had a positive effect on bird volume, except for nocturnal spring migration in the Urserental at daily and hourly scale and nocturnal autumn migration in Maloja at an hourly scale. For diurnal and nocturnal migration during both seasons, the positive effect of wind profit was strongest in Sempach. The weaker effect of wind profit at the Alpine sites could find an explanation in the result of a simulation made by Liechti et al., where the strongest tendency of birds to enter Alpine valleys for a mountain crossing was when birds were facing strong head winds (Liechti, Guélat and Komenda-Zehnder, 2013). Inside the Alps, wind fields would change frequently, and migrants would have a chance to reduce the amount of energy required, compared to the energy costs of continuing migration towards southeast through the lowlands, regardless of the energy needed for the climb over the pass heights.

The analysis of the variables for clouds and fog was not meaningful at a daily scale. Despite that there was a tendency towards a negative effect of fog and a thick cloud cover on an hourly scale, the effects were often insignificant, especially for the two Alpine sites. As the information on fog was not delivered by MeteoSwiss, I had to create an own fog indicator, using measurements of dew point and air temperature. Estimating fog from only these two variables is a very simple method, but leaves out other factors that influence the formation of fog, such as the presence of winds (Shim and Lee, 2017). Hence, when the temperature is equal to, or falls below the dew point, there is a fog situation. But despite having a relative humidity of 100%, what is required for the formation of fog, it is either possible that the water which is released from the atmosphere doesn't create fog but builds up clouds or settles on to the ground as dew. This problem probably is responsible for the relatively large confidence intervals for the effect of fog, especially during spring migration in Sempach. But it is similarly possible that despite some case studies highlight the adverse effect of for on their target species, most birds do not ignore fog, but still keep on flying when confronted with it (Griffin, 1972).

In comparison, the effect of heavy cloud cover was much clearer than for fog. It was most significantly negative for the lowland site in Sempach, while instead for the Alpine sites some estimates, although with insignificant p-values, were positive. So had clouds a positive effect on Resid_MTR for nocturnal spring and autumn migration in Maloja and almost no effect for nocturnal spring migration in the Urserental. While this was not as expected because heavy cloud cover increases the difficulty of nocturnal navigation, there are sources that observe that despite birds showing weak signs of disorientation when flying through clouds or fog, they were still able to follow a well-defined course (Griffin, 1972).

The strongly negative results for the occurrence of rain and its effect on the birds' decision to fly or not should be taken with a grain of salt. The reason is that when there is rain, the radar device is supposed to stop recording. However, because the rain needs to be strong enough and it needs to reach the ground, there can still be time intervals with data during rain events. Therefore, the effect is negative, but with rather large confidence intervals and differences between the locations.

In the beginning of my studies, I hypothesized that when birds profited from strong wind support when flying across the Alps or when strong headwinds increased the amount of energy required to fly around them, birds would prefer crossing the Alps before following the lowlands. After Figure 16, nocturnal autumn migration supports this hypothesis: while for Sempach there is a strong, significant positive effect of wind support on migration intensity, the two Alpine sites do not follow this trend. By comparing Figure 18 and Figure 20, it becomes clear that Sempach and the Urserental, despite lying relatively close to each other, are influenced very differently by the wind. Figure 18 shows the models of site-specific environmental influences on MTR residuals calculated by only using data from Sempach. The plot shows a positive effect of wind profit for Sempach, but a negative effect for the Urserental. Figure 20 instead illustrates the output of the model that explains site specific environmental effects on site specific MTR residuals and shows a positive effect of wind profit for the Urserental too – even if the effect size is slightly smaller than for Sempach. I think that this depicts the complicated role of the wind within and around a complex topographic structure and highlights the remarkable ability of migratory birds to seek out the best possible flyways for energy conservation. However, although these results give an impression on the factors and drivers of migratory birds' behaviour in topographically challenging regions, there definitely are gaps that remain unclear. Such gaps could be further closed by future tracking studies with geolocators such as GPS devices, or by using weather radar to analyse large-scale mass movements on a two- or three-dimensional spatial scale. Single flight tracks or also mass movements of birds through a continuous wind field could help us to further understand the complex interaction of topography and wind.

4.5 Consistency between Sites

I detected the highest correlations of bird volumes between the sites for nocturnal spring migration, especially between the two Alpine sites. I found the weakest correlation generally between Maloja and Sempach. Tschanz et al. demonstrated that in comparison, the continuity of bird volumes is much larger in the lowlands. They have calculated the Spearman's *rho* for MTR values between Sempach, Winterthur and Geneva and got back very high values of approximately 0.8 between all three sites (Tschanz *et al.*, 2019). For diurnal autumn migration, they found values for Spearman's *rho* between 0.55 and 0.75. During spring migration, the consistency in the lowlands was lower, with values between 0.3 and 0.7 for diurnal and 0.4 and 0.6 for nocturnal migration (Tschanz *et al.*, 2019). In contrast to the results of Tschanz et al., the correlations between the sites in the Alpine region was higher in spring than in autumn. During autumn, I assume that most birds follow the Alps westwards through the lowlands. For that reason, Tschanz et al. retrieved such high correlation coefficients during autumn. Birds that decided to fly westwards were reported to follow the northern foothills of the Alps, leading to this high connectivity, and birds that cross the Alps during autumn migration would usually be motivated by supportive winds or would be approaching the Alps on exceptionally high altitudes (Bruderer and Jenni, 1990). In spring instead, the Alps have no such strong function as a guidance for birds that migrate through the lowlands and birds migrating through the lowlands can just navigate more northwards. This would also be a possible explanation for the relatively low MTR values that I have found for Sempach during spring in both years and especially in the model for expected bird volumes which is based on measurements of five years.

During autumn, the low consistency between my own study sites could be explained by the fact that the upper Inntal, the Urserental and Sempach are not aligned – birds that pass by Maloja during autumn come from a totally different region than birds that fly through the Urserental. So, the volume of birds that pass by Maloja does not reflect the volume measured at Hospental or Sempach. Furthermore, because the weather inside the Alps can have large differences between regions, the three study sites could strongly differ in regard of wind and rain patterns, because they are influenced by different weather systems. The high correlations between the Alpine but also between Alpine and lowland sites during spring could be caused by first, the benefit of an early arrival and the fact that crossing the Alps is a more direct route for birds coming from the south and second, the arc-like shape of the Alps, which funnels birds approaching from the south and drives them into the Alpine valleys. When we focus only on those birds that cross the Alps by following valleys, birds that do so during autumn would enter the Inntal and the Reusstal which leads to the Urserental on very different places. The upper Reusstal is entered from Luzern in the centre of Switzerland, while the entrance of the Inntal is located south of Rosenheim, Austria, almost 300 km to the east. This possibly leads to the relatively low correlations I found for autumn migration. In spring instead, the entrances are much closer to each other. Spring migrants coming from northern Italy could be funnelled towards the region around Como, at least when they follow the southern foothills of the Alps likewise, they do during autumn along the northern slopes. In the region around Varese and Como, a further following of the slopes towards the northeast is no more possible and to further maintain a northerly course, birds must cross the Alps. The entrances of the valleys leading to the Maloja Pass or the Gotthard Pass are approximately 40 km away from each other and are just in this region of the mountain chain that probably marks the final point from which on a further following of the mountain slopes is no more reasonable. Figure 21 illustrates how in autumn birds that enter the Inntal in Rosenheim or the Reusstal in Flüelen may follow the course of valleys to move through the Alps, or how in spring, birds may enter these valleys in

Villeneuve VD, Locarno or Como to pass by one of the radar stations. However, under very good weather conditions, birds that approach the Alps from north or south were also found to just fly over the ridges and ignore these valleys (Zehnder *et al.*, 2001). A third possibility besides flying through valley and migrating independently of topography would be that birds may use the course of the valleys as a guiding landmark, but not be restricted to their orientation. However, it is likely that birds use the valleys as a passage, which is suggested by the investigation of their flight directions and their flight altitudes when they passed by the radar devices.

Summarizing the discussion of MTR correlations, I assume that birds that pass Maloja or Hospental during spring belong to the same group of birds which entered the area from the Po Valley. Sempach, from the perspective of a spring migrant over northern Italy, is located behind the Alps and the birds that pass by there probably came from Geneva and have flown over the Swiss Plateau or have elsewhere crossed the Alps. To pass by Sempach, birds that were detected in the Urserental before would have to make a detour from the preferred north-eastern flyway. In autumn, birds approach the Alps from north to north east and most of them will follow the Alps in parallel to the first ridges or over the Swiss Plateau (Bruderer and Jenni, 1990). Birds that cross the Alps during autumn belong to a different group that entered the area at very high altitudes or have split from the group that follows the ridges to fly into a valley (Bruderer and Jenni, 1990). The connectivity between Sempach and the Urserental in autumn, between the two Alpine locations in spring and between the Urserental and Sempach in spring is well illustrated by the results of this analysis.

Figure 21: Overview of the Alpine arc. The locations of the three radar stations are marked with pink circles. Entrance points of the study's Alpine valleys are marked with green circles. The course of the valleys is marked with a dark blue line.

5 Conclusion

This study investigated the influence of the Alps on migrating birds with the aim of finding evidence of a barrier effect. The results clearly speak for an influence of the topography on the birds' flight behaviour. First, the directional pattern of individual radar echoes at the Alpine sites highlighted a high degree of alignment of the flight trajectories, while at the lowland station in Sempach, there was a distinct difference between the directions for diurnal and nocturnal migrants, as well as an overall higher variability within the flight directions. Second, I found that wind profit and heavy cloud cover have a weaker effect on MTR deviations from the modelled expected bird volume at the Alpine sites than at the lowland site. Third, the Spearman's rank coefficients of MTR values between the sites revealed a different connectivity for spring and autumn migration, which indicates that while during spring migration, birds recorded at Maloja and Hospental came from the same pool that departed in the Po Valley in northern Italy, while during autumn migration, the two Alpine sites were only weakly correlated, suggesting that autumn migrants detected in the Urserental and in Maloja belong to different pools of birds. This speaks against a completely topography-independent bird migration over the Alps.

