

RESEARCH ARTICLE

High-intensity bird migration along Alpine valleys calls for protective measures against anthropogenically induced avian mortality

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Abstract

The Alps are a natural barrier for avian broad-front migration in Central Europe. While most birds that approach the Alps are deflected and circumvent the mountains, some choose to make the crossing. Here, they are funnelled and channelled in valleys, leading to high bird densities. Many Alpine valleys are suitable locations for wind farms, potentially creating a conflict between wind energy production and bird conservation. Collisions can be reduced by temporarily shutting down wind turbines. This however requires timely coordination, either by locally monitoring migration intensity or by extrapolating and forecasting migratory fluxes from other sites. However, little is known about the timing and intensity of bird migration in valleys of the central Alps, especially during spring migration. This study presents a 2-year quantification of avian migration across the Alps. We collected terrestrial radar data at three sites: two located in Alpine valleys and one in the lowland, close to the northern foothills of the Alps. We found high migration traffic rates (MTR) during both migration seasons in the Alpine valleys, with outstanding numbers of migrants during the spring season. The strong alignment of the flight directions with the main orientation of alpine valleys highlights the importance of valleys and the connected passes in channelling migratory fluxes through the Alps. However, extrapolating migration intensities and forecasting peak migration events for inner Alpine sites is difficult, likely due to how migratory patterns and activity are influenced by the complexity of the local topography and the associated dynamic wind and weather conditions. Instead, we call for year-round on-site monitoring of migration intensities and strategies tailored to the local context to reduce the risk of bird strikes at wind turbines in the Alps.

Introduction

Mountain ranges can play an important role in the evolution of migratory flyways (Bruderer & Salewski, 2008). Nocturnally migrating birds fly on a broad front (Nilsson et al., 2019), but mountain ranges mould, deflect and channel migratory bird fluxes (Cooke, 1915; Hardy, 1947; Lack & Lack, 1951). In the western flyway within the Palearctic-African migration system, the mountain range of the Alps poses a major topographic obstacle for broad-front migration (Aschwanden et al., 2020; Bruderer &

Jenni, 1990; Liechti et al., 1996). Like an arc, the Alps stretch from southern France in the west through Switzerland, northern Italy, and parts of southern Germany to eastern Austria.

Most birds that approach the Swiss Alps in autumn from the north circumvent the mountains by following its northern foothills to the southwest (Erni et al., 2005; Helbig, 1992). Birds on this route often face constant headwinds, as south-westerly winds are prevalent for the region (Erni et al., 2002). Birds that delay their onward journey because of too strong winds in order to continue

flying later during brief, favourable conditions cause migration intensities to pulsate strongly along this flight path (Erni et al., 2002; Nilsson et al., 2019). Flying with headwinds against the westerlies drifts numerous birds with a south western heading southwards, where they accumulate in high numbers along the northernmost ridges of the Alps (Liechti et al., 1996). Some of these birds find their way into Alpine valleys, where they migrate in higher numbers across mountain passes (Bruderer & Jenni, 1990; Komenda-Zehnder et al., 2010). Since 1952, bird ringing at Col de Bretolet, Switzerland, shows that over 100 bird species regularly cross the Alps and are concentrated on mountain passes (Jenni, 1984; Jenni & Naef-Daenzer, 1986). Visual observations confirm intermittent strong migration along valleys, even during heavy snowfall (Lohmann, 1960; Sutter, 1952, 1954). Contrary to autumn, spring migration is shorter and more condensed (Nussbaumer et al., 2021). During spring, the high mountains of the central part of the Alps seem to have a shadowing effect on the fluxes of birds, resulting in low migration intensities along the northern foothills (Liechti et al., 1996; Tschanz et al., 2019). Visual observations report migration with sometimes high intensities across mountain passes (Heilfurth, 1933; Kreienbühl, 1954) and over mountain peaks (Sick, 1954).

To our knowledge, the number of migratory birds crossing the Alps has never been fully quantified: no radar-based multi-site study inside the Alps covers full migration seasons. Existing studies based on moon-watching are limited to a few nights per season (Liechti et al., 1995; Liechti et al., 1996; Rössler & Schauer, 2014), thus failing to capture the whole migration phenology. Some studies have used tracking radar (Bruderer & Liechti, 1990; Liechti & Bruderer, 1986), retrieving the flight behaviour of individual birds but not providing a quantification of migratory fluxes (Schmaljohann et al., 2008). Furthermore, drawing conclusions for a more general migration pattern requires parallel measurements of migration intensity, which, so far, has not been done.

Declining population sizes are an increasing concern among scientists and conservationists (Both et al., 2006; Bowler et al., 2019; Petras & Vrezec, 2022; Sanderson et al., 2006). For migrants, conservation must target breeding and wintering habitats, as well as critical sites along the migration route (Runge et al., 2015). Collisions with human infrastructure stand out of other threats, killing billions of birds every year (Calvert et al., 2013; Erickson et al., 2005). Although these reviews summarize that most collisions are caused by illuminated buildings, wind turbines can potentially pose a high risk depending on their location (Drewitt & Langston, 2006; Smallwood & Thelander, 2008; Thaxter et al., 2019). The implementation

of effective conservation measures would require year-round quantification of migratory fluxes to identify key sites and flyways, where high densities of migrants frequently occur (Desholm et al., 2014; Drewitt & Langston, 2008; Kirby et al., 2008; Runge et al., 2015).