The relatively low flight altitudes and the high degree of parallelism in the flight directions which I found during the analysis of the data collected at the two Alpine sites suggest that many migratory birds use these valleys to either avoid high climbs over the mountain peaks when crossing the Alpine Mountain chain, or follow the valleys because of better wind conditions, or follow them for orientation. Either way, whether birds use these Alpine valleys for orientation or whether they allow them a relatively energy-efficient passage through the mountains, some valleys seem to be of high importance to birds. Because low flying migrants are obviously channelled inside the valleys, these flyways must be treated with a special focus on bird protection. This is also reflected by the map on the conflict potential of wind energy created by the Swiss Ornithological Institute on behalf of the Federal Office for the Environment FOEN (Horch *et al.*, 2013). The map shows most of the Alpine valleys and mountain passes, including the two sites examined here as areas with a high or very high potential for conflict. According to this, recently implemented projects such as the new wind farm on the Gotthard Pass (Lob, 2020) are in line with a sustainable energy strategy, but they represent a considerable risk for migratory birds. Valleys and pass heights are bottlenecks in the flyways of migratory birds that fly through the Alps. It was shown that the number of bird collisions at wind farms are strongly related to the migration phases in spring and autumn (Shamoun-Barnes, van Gasteren and Ross-Smith, 2017) and it is assumed that bad visibility increases the threat of bird collisions with artificial structures (Aschwanden *et al.*, 2018). Similarly, the powerlines which are used to transport the electricity to the consumers have been reported to be a danger to mainly larger bird species (Rubolini *et al.*, 2005). A danger on a much larger scale, is widespread lighting of our cities, settlements and other structures. Especially with low-altitude clouds, nocturnally migrating birds were observed to be attracted to brightly illuminated buildings and reported to collide with them or to become disoriented with the consequence of exhaustion (Erickson *et al.*, 2001; van Doren *et al.*, 2021).

Migratory birds are most vulnerable during migration. Unexpectedly narrow migration corridors as observed in a year-long tracking study suggest that some species target very distinct regions for stopover (Vardanis *et al.*, 2011; Tøttrup *et al.*, 2012). The survival of such species could therefore depend not the least on the preservation of these flyway corridors. Conservation efforts should, above all, facilitate migration and minimize the negative impact of man-made structures and human behaviour to birds. Some of the modern threats to birds are easy to mitigate. Experimental reduction of nightly illumination during critical times when high bird volumes were expected and clouds and winds drove birds towards regions with higher density of potentially dangerous structures, resulted in significantly lower numbers of bird fatalities (Evans Ogden, 2002). Because actual bird migration volumes were brought in relation to bird strikes (van Doren *et al.*, 2021), or collisions were mainly found during the migration seasons (Aschwanden *et al.*, 2018), the implementation of a large-scale real-time monitoring service in combination with consideration of local meteorologic conditions is thought to be a critical step in bird conservation efforts. Similarly, the implementation of bird warning systems in aviation have almost halved the number of bird strikes (van Gasteren *et al.*, 2019). An operational system should be able to temporarily reduce urban illumination and shut down wind turbines.

This study, like many related studies, has investigated how Switzerland is a special place in the palearctic migratory system due to its topography. Depending on the terrain, the currently dominant wind system and other meteorological factors such as the distribution of clouds, fog and rain, broad front bird migration is redirected, and birds are concentrated in very distinct areas. This improves our idea on the spatial extent of critical regions where the appearance of larger numbers of birds is possible and thus, of those regions where we need to focus our efforts for bird and nature conservation. Real-time data from the European weather radar network could be used for a large-scale monitoring service (Hüppop *et al.*, 2019). But for the Alps, other methods are needed because the mountains would cast a shadow in the radar recording (Bruderer, 1997) and birds moving through Alpine valleys remain hidden. To be able to interpolate real-time recordings of bird movements in the air or to be able to simulate bird movements in the Alps, we need to gather more knowledge on the drivers and the patterns of Alpine bird migration (Nussbaumer *et al.*, 2019). Therefore, we need to improve our understanding of how and when birds move through the Alps. Better models could be used in combination with the measurements from weather radars to fill gaps in the weather radar network.

References

Able, K. P. (1970) 'A Radar Study of the Altitude of Nocturnal Passerine Migration', *Bird-Branding*, 41(4), pp. 282–290.

Adamík, P. *et al.* (2016) 'Barrier crossing in small avian migrants: Individual tracking reveals prolonged nocturnal flights into the day as a common migratory strategy', *Scientific Reports*, 6. doi: 10.1038/srep21560.

Åkesson, S. *et al.* (2001) 'Reed warbler orientation: Initiation of nocturnal migratory flights in relation to visibility of celestial cues at dusk', *Animal Behaviour*, 61(1), pp. 181–189. doi: 10.1006/anbe.2000.1562.

Åkesson, S., Alerstam, T. and Hedenstrom, A. (1996) 'Flight Initiation of Nocturnal Passerine Migrants in Relation to Celestial Orientation Conditions at Twilight', *Journal of Avian Biology*, 27(2), p. 95. doi: 10.2307/3677138.

Åkesson, S. and Hedenström, A. (2000) 'Wind selectivity of migratory flight departures in birds', *Behavioral Ecology and Sociobiology*, 47(3), pp. 140–144. doi: 10.1007/s002650050004.

Åkesson, S. and Helm, B. (2020) 'Endogenous Programs and Flexibility in Bird Migration', *Frontiers in Ecology and Evolution*, 8(March). doi: 10.3389/fevo.2020.00078.

Alerstam, T. (1979) 'Wind as Selective Agent in Bird Migration', *Ornis Scandinavica*, 10(1), pp. 76–93.

Aschwanden, J. *et al.* (2018) 'Bird collisions at wind turbines in a mountainous area related to bird movement intensities measured by radar', *Biological Conservation*, 220(February), pp. 228–236. doi: 10.1016/j.biocon.2018.01.005.

Aschwanden, J. *et al.* (2020) 'Barrier effects of mountain ranges for broad-front bird migration', *Journal of Ornithology*, 161(1), pp. 59–71. doi: 10.1007/s10336-019-01704-4.

Aurbach, A. *et al.* (2018) 'Complex behaviour in complex terrain - Modelling bird migration in a high resolution wind field across mountainous terrain to simulate observed patterns', *Journal of Theoretical Biology*, 454, pp. 126–138. doi: 10.1016/j.jtbi.2018.05.039.

Aurbach, A. *et al.* (2020) 'Simulation of broad front bird migration across Western Europe', *Ecological Modelling*, 415(November 2019). doi: 10.1016/j.ecolmodel.2019.108879.

Bagg, A. M. *et al.* (1950) 'Barometric Pressure-Patterns and Spring Bird Migration', *The Wilson Bulletin*, 62(1), pp. 5–19.

Bauer, S. *et al.* (2019) 'The grand challenges of migration ecology that radar aeroecology can help answer', *Ecography*, 42(5), pp. 861–875. doi: 10.1111/ecog.04083.

Bauer, S. and Hoye, B. J. (2014) 'Migratory animals couple biodiversity and ecosystem functioning worldwide', *Science*, 344(6179). doi: 10.1126/science.1242552.

Boyle, W. A. and Conway, C. J. (2007) 'Why migrate? A test of the evolutionary precursor hypothesis', *American Naturalist*, 169(3), pp. 344–359. doi: 10.1086/511335.

Bradarić, M. *et al.* (2020) 'Winds at departure shape seasonal patterns of nocturnal bird migration over the North Sea', *Journal of Avian Biology*, 51(10), pp. 1–11. doi: 10.1111/jav.02562.

Brändle, M. *et al.* (2002) 'Dietary niche breadth for Central European birds: Correlations with species-specific traits', *Evolutionary Ecology Research*, 4(5), pp. 643–657.

Bruderer, B. (1996) 'Vogelzugforschung im Bereich der Alpen 1980-1995.pdf', *Der Ornithologische Beobachter*, 93, pp. 119–130.

Bruderer, B. (1997) 'The Study of Bird Migration by Radar', *Naturwissenschaften*, 84, pp. 1–8.

Bruderer, B. (2003) 'The Radar Window to Bird Migration', *Avian Migration*, pp. 347–358. doi: 10.1007/978-3-662-05957-9_24.

Bruderer, B. and Jenni, L. (1990) 'Migration across the Alps', in Gwinner, E. (ed.) *Bird Migration*. Springer, Berlin, Heidelberg, pp. 60–77. doi: https://doi.org/10.1007/978-3-642-74542-3_5.

Bruderer, B. and Peter, D. (2017) 'Windprofit als Ursache extremer Zughöhen', *Ornithologische Beobachter*, 114(2), pp. 73–86.

Bruderer, B., Peter, D. and Korner-Nievergelt, F. (2018) 'Vertical distribution of bird migration between the Baltic Sea and the Sahara', *Journal of Ornithology*, 159(2), pp. 315–336. doi: 10.1007/s10336-017-1506-z.

Buler, J. J. and Dawson, D. K. (2014) 'Radar analysis of fall bird migration stopover sites in the northeastern U.S.', *The Condor: Ornithological Applications*, 116(3), pp. 357–370. doi: 10.1650/CONDOR-13-162.1.

Dokter, A. M. *et al.* (2011) 'Bird migration flight altitudes studied by a network of operational weather radars', *Journal of the Royal Society Interface*, 8(54), pp. 30–43. doi: 10.1098/rsif.2010.0116.

Dokter, A. M. *et al.* (2013) 'High Altitude Bird Migration at Temperate Latitudes: A Synoptic Perspective on Wind Assistance', *PLoS ONE*, 8(1), pp. 1–8. doi: 10.1371/journal.pone.0052300.

van Doren, B. M. *et al.* (2021) 'Drivers of fatal bird collisions in an urban center', *Proceedings of the National Academy of Sciences of the United States of America*, 118(24). doi: 10.1073/pnas.2101666118.