In the central Swiss Alps, wind turbines could become a major problem for birds. The demand for electricity is increasing, as is the focus on the transition to renewable energy production (Meyer et al., 2022). For future development, a concept plan was developed by the Swiss federal administration, assessing the wind energy potential and possible conflict zones with either wildlife or human needs (Bundesamt für Raumentwicklung ARE, 2020). Most alpine valleys and mountain passes were considered as zones of least conflict where wind turbines pose no considerable threat (Liechti et al., 2013), but this view might be challenged when considering Alpine valleys as bottlenecks that channel and concentrate migratory fluxes. Assessing possible conflict is important during the planning stage, to implement mitigation measures such as increasing the visibility of objects (May et al., 2015), or estimating the frequency and duration or temporal turbine shutdowns (Drewitt & Langston, 2008; Horton et al., 2021).

As a first step to guide efficient conservation measures, our study aims to assess the role of Alpine valleys as bottlenecks for migratory birds. Previous research has shown that birds use Alpine valleys as passages through the mountains, but the actual amount could only be estimated. We hypothesize that due to funnelling and channelling, measured migration intensity during spring and autumn is higher at the Alpine sites than at the lowland site. Therefore, we analysed migratory fluxes across the central part of the Alps using the ornithological radar BirdScan MR1 during two full years. Radars were installed at three sites, one in the lowlands, two inside Alpine valleys. Because of topographic channelling, we hypothesize flight directions inside valleys to show a higher degree of alignment than in the lowland. Furthermore, we hypothesize that flight directions inside valleys rather match the valley's orientation than the preferred migration direction, which we derived from the lowland study site. To see whether active conservation measures can be coordinated through extrapolation and prediction between sites or if local monitoring is required, we analysed the correlation of peak migration events between the sites. We hypothesize that correlations of peak migration events are weaker between our study sites than they are along the lowland, implying that measurements from one Alpine valley cannot necessarily be projected to another Alpine valley. Finally, we analysed the cumulative migration traffic to estimate the eventual frequency of wind turbine shutdowns per site. We hypothesize less, but stronger peak

migration events inside the Alps, leading to a reduction of turbine shutdowns, compared to the lowland.

Methods

Study area and radar monitoring

The lowland site in Sempach ($47^{\circ}7'38.63''\text{N}/8^{\circ}11'32.47''\text{E}$, 505 m a.s.l. (above sea level)) is in the main flyway for autumn migration, 30 km north of the first peaks of the Alps.

The site in the Urseren Valley was initially located in Andermatt ($46^{\circ}38'30.26''\text{N}/8^{\circ}35'26.16''\text{E}$, 1430 m a.s.l.), but was moved 2.8 km southwest to Hospental at the end of July of the first study year to cover a more central location in the valley ($46^{\circ}37'16.28''\text{N}/8^{\circ}34'10.66''\text{E}$, 1454 m a.s.l.). The location lies at the junction of two main axes, east–west from the Furka Pass to the Oberalp

Pass, and north–south from the lowlands to the Gotthard Pass.

The site in the Inn Valley, Maloja ($46^{\circ}24'19.71''\text{N}/9^{\circ}42'8.51''\text{E}$, 1804 m a.s.l.), is close to the highest elevated point of the Inn Valley (1815 m a.s.l.). Here, the Inn Valley forms an almost straight channel through the Alps from the northeast (Rosenheim, Germany) to the southwest (Bregaglia Valley towards Lake Como, Italy), flanked by high mountain ridges on either side. Figure 1 gives an overview of the study area, relevant valleys, and mountain passes.

We analysed radar data from the years 2019 and 2020. Due to snowfall, maintenance and other technical issues, the radar systems were not continuously operational. In Sempach, we recorded birds from January 2 to December 31, 2019, and from January 3 to December 31, 2020, in the Urseren Valley from March 6 to November 27, 2019, and February 28 to November 18, 2020, in the Inn Valley