Van Doren, B. M. *et al.* (2017) 'High-intensity urban light installation dramatically alters nocturnal bird migration', *Proceedings of the National Academy of Sciences of the United States of America*, 114(42), pp. 11175–11180. doi: 10.1073/pnas.1708574114.

Dossman, B. C. *et al.* (2016) 'The effects of wind and fuel stores on stopover departure behavior across a migratory barrier', *Behavioral Ecology*, 27(2), pp. 567–574. doi: 10.1093/beheco/arv189.

Drent, R. H., Fox, A. D. and Stahl, J. (2006) 'Travelling to breed', *Journal of Ornithology*, 147(2), pp. 122–134. doi: 10.1007/s10336-006-0066-4.

Erickson, W. P. *et al.* (2001) *Avian Collisions with Wind Turbines: A Summary of Existing Studies and Comparisons to Other Sources of Avian Collision Mortality in the United States*. Washington D.C. Available at: www.nationalwind.org.

Erni, B. *et al.* (2002) 'Wind and rain govern the intensity of nocturnal bird migration in central Europe - A log-linear regression analysis', *Ardea*, 90(1), pp. 155–166.

Erni, B., Liechti, F. and Bruderer, B. (2005) 'The role of wind in passerine autumn migration between Europe and Africa', *Behavioral Ecology*, 16(4), pp. 732–740. doi: 10.1093/beheco/ari046.

Evans Ogden, L. J. (2002) *Summary report on the bird friendly building program: Effect of light reduction on collision of migratory birds*, *Fatal Light Awarences Program (FLAP)*.

Forstmeier, W. (2002) 'Benefits of early arrival at breeding grounds vary between males', *Journal of Animal Ecology*, 71(1), pp. 1–9. doi: 10.1046/j.0021-8790.2001.00569.x.

van Gasteren, H. *et al.* (2019) 'Aeroecology meets aviation safety: early warning systems in Europe and the Middle East prevent collisions between birds and aircraft', *Ecography*, 42(5), pp. 899–911. doi: 10.1111/ecog.04125.

Gauthreaux, S. A. (1991) 'The flight behavior of migrating birds in changing wind fields: Radar and visual analyses', *Integrative and Comparative Biology*, 31(1), pp. 187–204. doi: 10.1093/icb/31.1.187.

Greenberg, R. *et al.* (2000) ‘The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations’, *Ecology*, 81(6), pp. 1750–1755. doi: 10.1890/0012-9658(2000)081[1750:TIOAIO]2.0.CO;2.

Griffin, D. R. (1972) ‘Nocturnal bird migration in Opaque Clouds’, in Galler, S. R. et al. (eds) *Animal Orientation and Navigation*. Washington D.C.: National Aeronautics and Space Administration SP-262, Washington D.C. , U.S. Government Printing Office, pp. 169–188.

Haest, B. *et al.* (2019) ‘Autumn bird migration phenology: A potpourri of wind, precipitation and temperature effects’, *Global Change Biology*, 25(12), pp. 4064–4080. doi: 10.1111/gcb.14746.

Hahn, S. *et al.* (2014) ‘Variable detours in long-distance migration across ecological barriers and their relation to habitat availability at ground’, *Ecology and Evolution*, 4(21), pp. 4150–4160. doi: 10.1002/ece3.1279.

Hahn, S., Bauer, S. and Liechti, F. (2009) ‘The natural link between Europe and Africa - 2.1 billion birds on migration’, *Oikos*, 118(4), pp. 624–626. doi: 10.1111/j.1600-0706.2008.17309.x.

Hall, G. A. and Bell, R. K. (1981) ‘The diurnal migration of passerines along an Appalachian ridge’, *American Birds*, 35(2), pp. 135–138.

Halupka, L. *et al.* (2017) ‘Conditions at autumn stopover sites affect survival of a migratory passerine’, *Journal of Ornithology*, 158(4), pp. 979–988. doi: 10.1007/s10336-017-1472-5.

Hardesty-Moore, M. *et al.* (2018) ‘Migration in the anthropocene: How collective navigation, environmental system and taxonomy shape the vulnerability of migratory species’, *Philosophical Transactions of the Royal Society B: Biological Sciences*, 373(1746). doi: 10.1098/rstb.2017.0017.

Harper, W. G. (1958) ‘Detection of bird migration by centimetric radar - a cause of radar “angles”’, *Proceedings of the Royal Society B*. doi: 10.1098/rspb.1958.0088.

Horch, P. *et al.* (2013) *Konfliktpotenzialkarte Windenergie – Vögel Schweiz: Teilbereich Brutvögel, Gastvögel und Vogelschutzgebiete gemäss WZVV. Erläuterungsbericht. Aktualisierung 2013*. Sempach. Available at: http://www.vogelwarte.ch/konfliktpotenzialkarte.html.

Hüppop, O. *et al.* (2019) ‘Perspectives and challenges for the use of radar in biological conservation’, *Ecography*, 42(5), pp. 912–930. doi: 10.1111/ecog.04063.

Jenni, L. *et al.* (1991) ‘Jenni (1991) | Zugverhalten von Weissstörchen.pdf’, *Der Ornithologische Beobachter*, 88, pp. 287–319.

Jenni, L. and Naef-Daenzer, B. (1986) ‘Vergleich der Fanghäufigkeiten von Zugvögeln auf dem Alpenpass Col de Bretolet mit Brutbeständen im Herkunftsgebiet’, *Der Ornithologische Beobachter*, 83(2), pp. 95–110. Available at: http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Vergleich+der+Fangh�ufigkeiten+von+Zugv�geln+auf+dem+Alpenpass+Col+de+Bretolet+mit+Brutbest�nden+im+Herkunftsgebiet#0.

Johnson, R. J. *et al.* (2011) ‘Global Perspectives on Birds in Agricultural Landscapes’, in Campbell, B. W. and Ortiz, S. L. (eds) *Integrating Agriculture, Conservation and Ecotourism: Examples from the Field. Issues in Agroecology – Present Status and Future Prospectus, vol 1.* Dordrecht: Springer, pp. 55–140. doi: 10.1007/978-94-007-1309-3_3.

Karlsson, H. *et al.* (2011) ‘Nocturnal passerine migration without tailwind assistance’, *Ibis*, 153(3), pp. 485–493. doi: 10.1111/j.1474-919X.2011.01130.x.

Karlsson, H. *et al.* (2012) ‘Nocturnal passerine migrants fly faster in spring than in autumn: A test of the time minimization hypothesis’, *Animal Behaviour*, 83(1), pp. 87–93. doi: 10.1016/j.anbehav.2011.10.009.

Kelly, J. F. *et al.* (2012) 'Quantifying animal phenology in the aerosphere at a continental scale using NEXRAD weather radars', *Ecosphere*, 3(2), p. art16. doi: 10.1890/es11-00257.1.

Kemp, M. U. *et al.* (2010) 'Can wind help explain seasonal differences in avian migration speed?', *Journal of Avian Biology*, 41(6), pp. 672–677. doi: 10.1111/j.1600-048X.2010.05053.x.

Kestenholz, M. *et al.* (2009) 'Phänologie und wetterabhängigkeit des herbstzuges der ringeltaube Columba palumbus auf der Ulmethöchi im Jura: Massenzugtage nach zugstaulagen', *Der Ornithologische Beobachter*, 106(2), pp. 193–207.

Kokko, H. (1999) 'Competition for early arrival in migratory birds', *Journal of Animal Ecology*, 68(5), pp. 940–950. doi: 10.1046/j.1365-2656.1999.00343.x.

Lack, D. and Varley, C. G. (1945) 'Detection of birds by radar', *Nature*, 156(October 13), p. 446.

Liechti, F. (2006) 'Birds: Blowin' by the wind?', *Journal of Ornithology*, 147(2), pp. 202–211. doi: 10.1007/s10336-006-0061-9.

Liechti, F. *et al.* (2018) 'Miniaturized multi-sensor loggers provide new insight into year-round flight behaviour of small trans-Sahara avian migrants', *Movement Ecology*, 6(1), pp. 1–10. doi: 10.1186/s40462-018-0137-1.

Liechti, F., Guélat, J. Ô. and Komenda-Zehnder, S. (2013) 'Modelling the spatial concentrations of bird migration to assess conflicts with wind turbines', *Biological Conservation*, 162, pp. 24–32. doi: 10.1016/j.biocon.2013.03.018.

Liechti, F., Klaassen, M. and Bruderer, B. (2000) 'Predicting migratory flight altitudes by physiological migration models', *The Auk*, 117(1), pp. 205–214. doi: 10.1642/0004-8038(2000)117[0205:PMFABP]2.0.CO;2.

Liechti, F., Peter, D. and Lardelli, R. (1996) 'Die Alpen, ein Hindernis im nächtlichen Breitfrontzug - eine grossräumige Übersicht nach Mondbeobachtungen', *Journal für Ornithologie*, 137, pp. 337–356.

Liechti, F. and Schmaljohann, H. (2007) 'Wind-governed flight altitudes of nocturnal spring migrants over the Sahara', *Ostrich*, 78(2), pp. 337–341. doi: 10.2989/OSTRICH.2007.78.2.35.115.

Liu, H. (2008) *Generalized Additive Model*. Duluth: Department of Mathematics and Statistics University of Minnesota Duluth. doi: 10.4135/9781412952644.n184.

Lob, G. (2020) 'Ein kleiner Schub für die Windkraft: Auf dem Gotthard steht nun eine Windanlage', *Luzerner Zeitung*. Available at: https://www.luzernerzeitung.ch/schweiz/gotthard-fuenf-neue-windraeder-eingeweiht-ld.1268172.

Lowery, G. H. (1951) 'A Quantitative Study of the Nocturnal Migration of Birds', *University of Kansas Publications*, 3(2), pp. 361–472. doi: 10.2307/4510313.

Martin, G. R. (1990) 'The Visual Problems of Nocturnal Migration', in Gwinner, E. (ed.) *Bird Migration: Physiology and ecophysiology*. Berlin: Springer, pp. 185–197. doi: 10.1007/978-3-642-74542-3_13.

McLaren, J. D., Shamoun-Baranes, J. and Bouten, W. (2012) 'Wind selectivity and partial compensation for wind drift among nocturnally migrating passerines', *Behavioral Ecology*, 23(5), pp. 1089–1101. doi: 10.1093/beheco/ars078.

Mellone, U. *et al.* (2015) 'Seasonal differences in migration patterns of a soaring bird in relation to environmental conditions: a multi-scale approach', *Behavioral Ecology and Sociobiology*, 69(1), pp. 75–82. doi: 10.1007/s00265-014-1818-4.

Mettke-Hofmann, C. and Gwinner, E. (2003) 'Long-term memory for a life on the move', *Proceedings of the National Academy of Sciences of the United States of America*, 100(10), pp. 5863–5866. doi: 10.1073/pnas.1037505100.

Morrison, C. A. *et al.* (2019) 'Why do earlier-arriving migratory birds have better breeding success?', *Ecology and Evolution*, 9(15), pp. 8856–8864. doi: 10.1002/ece3.5441.

Mukhin, A., Grinkevich, V. and Helm, B. (2009) 'Under cover of darkness: Nocturnal life of diurnal birds', *Journal of Biological Rhythms*, 24(3), pp. 225–231. doi: 10.1177/0748730409335349.

Newton, I. (2006) 'Can conditions experienced during migration limit the population levels of birds?', *Journal of Ornithology*, 147(2), pp. 146–166. doi: 10.1007/s10336-006-0058-4.

Newton, I. (2007) 'Weather-related mass-mortality events in migrants', *Ibis*, 149(3), pp. 453–467. doi: 10.1111/j.1474-919X.2007.00704.x.

Nilsson, C. *et al.* (2018) 'Field validation of radar systems for monitoring bird migration', *Journal of Applied Ecology*, 55(6), pp. 2552–2564. doi: 10.1111/1365-2664.13174.

Nilsson, C. *et al.* (2019) 'Revealing patterns of nocturnal migration using the European weather radar network', *Ecography*, 42(5), pp. 876–886. doi: 10.1111/ecog.04003.

Nilsson, C., Klaassen, R. H. G. and Alerstam, T. (2013) 'Differences in speed and duration of bird migration between spring and autumn', *American Naturalist*, 181(6), pp. 837–845. doi: 10.1086/670335.

Nussbaumer, R. *et al.* (2019) 'A geostatistical approach to estimate high resolution nocturnal bird migration densities from a weather radar network', *Remote Sensing*, 11(19). doi: 10.3390/rs11192233.

Nussbaumer, R. *et al.* (2021) 'Quantifying year-round nocturnal bird migration with a fluid dynamics model', *Journal of the Royal Society Interface*, 18(179). doi: 10.1098/rsif.2021.0194.

Panuccio, M. *et al.* (2019) 'Migrating birds avoid flying through fog and low clouds', *International Journal of Biometeorology*, 63(2), pp. 231–239. doi: 10.1007/s00484-018-01656-z.

Pastorino, A. *et al.* (2017) 'Fog and rain lead migrating White storks Ciconia ciconia to perform reverse migration and to land', *Avocetta*, 41(1), pp. 5–12.

Patchett, R. and Cresswell, W. (2020) 'Regional wind patterns likely shape a seasonal migration detour', *Journal of Avian Biology*, 51(11), pp. 1–6. doi: 10.1111/jav.02466.

Pedersen, E. J. *et al.* (2019) 'Hierarchical generalized additive models in ecology: An introduction with mgcv', *PeerJ*, 2019(5). doi: 10.7717/peerj.6876.

Peter, D., Trösch, B. and Lücker, L. (1999) 'Intensiver Vogelzug im Spätherbst als Folge einer Stauentladung', *Der Ornithologische Beobachter*, 96, pp. 285–292.

Richardson, W. J. (1978) 'Timing and Amount of Bird Migration in Relation to Weather: A Review', *OIKOS*, 30(2), pp. 224–272.

Rubolini, D. *et al.* (2005) 'Birds and powerlines in Italy: An assessment', *Bird Conservation International*, 15(2), pp. 131–145. doi: 10.1017/S0959270905000109.

Rubolini, D. *et al.* (2007) 'Intraspecific consistency and geographic variability in temporal trends of spring migration phenology among european bird species', *Climate Research*, 35(1–2), pp. 135–146. doi: 10.3354/cr00720.

Saino, N. *et al.* (2010) 'Spring migration decisions in relation to weather are predicted by wing morphology among trans-Mediterranean migratory birds', *Functional Ecology*, 24(3), pp. 658–669. doi: 10.1111/j.1365-2435.2009.01659.x.

Salewski, V. and Bruderer, B. (2007) 'The evolution of bird migration - A synthesis', *Naturwissenschaften*, 94(4), pp. 268–279. doi: 10.1007/s00114-006-0186-y.

Sánchez, M. I., Green, A. J. and Castellanos, E. M. (2006) 'Internal transport of seeds by migratory waders in the Odiel marshes, south-west Spain: Consequences for long-distance dispersal', *Journal of Avian Biology*, 37(3), pp. 201–206. doi: 10.1111/j.2006.0908-8857.03719.x.

Sanderson, F. J. *et al.* (2006) 'Long-term population declines in Afro-Palearctic migrant birds', *Biological Conservation*, 131(1), pp. 93–105. doi: 10.1016/j.biocon.2006.02.008.

Schaub, M., Liechti, F. and Jenni, L. (2004) 'Departure of migrating European robins, Erithacus rubecula, from a stopover site in relation to wind and rain', *Animal Behaviour*, 67(2), pp. 229–237. doi: 10.1016/j.anbehav.2003.03.011.

Schmid, B. *et al.* (2019) 'Size matters in quantitative radar monitoring of animal migration: estimating monitored volume from wingbeat frequency', *Ecography*, 42(5), pp. 931–941. doi: 10.1111/ecog.04025.

Shamoun-Barnes, J., van Gasteren, H. and Ross-Smith, V. (2017) 'Sharing the Aerosphere: Conflicts and Potential Solutions', in Chilson, P. P. et al. (eds) *Aeroecology*. Norman, Oklahoma USA: Springer International Publishing AG, pp. 465–497. doi: 10.1007/978-3-319-68576-2_17.

Shi, X. *et al.* (2021) 'Seasonal Trends in Movement Patterns of Birds and Insects Aloft Simultaneously Recorded by Radar', *Remote Sensing*, 13. doi: https://doi.org/10.3390/rs13091839.

Shim, H. and Lee, Y. (2017) '국지풍이 내륙의 안개발생에 미치는 영향', 27(2), pp. 213–224.

Sjöberg, S. and Moore, F. R. (2015) *Stopover behaviour in migratory songbirds: timing, orientation and departures*, *Ecology Building*.

Somveille, M., Rodrigues, A. S. L. and Manica, A. (2015) 'Why do birds migrate? A macroecological perspective', *Global Ecology and Biogeography*, 24(6), pp. 664–674. doi: 10.1111/geb.12298.

Steuri, T. (2012) *Estimation of flight direction and speed*. Available at: https://swiss-birdradar.com/detection-of-flight-speed-and-direction.html (Accessed: 9 July 2021).

Strandberg, R. and Alerstam, T. (2007) 'The strategy of fly-and-forage migration, illustrated for the osprey (Pandion haliaetus)', *Behavioral Ecology and Sociobiology*, 61(12), pp. 1865–1875. doi: 10.1007/s00265-007-0426-y.

Tankersley, J. R. and Orvis, K. (2003) 'Modeling the geography of migratory pathways and stopover habitats for neotropical migratory birds', *Conservation Ecology*, 7(1). doi: 10.5751/es-00483-070107.

Thoma, M. and Althaus, S. (2016) 'Inneralpines auftreten ziehender watvögel: Diversität, häufigkeit und phänologie durchziehender limikolen auf dem col de bretolet', *Ornithologische Beobachter*, 113(1), pp. 31–52.

Tøttrup, A. P. *et al.* (2012) 'The annual cycle of a trans-equatorial Eurasian-African passerine migrant: Different spatio-temporal strategies for autumn and spring migration', *Proceedings of the Royal Society B: Biological Sciences*, 279(1730), pp. 1008–1016. doi: 10.1098/rspb.2011.1323.

Tøttrup, A. P., Thorup, K. and Rahbek, C. (2006) 'Patterns of change in timing of spring migration in North European songbird populations', *Journal of Avian Biology*, 37(1), pp. 84–92.

Tryjanowski, P. *et al.* (2013) 'Bird Migration Advances More Strongly in Urban Environments', *PLoS ONE*, 8(5), pp. 1–6. doi: 10.1371/journal.pone.0063482.

Tschanz, P. *et al.* (2019) 'Consistency of spatio-temporal patterns of avian migration across the Swiss lowlands', *Remote Sensing in Ecology and Conservation*, pp. 1–14. doi: 10.1002/rse2.143.

Tyagi, T. and Bhardwaj, S. K. (2021) 'Orientation cues and mechanisms used during avian navigation: A review', *Journal of Applied and Natural Science*, 13(2), pp. 627–640. doi: 10.31018/JANS.V13I2.2684.

Vardanis, Y. *et al.* (2011) 'Individuality in bird migration: Routes and timing', *Biology Letters*, 7(4), pp. 502–505. doi: 10.1098/rsbl.2010.1180.

Williams, T. C. *et al.* (2001) 'Bird migration through a mountain pass studied with high resolution radar, ceilometers, and census', *Auk*, 118(2), pp. 389–403. doi: 10.2307/4089800.