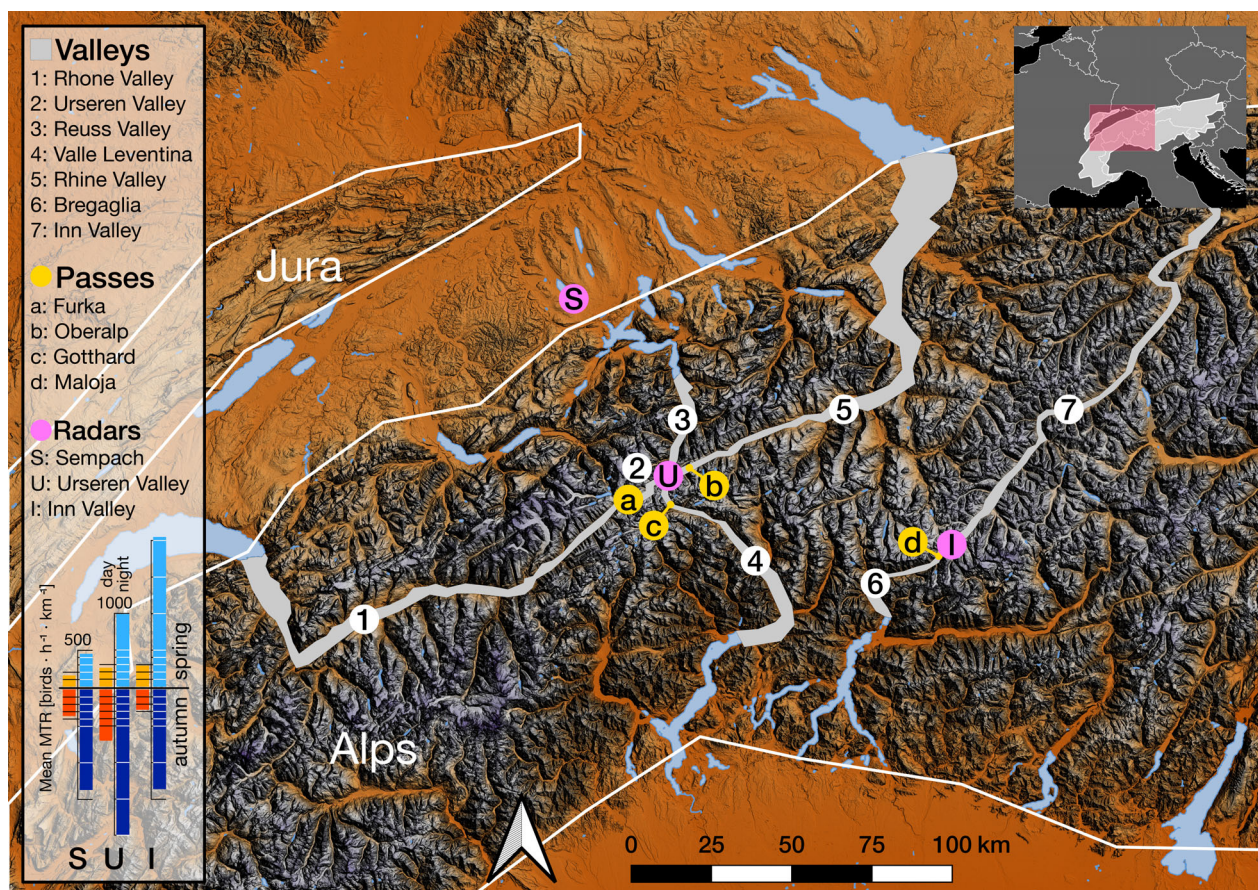


Figure 1. Map overview of the study region. The map shows the location of the mountain ranges of the Jura and the Alps with the Swiss lowlands in between. The study sites where ornithological radars were installed are marked with purple circles. Relevant valleys (red) and mountain passes (yellow) are marked and labelled. The inset map shows the larger-scale topography of the Jura and the Alps. Mean MTR of both years are shown in the legend panel. (DTM by Farr & Kobrick, 2000).

from February 21 to October 22, 2019, and from February 25 to November 12, 2020.

We monitored the migration intensity and flight directions of birds with three bird radar devices (BirdScan MR1, Swiss Birdradar Solution AG, 2022), one at each study site. Technical details on the radar and the signal processing are provided in Appendix S1.

The radar software interrupts the detection of echoes during steady precipitation due to inaccurate echo classification. We manually extended interruption periods to reduce the risk of remaining meteorological echoes being falsely classified as bird. We considered the migration traffic rate (MTR in birds per hour per virtual transect of 1 km, Lowery, 1951; Liechti et al., 1995, supporting information) of precipitation periods as zero when no animal movement still was visible in the raw radar signal or as NA otherwise.

Hourly MTRs were assigned day- or nighttime depending on whether day or night dominated the time interval. We used civil twilight as the boundary between day and night, which calculated per site using the function *getSunlightTimes* from R package *suncalc* (Thieurmél & Elmarhraoui, 2022). To summarize, we averaged hourly MTRs for each day and night.

Identifying migration seasons

To exclude times dominated by non-migratory aerial movements from the migration seasons, we computed an index using the concentration of flight directions as mean resultant vector length (Batschelet, 1981), multiplied by the normalized migration intensity, pooled over all sites. We determined the interval for spring and autumn migration using locally estimated scatterplot smoothing (detailed description in Appendix S1). We inferred the spring migration season to span from February 25 to May 3 in 2019, and February 29 to April 28 in 2020, and the autumn migration season from August 5 to November 11 in 2019, and August 9 to November 10 in 2020 (Figure S1).

Analysis of flight directions

To assess the similarity of flight direction distributions between night and day, we applied Watson Williams test (Landler et al., 2021), as implemented in the function *Watson.williams.test* in the R package *circular* (Agostinelli & Lund, 2023) for each year, season and site. We quantified the directional concentration as the mean resultant vector length with the function *summary.circular* from the R package *circular* (Agostinelli & Lund, 2023). Because of the channelling effect caused by topography, we expected to find a longer seasonal mean resultant vector for the Alpine sites compared to the lowland. Furthermore, we expected

to find a high level of agreement between diurnal and nocturnal flight direction distributions for the Alpine sites, while we expected larger differences in the lowlands. Both would indicate a high degree of channelling of migratory fluxes by Alpine valley topography.

Migration intensity

We estimated the mean daily MTR for all sites for day and night (Fig. 2) and the median MTR and interquartile ranges per year, season, daytime and site (Fig. 3). Migration intensity can vary greatly between consecutive days. To compare the magnitude of peak migration events between Alpine and lowland sites, we ordered the mean daily MTR from highest to lowest and computed cumulative sums, which we normalized to [0, 1] (Fig. 4). We used these normalized cumulative sums to determine the minimum number of days until 50% of the seasonal migration passage had passed at each site.

We used COSMO-1E reanalysis weather data provided by the Federal Office of Meteorology and Climatology MeteoSwiss (<https://www.meteoswiss.admin.ch>) to explain noticeable phenomena in the measurement series.

Between-site correlation

We analysed the correlation of peak migration events between all three sites. Peak migration events are intervals with high migration intensity relative to the expected seasonal trend at the site (Horton et al., 2021; Nussbaumer et al., 2021). This first requires evaluating the seasonal trend. We modelled the seasonal and daily trend of bird flight activity (MTR) at each study site with a generalized additive model (GAM) using the *gam* function from the R package *mgcv* (Wood, 2023) (Fig. 2; details in Appendix S1 and Figure S2).

To compare the correlation of peak migration events between the sites on a daily scale, we computed the residuals between the daily mean GAM output and the measured migration intensities for each site. Next, we computed Spearman's rank correlation coefficient (ρ) to quantify the correlation of the MTR and of the residuals between GAM output and MTR between the sites, following the approach by Tschanz et al. (2019), who analysed the connectivity of migration intensity in the Swiss lowlands. As MTRs do not follow a normal distribution and are on an interval measurement scale, using rank correlation is suitable, because it does not make any assumptions about the frequency distribution of a variable.

We computed ρ for the measured MTR and the residuals between the MTR and the GAM for each combination of diurnal, nocturnal, autumn and spring

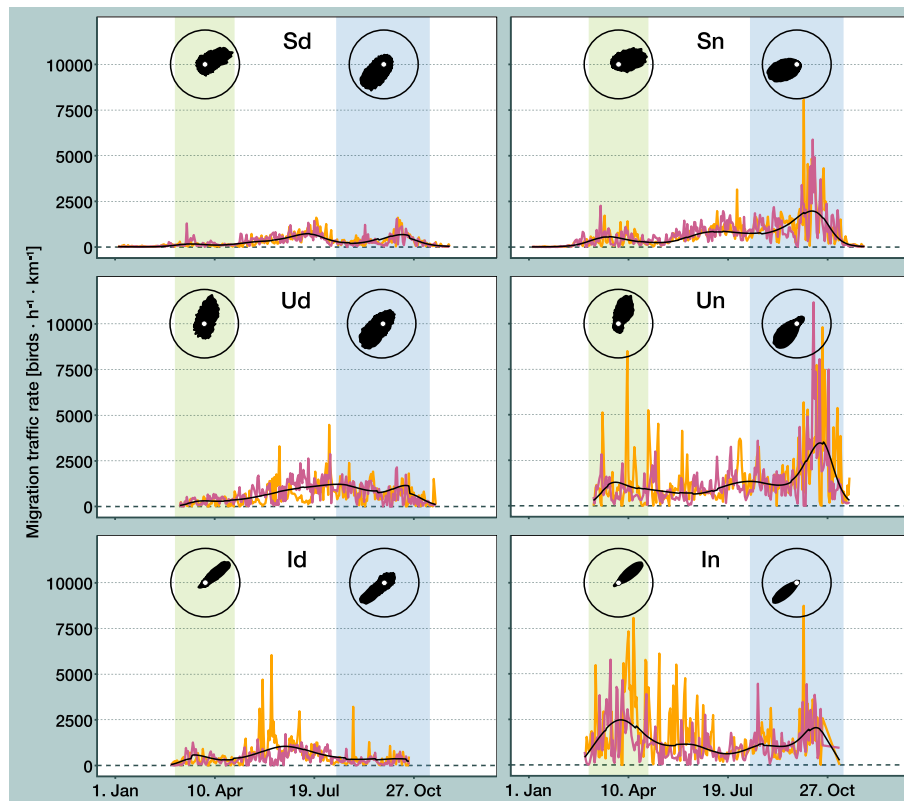


Figure 2. Mean daily MTR for each site (top: Sempach, 'S'; middle: Urseren Valley, 'U'; bottom: Inn Valley, 'I') for daytime (left, 'd') and nighttime (right, 'n') in 2019 (orange) and 2020 (purple). The black line denotes the trend in migration intensity modelled with a generalized additive model. The y-axis depicts MTR, the x-axis marks the day of the year. The migration seasons are highlighted in light green (spring season) and light blue (autumn season). Circular plots show the distribution of flight directions for spring and autumn migration (north at the top, 3° bin size). The small white circles mark the centre.