Wood, S. (2021) *Mixed GAM Computation Vehicle with Automatic Smoothness Estimation*. doi: 10.1201/9781315370279.

Yokoyama, K. and Farner, D. S. (1978) 'Induction of Zugunruhe by photostimulation of encephalic receptors in white-crowned sparrows', *Science*, 201(4350), pp. 76–79. doi: 10.1126/science.566467.

Zaugg, S. *et al.* (2008) 'Automatic identification of bird targets with radar via patterns produced by wing flapping', *Journal of the Royal Society Interface*, 5(26), pp. 1041–1053. doi: 10.1098/rsif.2007.1349.

Zehnder, S. *et al.* (2001) 'Gibt es topographie-unabhängigen Nachtzug über den Alpen', *Der Ornithologische Beobachter*, 98, pp. 215–222.

ZHAW (2021) *BirdScan MR1*. Available at: https://www.zhaw.ch/de/engineering/institute-zentren/isc/referenzprojekte/birdscan-mr1/ (Accessed: 9 July 2021).

Zúñiga, D. *et al.* (2016) 'Abrupt switch to migratory night flight in a wild migratory songbird', *Scientific Reports*, 6, pp. 1–10. doi: 10.1038/srep34207.

Zurell, D. *et al.* (2018) 'Long-distance migratory birds threatened by multiple independent risks from global change', *Nature Climate Change*, 8(11), pp. 992–996. doi: 10.1038/s41558-018-0312-9.

Appendix

I Model Output: Influence of the Environment by Day

The following tables show the fixed effects extracted from the summary outputs of the models that explain Resid_MTR with the scaled environmental variables on a daily basis. The models are of the type

```
model <- lmer(formula=scale(MTR_Resid) ~ scale(WiDir_Std) +
scale(Wind_Prof) + scale(AirPresPa) + scale(ATemp_Mea) +
scale(D_ATempMean) + scale(D_AirPresPa) + scale(D_Wind_Prof) +
Precip_TF + FogSit_TF + Clouds_TF + (1|Year), data=data)
```

Table 4: Nocturnal spring migration in Sempach.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	-0.001476	0.168545	117.000000	-0.009	0.99303	
scale(WiDir_Std)	-0.007826	0.085801	117.000000	-0.091	0.92748	
scale(Wind_Prof)	0.304306	0.093891	117.000000	3.241	0.00155	**
scale(AirPresPa)	0.082729	0.095071	117.000000	0.870	0.38599	
scale(ATemp_Mea)	0.478375	0.098198	117.000000	4.872	3.51e-06	***
scale(D_ATempMean)	0.060736	0.084157	117.000000	0.722	0.47192	
scale(D_AirPresPa)	-0.055650	0.080944	117.000000	-0.688	0.49313	
scale(D_Wind_Prof)	-0.036665	0.088022	117.000000	-0.417	0.67777	
Precip_TFRain	-0.069520	0.495526	117.000000	-0.140	0.88867	
FogSit_TFFoggy	0.748188	0.844572	117.000000	0.886	0.37750	
Clouds_TFCloudy	-0.003854	0.213390	117.000000	-0.018	0.98562	

Table 5: Diurnal spring migration in Sempach.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.253166	0.207151	7.295443	1.222	0.259670	
scale(WiDir_Std)	0.009761	0.090683	116.233763	0.108	0.914468	
scale(Wind_Prof)	0.326371	0.096545	116.208392	3.381	0.000986	***
scale(AirPresPa)	0.202003	0.109586	116.994997	1.843	0.067812	.
scale(ATemp_Mea)	0.352721	0.102317	116.998700	3.447	0.000787	***
scale(D_ATempMean)	-0.011936	0.085636	116.098875	-0.139	0.889388	
scale(D_AirPresPa)	-0.109533	0.085917	116.670815	-1.275	0.204891	
scale(D_Wind_Prof)	-0.177564	0.092587	116.052935	-1.918	0.057592	.
Precip_TFRain	-0.302042	0.311429	116.003055	-0.970	0.334135	
FogSit_TFFoggy	-0.359560	0.285575	116.079173	-1.259	0.210530	
Clouds_TFCloudy	-0.266765	0.228590	116.728314	-1.167	0.245589	

Table 6: Nocturnal spring migration in Maloja.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.12787	0.25569	2.81342	0.500	0.65347	
scale(WiDir_Std)	-0.01088	0.10071	116.06996	-0.108	0.91415	
scale(Wind_Prof)	0.25687	0.12466	116.99909	2.061	0.04157	*
scale(AirPresPa)	-0.19915	0.13273	116.76703	-1.500	0.13622	
scale(ATemp_Mea)	0.19982	0.13151	116.39796	1.519	0.13135	
scale(D_ATempMean)	-0.13811	0.11749	116.03670	-1.176	0.24218	
scale(D_AirPresPa)	0.32473	0.10915	116.39685	2.975	0.00356	**
scale(D_Wind_Prof)	0.03412	0.11037	116.51326	0.309	0.75777	
Precip_TFRain	-0.53088	0.32285	116.00826	-1.644	0.10281	
FogSit_TFFoggy	-1.15143	0.38326	116.41809	-3.004	0.00326	**
Clouds_TFCloudy	-0.02167	0.21974	116.99961	-0.099	0.92159	

Table 7: Diurnal spring migration in Maloja.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.27450	0.21350	3.53515	1.286	0.27629	
scale(WiDir_Std)	-0.12382	0.10068	116.41728	-1.230	0.22122	
scale(Wind_Prof)	0.38166	0.12050	116.64132	3.167	0.00196	**
scale(AirPresPa)	-0.07230	0.14080	116.98261	-0.513	0.60859	
scale(ATemp_Mea)	0.36189	0.13461	116.86438	2.688	0.00823	**
scale(D_ATempMean)	-0.11928	0.11623	116.10009	-1.026	0.30690	
scale(D_AirPresPa)	0.11247	0.10828	116.21988	1.039	0.30113	
scale(D_Wind_Prof)	-0.09175	0.10994	116.12778	-0.835	0.40568	
Precip_TFRain	-0.03179	0.28562	116.48634	-0.111	0.91156	
FogSit_TFFoggy	-0.26728	0.30464	116.27256	-0.877	0.38210	
Clouds_TFCloudy	-0.36172	0.21308	116.81560	-1.698	0.09225	.

Table 8: Nocturnal spring migration in the Urserental.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	-0.113749	0.338577	2.226822	-0.336	0.76595	
scale(WiDir_Std)	0.002558	0.111110	106.357176	0.023	0.98168	
scale(Wind_Prof)	-0.198746	0.153754	106.034632	-1.293	0.19895	
scale(AirPresPa)	-0.154181	0.139923	106.916688	-1.102	0.27298	
scale(ATemp_Mea)	0.446299	0.155942	106.823405	2.862	0.00507	**
scale(D_ATempMean)	0.012608	0.136934	106.307921	0.092	0.92681	
scale(D_AirPresPa)	0.079167	0.112605	106.103290	0.703	0.48357	
scale(D_Wind_Prof)	0.103177	0.120290	106.085032	0.858	0.39297	
Precip_TFRain	-0.903974	0.340634	106.952401	-2.654	0.00917	**
FogSit_TFFoggy	0.374925	0.410614	106.078159	0.913	0.36327	
Clouds_TFCloudy	0.265138	0.252666	106.843928	1.049	0.29638	

Table 9: Diurnal spring migration in the Urserental.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.15928	0.15881	5.40371	1.003	0.358669	
scale(WiDir_Std)	0.04309	0.09132	102.98522	0.472	0.638011	
scale(Wind_Prof)	0.10431	0.11790	106.14816	0.885	0.378329	
scale(AirPresPa)	0.09207	0.11268	98.80016	0.817	0.415824	
scale(ATemp_Mea)	0.50804	0.12360	94.28614	4.111	8.42e-05	***
scale(D_ATempMean)	-0.19411	0.10739	106.79288	-1.808	0.073496	.
scale(D_AirPresPa)	-0.01295	0.08913	106.29304	-0.145	0.884757	
scale(D_Wind_Prof)	0.10439	0.09739	106.01774	1.072	0.286243	
Precip_TFRain	-0.79585	0.22660	106.99171	-3.512	0.000652	***
FogSit_TFFoggy	0.09614	0.23688	86.27565	0.406	0.685859	
Clouds_TFCloudy	-0.07805	0.18355	106.36907	-0.425	0.671523	

Table 10: Nocturnal autumn migration in Sempach.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	-0.15300	0.22732	15.71094	-0.673	0.510683	
scale(WiDir_Std)	0.12508	0.07362	181.00237	1.699	0.091060	.
scale(Wind_Prof)	0.02236	0.08940	181.62012	0.250	0.802785	
scale(AirPresPa)	0.27891	0.10248	181.19646	2.722	0.007129	**
scale(ATemp_Mea)	-0.26586	0.09386	181.00082	-2.832	0.005143	**
scale(D_ATempMean)	0.29675	0.07685	181.00063	3.861	0.000157	***
scale(D_AirPresPa)	-0.19852	0.07524	181.03198	-2.638	0.009058	**
scale(D_Wind_Prof)	0.15292	0.07684	181.13068	1.990	0.048083	*
Precip_TFRain	-0.59600	0.20479	181.46478	-2.910	0.004064	**
FogSit_TFFoggy	-0.19598	0.27075	181.64073	-0.724	0.470093	
Clouds_TFCloudy	0.29109	0.22020	181.06749	1.322	0.187855	