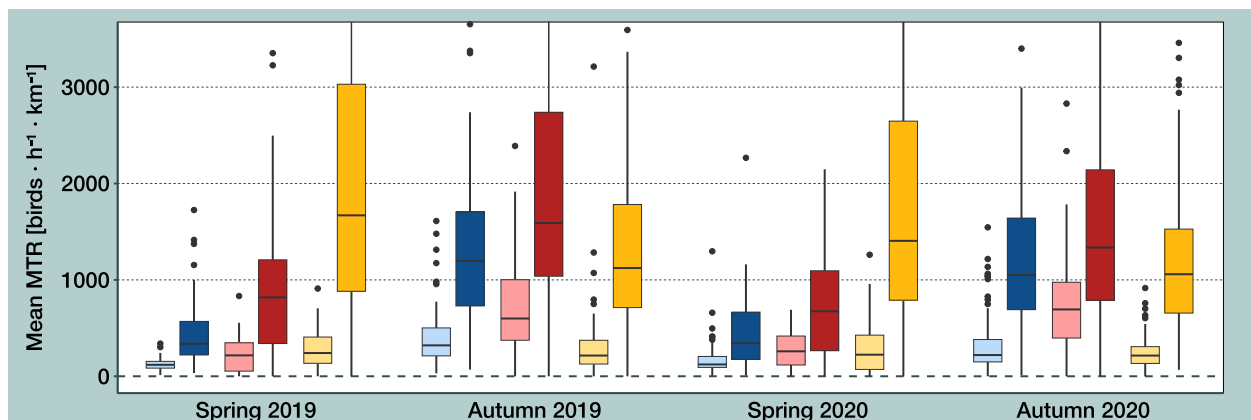


Figure 3. MTR statistics per year, season, site, and daytime. The y-axis displays MTR in birds per hour per kilometre. The coloured boxes display the interquartile range. Horizontal black strokes display the median MTR. For better visualization, the y-axis ends at an MTR of 3500, which cuts off some extreme MTR values. Blue boxes mark MTR for Sempach, red boxes the Urseren Valley, and yellow boxes the Inn Valley. For each site, the pair of boxes with diurnal MTR is on the left, and nocturnal MTR is on the right side.

migration, both per individual year (Figures S3 and S4) and pooled over the 2 years (Fig. 5). We compared diurnal to nocturnal and spring to autumn correlation

coefficients with Fisher's Z test using the function *cocor.indep.groups* from the R package *cocor* (Diedenhofer & Musch, 2022).

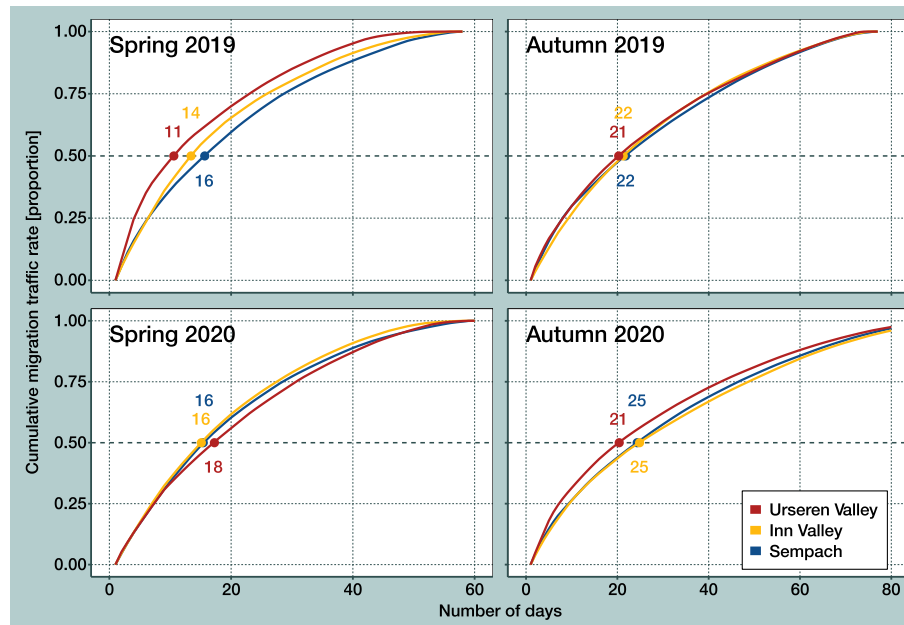


Figure 4. Cumulative MTR sorted from nights with highest to lowest migration intensity. On the x-axis is the number of nights and on the y-axis is the proportion of birds that have crossed the site, relative to the total site-specific migration volume per season. The number of days it takes for 50% of the birds to pass by a location was noted on the 50% line, in red for the Urseren Valley, yellow for the Inn Valley and blue for the lowland site in Sempach.