Table 11: Diurnal autumn migration in Sempach.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	-0.04380	0.22062	6.36831	-0.199	0.848797	
scale(WiDir_Std)	-0.01776	0.08000	181.00326	-0.222	0.824572	
scale(Wind_Prof)	0.09424	0.09241	181.78078	1.020	0.309140	
scale(AirPresPa)	-0.02810	0.10369	181.00703	-0.271	0.786734	
scale(ATemp_Mea)	0.10670	0.09709	181.10990	1.099	0.273273	
scale(D_ATempMean)	0.12618	0.08198	181.03099	1.539	0.125511	
scale(D_AirPresPa)	-0.02289	0.07660	181.03580	-0.299	0.765399	
scale(D_Wind_Prof)	0.15395	0.07821	181.13360	1.968	0.050547	.
Precip_TFRain	-0.55645	0.23797	181.04150	-2.338	0.020460	*
FogSit_TFFoggy	-0.81699	0.23720	181.50868	-3.444	0.000711	***
Clouds_TFCloudy	0.23421	0.20137	181.90980	1.163	0.246332	

Table 12: Nocturnal autumn migration in Maloja.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	-0.15167	0.19967	25.96333	-0.760	0.4543	
scale(WiDir_Std)	0.01524	0.07571	177.05554	0.201	0.8407	
scale(Wind_Prof)	0.13192	0.10059	177.85349	1.311	0.1914	
scale(AirPresPa)	0.12191	0.15538	177.12368	0.785	0.4337	
scale(ATemp_Mea)	0.01368	0.14987	177.69419	0.091	0.9274	
scale(D_ATempMean)	0.18775	0.12022	177.36164	1.562	0.1202	
scale(D_AirPresPa)	-0.10518	0.11636	177.04007	-0.904	0.3673	
scale(D_Wind_Prof)	-0.03715	0.09122	177.44344	-0.407	0.6843	
Precip_TFRain	-0.00102	0.23254	177.08354	-0.004	0.9965	
FogSit_TFFoggy	-0.47541	0.25351	177.69780	-1.875	0.0624	.
Clouds_TFCloudy	0.26301	0.21101	177.07128	1.246	0.2143	

Table 13: Diurnal autumn migration in Maloja.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	0.098473	0.169552	178.000000	0.581	0.5621	
scale(WiDir_Std)	0.073374	0.068385	178.000000	1.073	0.2847	
scale(Wind_Prof)	0.430632	0.095569	178.000000	4.506	1.19e-05	***
scale(AirPresPa)	-0.007902	0.134443	178.000000	-0.059	0.9532	
scale(ATemp_Mea)	0.307923	0.130839	178.000000	2.353	0.0197	*
scale(D_ATempMean)	-0.026580	0.101742	178.000000	-0.261	0.7942	
scale(D_AirPresPa)	-0.015187	0.099461	178.000000	-0.153	0.8788	
scale(D_Wind_Prof)	-0.141129	0.082137	178.000000	-1.718	0.0875	.
Precip_TFRain	-0.027960	0.233487	178.000000	-0.120	0.9048	
FogSit_TFFoggy	-0.215430	0.230083	178.000000	-0.936	0.3504	
Clouds_TFCloudy	-0.070748	0.183296	178.000000	-0.386	0.7000	

Table 14: Nocturnal autumn migration in the Urserental.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	0.161407	0.317983	2.271173	0.508	0.6568	
scale(WiDir_Std)	0.001938	0.069552	181.835139	0.028	0.9778	
scale(Wind_Prof)	0.136557	0.084592	181.687574	1.614	0.1082	
scale(AirPresPa)	0.215165	0.135849	181.010828	1.584	0.1150	
scale(ATemp_Mea)	-0.534377	0.127874	181.045055	-4.179	4.55e-05	***
scale(D_ATempMean)	0.257800	0.110070	181.029669	2.342	0.0203	*
scale(D_AirPresPa)	-0.156663	0.099887	181.002010	-1.568	0.1185	
scale(D_Wind_Prof)	0.103158	0.089718	181.078460	1.150	0.2517	
Precip_TFRain	-0.416823	0.198292	181.210893	-2.102	0.0369	*
FogSit_TFFoggy	0.237731	0.191637	181.536010	1.241	0.2164	
Clouds_TFCloudy	-0.132758	0.205889	181.041966	-0.645	0.5199	

Table 15: Diurnal autumn migration in the Urserental.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	0.12785	0.41539	1.15887	0.308	0.8043	
scale(WiDir_Std)	0.07924	0.05136	181.11821	1.543	0.1246	
scale(Wind_Prof)	0.40858	0.06273	181.12822	6.514	7.01e-10	***
scale(AirPresPa)	-0.40812	0.09714	181.00010	-4.201	4.16e-05	***
scale(ATemp_Mea)	0.77533	0.09358	181.03033	8.285	2.57e-14	***
scale(D_ATempMean)	-0.07372	0.08019	181.00010	-0.919	0.3591	
scale(D_AirPresPa)	0.18093	0.07034	181.00251	2.572	0.0109	*
scale(D_Wind_Prof)	-0.12588	0.06680	181.01162	-1.884	0.0611	.
Precip_TFRain	-0.30036	0.16399	181.01340	-1.832	0.0687	.
FogSit_TFFoggy	-0.30318	0.15307	181.04648	-1.981	0.0491	*
Clouds_TFCloudy	-0.02910	0.13335	181.00206	-0.218	0.8275	

II Model Output: Influence of the Environment by Hour and Day

The following tables show the fixed effects extracted from the summary outputs of the models that explain Resid_MTR with the scaled environmental variables on an hourly basis. The models are of the type

```
model <- lmer(formula=scale(MTR_Resid) ~ scale(WiDir_Std) +
scale(Wind_Prof) + scale(AirPresPa) + scale(ATemp_Mea) +
scale(D_ATempMean) + scale(D_AirPresPa) + scale(D_Wind_Prof) +
Precip_TF + FogSit_TF + Clouds_TF + (1|Year), data=data)
```

Table 16: Nocturnal spring migration in Sempach.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	2.593e-01	3.467e-02	1.305e+03	7.480	1.36e-13	***
scale(WiDir_Std)	-3.818e-02	2.374e-02	1.305e+03	-1.608	0.10801	
scale(Wind_Prof)	1.924e-01	2.872e-02	1.305e+03	6.699	3.10e-11	***
scale(AirPresPa)	-2.447e-01	2.900e-02	1.305e+03	-8.438	< 2e-16	***
scale(ATemp_Mea)	3.896e-01	2.429e-02	1.305e+03	16.037	< 2e-16	***
scale(D_ATempMean)	-7.991e-03	2.797e-02	1.305e+03	-0.286	0.77518	
scale(D_AirPresPa)	6.278e-02	2.812e-02	1.305e+03	2.233	0.02574	*
scale(D_Wind_Prof)	-6.382e-02	2.351e-02	1.305e+03	-2.715	0.00671	**
Precip_TFRain	-6.175e-01	1.334e-01	1.305e+03	-4.630	4.03e-06	***
FogSit_TFFoggy	-3.458e-01	2.215e-01	1.305e+03	-1.561	0.11876	
Clouds_TFCloudy	-4.460e-01	4.986e-02	1.305e+03	-8.945	< 2e-16	***

Table 17: Diurnal spring migration in Sempach.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	0.19398	0.11519	1.10689	1.684	0.32294	
scale(WiDir_Std)	0.05138	0.02299	1712.33922	2.235	0.02554	*
scale(Wind_Prof)	0.14523	0.02635	1712.88667	5.512	4.08e-08	***
scale(AirPresPa)	-0.07964	0.02495	1712.29417	-3.192	0.00144	**
scale(ATemp_Mea)	0.18189	0.02339	1712.99980	7.777	1.27e-14	***
scale(D_ATempMean)	-0.07481	0.02358	1712.08475	-3.172	0.00154	**
scale(D_AirPresPa)	0.01730	0.02344	1712.41051	0.738	0.46063	
scale(D_Wind_Prof)	-0.01591	0.02353	1712.10440	-0.676	0.49908	
Precip_TFRain	-0.64785	0.14502	1712.00353	-4.467	8.44e-06	***
FogSit_TFFoggy	-0.16427	0.25882	1712.54390	-0.635	0.52572	
Clouds_TFCloudy	-0.30610	0.04840	1712.41666	-6.324	3.25e-10	***

Table 18: Nocturnal spring migration in Maloja.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	1.267e-02	6.069e-02	1.634e+00	0.209	0.85770	
scale(WiDir_Std)	-9.453e-02	2.879e-02	1.260e+03	-3.283	0.00105	**
scale(Wind_Prof)	1.556e-01	3.251e-02	1.259e+03	4.787	1.89e-06	***
scale(AirPresPa)	1.642e-03	3.128e-02	7.409e+02	0.053	0.95814	
scale(ATemp_Mea)	1.760e-01	2.972e-02	1.260e+03	5.923	4.06e-09	***
scale(D_ATempMean)	-6.198e-02	3.407e-02	1.259e+03	-1.819	0.06914	.
scale(D_AirPresPa)	5.128e-02	3.442e-02	1.260e+03	1.490	0.13657	
scale(D_Wind_Prof)	-2.302e-02	2.788e-02	1.259e+03	-0.826	0.40909	
Precip_TFRain	-7.766e-01	1.275e-01	1.259e+03	-6.088	1.51e-09	***
FogSit_TFFoggy	-4.247e-02	1.147e-01	1.259e+03	-0.370	0.71131	
Clouds_TFCloudy	4.795e-02	5.834e-02	1.253e+03	0.822	0.41133	

Table 19: Diurnal spring migration in Maloja.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	8.002e-02	4.893e-02	1.816e+00	1.636	0.25581	
scale(WiDir_Std)	-2.614e-02	2.577e-02	1.688e+03	-1.014	0.31063	
scale(Wind_Prof)	9.303e-02	2.849e-02	1.661e+03	3.266	0.00111	**
scale(AirPresPa)	-5.488e-02	2.616e-02	1.565e+03	-2.098	0.03609	*
scale(ATemp_Mea)	7.162e-02	2.669e-02	1.646e+03	2.684	0.00735	**
scale(D_ATempMean)	-3.903e-02	2.544e-02	1.687e+03	-1.534	0.12524	
scale(D_AirPresPa)	9.222e-02	2.527e-02	1.685e+03	3.650	0.00027	***
scale(D_Wind_Prof)	-2.358e-03	2.463e-02	1.687e+03	-0.096	0.92374	
Precip_TFRain	-3.660e-01	1.165e-01	1.687e+03	-3.143	0.00170	**
FogSit_TFFoggy	-2.691e-01	1.147e-01	1.687e+03	-2.347	0.01906	*
Clouds_TFCloudy	-9.908e-02	5.209e-02	1.681e+03	-1.902	0.05732	.

Table 20: Nocturnal spring migration in the Urserental.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	4.928e-02	1.741e-01	1.080e+00	0.283	0.822	
scale(WiDir_Std)	2.352e-02	2.891e-02	1.162e+03	0.814	0.416	
scale(Wind_Prof)	-2.871e-02	3.403e-02	1.162e+03	-0.844	0.399	
scale(AirPresPa)	3.477e-02	3.150e-02	1.163e+03	1.104	0.270	
scale(ATemp_Mea)	1.775e-01	3.509e-02	1.163e+03	5.059	4.91e-07	***
scale(D_ATempMean)	2.932e-02	4.431e-02	1.162e+03	0.662	0.508	
scale(D_AirPresPa)	1.991e-02	4.460e-02	1.162e+03	0.446	0.655	
scale(D_Wind_Prof)	9.428e-03	2.936e-02	1.162e+03	0.321	0.748	
Precip_TFRain	-6.748e-01	1.287e-01	1.163e+03	-5.243	1.87e-07	***
FogSit_TFFoggy	4.796e-02	1.042e-01	1.162e+03	0.460	0.645	
Clouds_TFCloudy	-1.383e-02	6.324e-02	1.163e+03	-0.219	0.827	

Table 21: Diurnal spring migration in the Urserental.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.15591	0.06733	1.25228	2.316	0.2173	
scale(WiDir_Std)	0.04113	0.02438	1378.67773	1.687	0.0918	.
scale(Wind_Prof)	0.04850	0.02776	1554.88023	1.747	0.0808	.
scale(AirPresPa)	-0.01414	0.02514	1550.63628	-0.562	0.5739	
scale(ATemp_Mea)	0.31729	0.02889	1523.44825	10.983	< 2e-16	***
scale(D_ATempMean)	-0.05885	0.02768	1554.72098	-2.126	0.0336	*
scale(D_AirPresPa)	0.14423	0.02744	1554.91508	5.257	1.67e-07	***
scale(D_Wind_Prof)	-0.04086	0.02376	1554.04115	-1.720	0.0857	.
Precip_TFRain	-0.64978	0.10276	1551.17187	-6.323	3.34e-10	***
FogSit_TFFoggy	-0.05058	0.09539	1550.86220	-0.530	0.5960	
Clouds_TFCloudy	-0.23165	0.04989	1542.63090	-4.643	3.72e-06	***

Table 22: Nocturnal autumn migration in Sempach.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	2.947e-01	6.209e-02	1.836e+00	4.747	0.04902	*
scale(WiDir_Std)	3.961e-02	2.073e-02	2.080e+03	1.911	0.05615	.
scale(Wind_Prof)	2.114e-01	2.191e-02	2.081e+03	9.649	< 2e-16	***
scale(AirPresPa)	-6.615e-02	2.231e-02	2.080e+03	-2.965	0.00306	**
scale(ATemp_Mea)	-3.432e-02	2.313e-02	2.081e+03	-1.484	0.13805	
scale(D_ATempMean)	9.778e-03	2.255e-02	2.080e+03	0.434	0.66456	
scale(D_AirPresPa)	3.192e-02	2.238e-02	2.080e+03	1.426	0.15388	
scale(D_Wind_Prof)	-6.668e-02	2.110e-02	2.080e+03	-3.160	0.00160	**
Precip_TFRain	-6.623e-01	7.931e-02	2.081e+03	-8.351	< 2e-16	***
FogSit_TFFoggy	-1.330e-01	1.038e-01	2.070e+03	-1.282	0.20008	
Clouds_TFCloudy	-3.453e-01	4.711e-02	2.068e+03	-7.328	3.32e-13	***

Table 23: Diurnal autumn migration in Sempach.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	8.865e-02	6.143e-02	1.594e+00	1.443	0.3143	
scale(WiDir_Std)	-1.251e-03	1.981e-02	2.477e+03	-0.063	0.9496	
scale(Wind_Prof)	1.261e-01	2.074e-02	2.478e+03	6.079	1.39e-09	***
scale(AirPresPa)	-4.106e-02	2.176e-02	2.468e+03	-1.888	0.0592	.
scale(ATemp_Mea)	5.245e-02	2.193e-02	2.477e+03	2.392	0.0168	*
scale(D_ATempMean)	-3.755e-02	2.028e-02	2.477e+03	-1.851	0.0642	.
scale(D_AirPresPa)	-3.627e-02	1.985e-02	2.477e+03	-1.827	0.0678	.
scale(D_Wind_Prof)	-4.039e-02	2.011e-02	2.477e+03	-2.008	0.0447	*
Precip_TFRain	-6.930e-01	8.273e-02	2.477e+03	-8.377	< 2e-16	***
FogSit_TFFoggy	-4.655e-02	1.163e-01	2.478e+03	-0.400	0.6889	
Clouds_TFCloudy	-6.796e-02	4.398e-02	2.478e+03	-1.546	0.1223	

Table 24: Nocturnal autumn migration in Maloja.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.05018	0.03723	1837.00000	1.348	0.17791	
scale(WiDir_Std)	0.07845	0.02398	1837.00000	3.272	0.00109	**
scale(Wind_Prof)	-0.02965	0.02572	1837.00000	-1.153	0.24922	
scale(AirPresPa)	-0.08700	0.03057	1837.00000	-2.846	0.00448	**
scale(ATemp_Mea)	0.07040	0.03016	1837.00000	2.334	0.01970	*
scale(D_ATempMean)	-0.05686	0.02746	1837.00000	-2.070	0.03855	*
scale(D_AirPresPa)	0.05863	0.02714	1837.00000	2.160	0.03091	*
scale(D_Wind_Prof)	-0.02786	0.02351	1837.00000	-1.185	0.23617	
Precip_TFRain	-0.82522	0.08363	1837.00000	-9.867	< 2e-16	***
FogSit_TFFoggy	-0.27087	0.09266	1837.00000	-2.923	0.00351	**
Clouds_TFCloudy	0.06900	0.04953	1837.00000	1.393	0.16375	

Table 25: Diurnal autumn migration in Maloja.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.04080	0.03331	2226.00000	1.225	0.220669	
scale(WiDir_Std)	0.03135	0.02131	2226.00000	1.471	0.141518	
scale(Wind_Prof)	0.06737	0.02361	2226.00000	2.854	0.004363	**
scale(AirPresPa)	0.02306	0.02854	2226.00000	0.808	0.419115	
scale(ATemp_Mea)	0.07597	0.02985	2226.00000	2.545	0.010988	*
scale(D_ATempMean)	0.03293	0.02266	2226.00000	1.453	0.146366	
scale(D_AirPresPa)	-0.01661	0.02267	2226.00000	-0.733	0.463865	
scale(D_Wind_Prof)	-0.05660	0.02182	2226.00000	-2.594	0.009551	**
Precip_TFRain	-0.32174	0.08893	2226.00000	-3.618	0.000304	***
FogSit_TFFoggy	-0.14163	0.09298	2226.00000	-1.523	0.127831	
Clouds_TFCloudy	-0.01818	0.04534	2226.00000	-0.401	0.688462	

Table 26: Nocturnal autumn migration in the Urserental.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.12884	0.03590	2110.00000	3.589	0.00034	***
scale(WiDir_Std)	-0.05259	0.02117	2110.00000	-2.484	0.01308	*
scale(Wind_Prof)	0.01972	0.02345	2110.00000	0.841	0.40050	
scale(AirPresPa)	0.12104	0.02341	2110.00000	5.170	2.57e-07	***
scale(ATemp_Mea)	-0.24038	0.02426	2110.00000	-9.909	< 2e-16	***
scale(D_ATempMean)	0.05362	0.02951	2110.00000	1.817	0.06936	.
scale(D_AirPresPa)	-0.06391	0.02874	2110.00000	-2.224	0.02629	*
scale(D_Wind_Prof)	-0.02436	0.02219	2110.00000	-1.098	0.27226	
Precip_TFRain	-0.71687	0.08392	2110.00000	-8.542	< 2e-16	***
FogSit_TFFoggy	-0.06748	0.07494	2110.00000	-0.900	0.36798	
Clouds_TFCloudy	-0.10895	0.04692	2110.00000	-2.322	0.02032	*

Table 27: Diurnal autumn migration in the Urserental.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	0.11490	0.10654	1.08970	1.079	0.46409	
scale(WiDir_Std)	-0.01329	0.02065	2561.00094	-0.643	0.51996	
scale(Wind_Prof)	0.12286	0.02207	2561.09947	5.566	2.87e-08	***
scale(AirPresPa)	-0.05283	0.02586	2446.27138	-2.043	0.04113	*
scale(ATemp_Mea)	0.32830	0.02482	2552.01724	13.230	< 2e-16	***
scale(D_ATempMean)	0.05443	0.02149	2561.10500	2.533	0.01136	*
scale(D_AirPresPa)	0.01984	0.02057	2561.63517	0.965	0.33480	
scale(D_Wind_Prof)	-0.01352	0.01906	2561.00378	-0.709	0.47836	
Precip_TFRain	-0.51756	0.07087	2561.82719	-7.303	3.74e-13	***
FogSit_TFFoggy	-0.06957	0.07965	2561.65829	-0.874	0.38246	
Clouds_TFCloudy	-0.10774	0.04032	2561.00031	-2.672	0.00758	**

III Model Output: Influence of the Environment by Hour and Day with Variable Selection