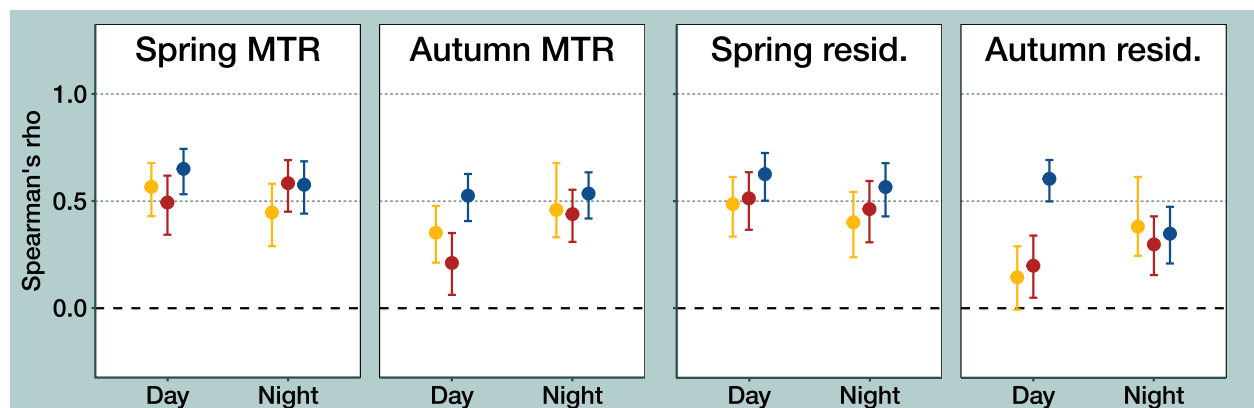


Figure 5. Between-site correlations of measured daily mean MTR (two left-hand panels) and residuals between the GAM and measured MTR (two right-hand panels). Correlations for spring migration are illustrated in the left panel and for autumn migration in the right panel of each pair, with diurnal migration on the left and nocturnal migration on the right. The y-axis shows Spearman's correlation coefficient (ρ), computed on both study years' pooled data, with error bars indicating the 95% confidence interval. The colours denote the between-site combinations, yellow for Sempach/Inn Valley, red for Sempach/Urseren Valley and blue for Inn Valley/Urseren Valley.

Results

Migration intensity

In the lowland site in Sempach and the Urseren Valley, the mean nocturnal spring migration intensities were lower than in autumn (2-year mean MTR in Sempach: spring = 449, autumn = 1376; Urseren

Valley: spring = 992, autumn = 1990, Fig. 3). Only in the Inn Valley, nocturnal spring migration was more intense than in autumn (2-year mean MTR in the Inn Valley: spring = 2049, autumn = 1362, Fig. 3).

For each site and season, the mean migration intensity was higher during the nighttime than the daytime (Fig. 3, Table 1).

TABLE 1. Statistics for the three sites and the two migration seasons pooled over both study years.

Site	Season	Daytime	Max MTR [n h ⁻¹ km ⁻¹]	Mean MTR [n h ⁻¹ km ⁻¹]	Median MTR [n h ⁻¹ km ⁻¹]	Direction [°]	Vector length
Sempach	Spring	Day	1297	153	119	61	0.59
		Night	2267	449	338	62	0.59
	Autumn	Day	1611	363	279	215	0.49
		Night	8062	1376	1120	239	0.57
Urseren Valley	Spring	Day	833	258	227	21	0.36
		Night	8493	992	726	20	0.48
	Autumn	Day	2389	701	608	221	0.27
		Night	11 171	1990	1404	225	0.45
Inn Valley	Spring	Day	1261	289	236	46	0.58
		Night	8073	2049	1581	46	0.66
	Autumn	Day	3212	276	212	222	0.39
		Night	8737	1362	1088	226	0.73

The columns are from left to right: maximum measured mean daily MTR, mean MTR, median MTR (MTR in number of birds per km per hour), mean flight direction (in degrees with north as zero) and the mean resultant length of the flight direction vectors, indicating directional concentration. Directional concentration is minimal at a value of 0 (random distribution of flight directions) and maximal at a value of 1 (parallel flight directions).