Here I show the summary tables of the models that explain Resid_MTR with environmental factors, excluding change variables and wind direction variability. The models are of the type

```
model <- lmer(formula=scale(MTR_Resid) ~ scale(Wind_Prof) +
scale(AirPresPa) + scale(ATemp_Mea) + Precip_TF + FogSit_TF +
Clouds_TF + (1|Year), data=data)
```

Table 28: Nocturnal spring migration in Sempach.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	0.24873	0.03558	3.66157	6.991	0.00304	**
scale(Wind_Prof)	0.19076	0.02805	174.97077	6.801	1.59e-10	***
scale(AirPresPa)	-0.23243	0.02813	140.16156	-8.264	9.63e-14	***
scale(ATemp_Mea)	0.38000	0.02379	1243.46759	15.973	< 2e-16	***
Precip_TFRain	-0.64652	0.13361	1293.95270	-4.839	1.46e-06	***
FogSit_TFFoggy	-0.33751	0.22235	1308.59838	-1.518	0.12927	
Clouds_TFCloudy	-0.42461	0.04958	1260.63951	-8.564	< 2e-16	***

Table 29: Diurnal spring migration in Sempach.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	0.18481	0.11597	1.10324	1.594	0.339545	
scale(Wind_Prof)	0.14007	0.02541	1716.97336	5.512	4.09e-08	***
scale(AirPresPa)	-0.08825	0.02473	1716.23917	-3.569	0.000368	***
scale(ATemp_Mea)	0.17803	0.02337	1716.98671	7.618	4.22e-14	***
Precip_TFRain	-0.61001	0.14453	1716.01235	-4.221	2.56e-05	***
FogSit_TFFoggy	-0.19317	0.25884	1716.57383	-0.746	0.455594	
Clouds_TFCloudy	-0.29063	0.04799	1716.49194	-6.056	1.71e-09	***

Table 30: Nocturnal spring migration in Maloja.

	Estimate	Std.Error	df	t value	Pr(>|t|)	
(Intercept)	-0.00911	0.10414	1.16609	-0.087	0.94286	
scale(Wind_Prof)	0.09374	0.03088	1260.04096	3.035	0.00245	**
scale(AirPresPa)	-0.08367	0.03086	1204.52166	-2.712	0.00679	**
scale(ATemp_Mea)	0.13980	0.02939	1260.50996	4.757	2.20e-06	***
Precip_TFRain	-0.82937	0.12821	1260.05822	-6.469	1.41e-10	***
FogSit_TFFoggy	-0.02659	0.11361	1260.01942	-0.234	0.81500	
Clouds_TFCloudy	0.08336	0.05850	1260.99963	1.425	0.15442	

Table 31: Diurnal spring migration in Maloja.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.05709	0.05994	1.44035	0.952	0.47295	
scale(Wind_Prof)	0.08894	0.02719	1683.03998	3.272	0.00109	**
scale(AirPresPa)	-0.06843	0.02585	1652.87482	-2.648	0.00819	**
scale(ATemp_Mea)	0.12479	0.02615	1674.04782	4.772	1.98e-06	***
Precip_TFRain	-0.29572	0.11501	1687.06791	-2.571	0.01022	*
FogSit_TFFoggy	-0.10471	0.11297	1687.96500	-0.927	0.35413	
Clouds_TFCloudy	-0.08069	0.05155	1685.59943	-1.565	0.11772	

Table 32: Nocturnal spring migration in the Urserental.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	-0.01280	0.14102	1.12525	-0.091	0.9411	
scale(Wind_Prof)	-0.05702	0.03359	1163.41060	-1.698	0.0898	.
scale(AirPresPa)	-0.02760	0.03156	1162.02706	-0.875	0.3819	
scale(ATemp_Mea)	0.15747	0.03505	1163.80094	4.493	7.73e-06	***
Precip_TFRain	-0.66185	0.13150	1163.97939	-5.033	5.59e-07	***
FogSit_TFFoggy	-0.02585	0.10518	1163.18151	-0.246	0.8059	
Clouds_TFCloudy	0.10269	0.06371	1163.77785	1.612	0.1073	

Table 33: Diurnal spring migration in the Urserental.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	1.619e-01	6.310e-02	1.339e+00	2.566	0.1826	
scale(Wind_Prof)	8.155e-03	2.751e-02	1.554e+03	0.296	0.7669	
scale(AirPresPa)	-1.490e-01	2.559e-02	1.553e+03	-5.822	7.03e-09	***
scale(ATemp_Mea)	2.785e-01	2.920e-02	1.533e+03	9.536	< 2e-16	***
Precip_TFRain	-6.488e-01	1.057e-01	1.552e+03	-6.136	1.07e-09	***
FogSit_TFFoggy	-1.731e-01	9.729e-02	1.553e+03	-1.779	0.0754	.
Clouds_TFCloudy	-2.250e-01	5.119e-02	1.547e+03	-4.395	1.18e-05	***

Table 34: Nocturnal autumn migration in Sempach.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.29901	0.05889	1.99202	5.078	0.03697	*
scale(Wind_Prof)	0.19533	0.02120	2084.97617	9.215	< 2e-16	***
scale(AirPresPa)	-0.06987	0.02194	2083.76135	-3.185	0.00147	**
scale(ATemp_Mea)	-0.03117	0.02292	2084.78643	-1.360	0.17398	
Precip_TFRain	-0.67554	0.07913	2084.01314	-8.537	< 2e-16	***
FogSit_TFFoggy	-0.08674	0.10342	2071.53276	-0.839	0.40171	
Clouds_TFCloudy	-0.35273	0.04710	2066.49011	-7.489	1.02e-13	***

Table 35: Diurnal autumn migration in Sempach.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.08073	0.06100	1.58303	1.323	0.3448	
scale(Wind_Prof)	0.11428	0.02004	2481.47808	5.704	1.31e-08	***
scale(AirPresPa)	-0.05056	0.02139	2469.49894	-2.364	0.0182	*
scale(ATemp_Mea)	0.05839	0.02175	2481.02157	2.685	0.0073	**
Precip_TFRain	-0.67212	0.08130	2481.02743	-8.267	< 2e-16	***
FogSit_TFFoggy	-0.03176	0.11568	2481.73937	-0.275	0.7837	
Clouds_TFCloudy	-0.05851	0.04368	2481.75017	-1.339	0.1806	

Table 36: Nocturnal autumn migration in Maloja.

	Estimate	**Std.Error**	**df**	**T value**	**Pr(>|t|)**	
(Intercept)	9.415e-02	3.689e-02	1.839e+03	2.552	0.010778	*
scale(Wind_Prof)	-8.321e-02	2.389e-02	1.839e+03	-3.483	0.000507	***
scale(AirPresPa)	-8.403e-02	2.991e-02	1.839e+03	-2.810	0.005009	**
scale(ATemp_Mea)	1.604e-02	2.984e-02	1.839e+03	0.538	0.590866	
Precip_TFRain	-9.067e-01	8.265e-02	1.839e+03	-10.970	< 2e-16	***
FogSit_TFFoggy	-2.785e-01	9.116e-02	1.839e+03	-3.055	0.002283	**
Clouds_TFCloudy	9.783e-03	4.915e-02	1.839e+03	0.199	0.842253	

Table 37: Diurnal autumn migration in Maloja.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	5.504e-02	3.534e-02	3.508e+00	1.557	0.2041	
scale(Wind_Prof)	2.498e-02	2.300e-02	2.223e+03	1.086	0.2776	
scale(AirPresPa)	-1.168e-03	2.835e-02	1.019e+02	-0.041	0.9672	
scale(ATemp_Mea)	-4.083e-02	2.966e-02	2.165e+03	-1.377	0.1687	
Precip_TFRain	-3.847e-01	8.773e-02	2.224e+03	-4.385	1.21e-05	***
FogSit_TFFoggy	-2.073e-01	9.273e-02	2.177e+03	-2.236	0.0255	*
Clouds_TFCloudy	-2.807e-02	4.552e-02	2.084e+03	-0.617	0.5376	

Table 38: Nocturnal autumn migration in the Urserental.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.15753	0.03574	2110.00000	4.408	1.10e-05	***
scale(Wind_Prof)	0.11657	0.02291	2110.00000	5.089	3.93e-07	***
scale(AirPresPa)	0.09105	0.02309	2110.00000	3.944	8.28e-05	***
scale(ATemp_Mea)	-0.14223	0.02403	2110.00000	-5.918	3.80e-09	***
Precip_TFRain	-0.77297	0.08328	2110.00000	-9.282	< 2e-16	***
FogSit_TFFoggy	-0.14492	0.07423	2110.00000	-1.952	0.0510	.
Clouds_TFCloudy	-0.13386	0.04683	2110.00000	-2.858	0.0043	**

Table 39: Diurnal spring migration in the Urserental.

	Estimate	**Std.Error**	**df**	**t value**	**Pr(>|t|)**	
(Intercept)	0.16704	0.16962	1.03606	0.985	0.500283	
scale(Wind_Prof)	0.03651	0.01995	2561.09584	1.830	0.067404	.
scale(AirPresPa)	-0.14609	0.02606	2548.02654	-5.606	2.29e-08	***
scale(ATemp_Mea)	0.14029	0.02562	2561.63417	5.476	4.78e-08	***
Precip_TFRain	-0.61013	0.07289	2561.41073	-8.371	< 2e-16	***
FogSit_TFFoggy	-0.24829	0.08218	2561.29964	-3.021	0.002543	**
Clouds_TFCloudy	-0.15756	0.04183	2561.00160	-3.767	0.000169	***

Personal Declaration

Personal declaration: I hereby declare that the material contained in this thesis is my own original work. Any quotation or paraphrase in this thesis from the published or unpublished work of another individual or institution has been duly acknowledged. I have not submitted this thesis, or any part of it, previously to any institution for assessment purposes.

Signature: Simon Hirschhofer