Flight directions

During spring migration 2019, differences in flight directions between daytime and nighttime were smaller than during autumn. At the lowland site in Sempach, the diurnal and nocturnal flight directions differed by 2.8° (md = 59.96°, mn = 62.75°, $F = 7.28$, d.f. = 24 865, $P < 0.05$). The Urseren Valley had the largest difference, 8.12° (md = 22.66°, mn = 14.54, $F = 62.41$, d.f. = 54 414, $P < 0.05$) and the Inn Valley the smallest, 1.13° (md = 46.56°, mn = 45.43°, $F = 4.67$, $P < 0.05$). The results in 2020 were similar, with a difference of 1.06° in Sempach (md = 61.14°, mn = 62.20°, $F = 2.18$, d.f. = 30 704, $P = 0.14$), 3.67° in the Urseren Valley (md = 19.88, mn = 23.54, $F = 29.07$, d.f. = 56 290, $P < 0.05$), and 0.38° in the Inn Valley (md = 46.02°, mn = 45.64°, $F = 0.75$, d.f. = 99 187, $P = 0.39$). The mean resultant vector length was smaller during daytime than nighttime (Sempach: 0.51 during daytime and 0.56 during nighttime in 2019, 0.64 and 0.62 in 2020; Urseren Valley: 0.27 and 0.36 in 2019, 0.44 and 0.6 in 2020; Inn Valley: 0.54 and 0.6 in 2019, 0.62 and 0.72 in 2020). In Sempach and the Inn Valley, these flight directions match the preferred migration direction for the region, but in the Urseren Valley, birds deviate to the north (Fig. 2), following the Reuss river on the shortest way to the lowlands. Additionally, the nocturnal flight directions in the Urseren Valley show a bimodality, as there appears to be a second group of birds moving towards southwest. The concentration of flight directions was highest in the Inn Valley, followed by Sempach and the Urseren Valley.

During the autumn migration season of 2019, the diurnal and nocturnal flight directions at the lowland site in

Sempach differed by 23.82° (Watson-Williams test: mean diurnal (md) = 213.77°, mean nocturnal (mn) = 237.59°, F statistic (F) = 1890.8, degrees of freedom for the echoes (d.f.) = 116 685, P -value (P) < 0.05). The differences at the two Alpine sites were much smaller: 4.11° for the Urseren Valley (md = 223.33°, mn = 227.44°, $F = 57.82$, d.f. = 203 349, $P < 0.05$) and 5.52° for the Inn Valley (md = 221.33, mn = 226.85°, $F = 74.83$, d.f. = 96 296, $P < 0.05$). In 2020, the pattern was similar with a day-to-night difference of 23.76° in Sempach (md = 217.05°, mn = 240.81°, $F = 1925.42$, d.f. = 111 190, $P < 0.05$), 4.15° in the Urseren Valley (md = 217.54°, mn = 222.69°, $F = 57.25$, d.f. = 177 136, $P < 0.05$), and 2.74° in the Inn Valley (md = 223.03°, mn = 225.77°, $F = 31.06$, d.f. = 125 735, $P < 0.05$). For all three sites, the concentration of flight directions was smaller during day- than nighttime. It was highest in the Inn Valley (0.33 during daytime and 0.72 during nighttime in 2019, 0.44 and 0.73 in 2020) followed by the lowland site in Sempach (0.48 and 0.58 in 2019, 0.5 and 0.57 in 2020). The lowest directional concentration was in the Urseren Valley (0.26 and 0.44 in 2019, 0.29 and 0.47 in 2020). Flight directions in the Inn Valley pointed southwest, matching the valley's orientation. In the Urseren Valley, migration followed the valley southwest towards the Furka Pass. We also checked whether the relocation of the radar in the Urseren Valley influenced flight directions, but at both radar sites, Andermatt and Hospental, the results were very similar.

In short, during both seasons, the flight directions collected at the Alpine sites match the local valley topography. Between day and night, the distribution and mean of flight directions were more similar at the two Alpine sites than in the lowland (Fig. 2, Table 1).

Between-site correlations

We modelled the expected migration intensity for each day of the year and hour of the day using a generalized additive model (GAM). For all sites, the GAM explained approximately half of the variability in the measured MTR and resulted in highly significant smooth terms (Sempach: effective degrees of freedom (e.d.f.) = 136.3, $F = 26.59$, $P < 0.05$, deviance explained (de) = 44.9%; Urseren Valley: e.d.f. = 92.05, $F = 17.2$, $P < 0.05$, de = 52.1%; Inn Valley: e.d.f. = 111.6, $F = 11.24$, $P < 0.05$, de = 51%).

The between-site correlations for the measured MTR and the residuals between the MTR and the GAM were consistently positive (Fig. 5, Figures S3 and S4). Most correlations were significant, but for a few exceptions (the diurnal MTR between Sempach and the Urseren Valley in autumn 2019, the diurnal residuals between Sempach and the Urseren Valley in 2019, and between Sempach and the Inn Valley in 2019 and 2020).

The correlation coefficients of MTR residuals were generally higher in spring than in autumn, with significant diurnal differences between Sempach and the Inn Valley in 2019 ($z = 2.6$, $P = 0.09$), and 2020 ($z = 2.29$, $P < 0.05$), and between Sempach and the Urseren Valley in 2019 ($z = 3.22$, $P < 0.05$). During nighttime, there were significant differences between Sempach and the Urseren Valley in 2020 ($z = 1.73$, $P = 0.084$) and between the Inn Valley and the Urseren Valley in 2019 ($z = 1.66$, $P = 0.098$), and 2020 ($z = 1.76$, $P = 0.079$).

The correlation coefficients of MTR residuals were generally lower during daytime than nighttime, but only significantly between Sempach and the Inn Valley in autumn 2020 (Fisher's Z test: $z = -2.44$, $P < 0.05$), between the Urseren Valley and the Inn Valley in autumn 2019 ($z = 3.06$, $P = 0.002$) and spring 2019 ($z = 0.49$, $P = 0.061$).

Cumulative migration intensity

The magnitude of peak migration events showed similar patterns between sites and years (Fig. 4). During both spring seasons, 2019 and 2020, it took fewer days until 50% of the total migration volume passed a site than in autumn (Number of days in spring, 2019 and 2020, respectively: 16–16 in Sempach, 11–18 in the Urseren Valley, 14–16 in the Inn Valley; in autumn: 22–25 in Sempach, 21–21 in the Urseren Valley, 22–25 in the Inn Valley).

Discussion

We studied bird migration at two sites in the Alps and at one lowland site to confirm suspected channelling of migratory fluxes in mountain valleys and to draw

conclusions about conservation practices for birds that migrate along valleys of the central Swiss Alps.

Migration intensity

We investigated migration intensity to answer the question if migratory fluxes are channelled inside valleys. Such a channelling would result in higher migration intensities, compared to the lowland. With small deviations, the data showed that migration intensity was stronger at the Alpine study sites for both years and both migration seasons, spring, and autumn. This suggests that the Alpine valleys guide and channel bird migration.

Research shows that in spring, migration intensities are usually lower than in autumn: cumulative mortality along the migration and during overwintering reduces migration intensities in spring, compared to autumn (Dokter et al., 2018; Nussbaumer et al., 2021), especially affecting juveniles on their first migration (Newton, 2006). Contrary to this, we found spring migration intensities to exceed those recorded in autumn in the Inn Valley. This pattern was consistent for both study years, 2019 and 2020. Our data do not allow us to give a solid reason for this phenomenon. However, birds approaching the Alps from the south in spring have the choice to either cross the Alpine arc or circumvent it towards the east (Rössler & Schauer, 2014), and the orientation of the two valleys we studied might promote a crossing of the Alps in spring, as the axis from Rhone to Urseren to Rhine Valley and from the Bregaglia to Inn Valley both match the preferred southwest to northeast spring migration direction (Bruderer et al., 2022; Bruderer & Liechti, 1990; Bruderer & Peter, 2022). At the lowland site in Sempach, we only measured very low migration intensities. Sempach lies south of the axis between the Alps and Jura where most birds migrate in spring (Tschanz et al., 2019). The mountains southwest to Sempach are very high, and therefore, birds approaching the Alps from the Iberian Peninsula and the Rhone Valley are likely deflected northwards. Ultimately, this would lead to the generally low migration intensities as we measured them in Sempach.

In the autumn migration season of both years, the highest MTRs occurred in the Urseren Alpine Valley. The radar site in the Urseren Valley is located at the intersection of two topographic axes: first, east to west, from the Rhine Valley to the Oberalp Pass, Urseren Valley, Furka Pass into the Rhone Valley, and second, north to south, from the lowlands to the Reuss Valley, Urseren Valley and Gotthard Pass. These valleys form large, relatively straight corridors through the Alps. The channelled migratory fluxes along these valleys are summed up at the intersection, likely leading to these high mean MTRs at the radar site in the Urseren Valley in autumn. In the Inn

Valley, the maximum of the measured MTR was higher, compared to Sempach, while Sempach had a slightly higher mean MTR. In contrast to the Urseren Valley, the Inn Valley forms a single, straight corridor along a north-east to southwest axis. Migration intensities at the radar site in the Inn Valley result from the concentrated migratory flux along this single corridor. This might likely be the reason why in the Urseren Valley, where two larger valleys intersect, autumn migration is much stronger than it is in the Inn Valley. The lowland site in Sempach lies in the main flyway for autumn migration (Bruderer & Jenni, 1990; Bruderer & Liechti, 1990; Liechti et al., 1995; Liechti et al., 1996; Liechti & Bruderer, 1986), which might explain why migration intensities were almost as high as at the site in the Inn Valley.

Besides topography, research shows that migratory fluxes are strongly influenced by local weather conditions (Erni et al., 2002; Erni et al., 2005). But how weather shapes the migration intensity in the lowlands and Alps needs to be the subject of further studies. However, we were able to capture one phenomenon where wind clearly was the main cause of sudden shifts in migration intensity. On October 3, 2019 (day 276, Fig. 2), we measured a synchronous peak migration event across all three sites. Underlying was a longer period of larger-scale adverse weather (Erni et al., 2002) with medium to strong winds from the southwest, typical for the region. On that day, the wind direction changed from southwest to north, creating beneficial conditions for autumn migration. The inconsistent effect of winds on migration intensities at the Alpine sites could be explained by the fact that Alpine valleys also channel winds. Birds that cross the Alps might therefore benefit from not having to compensate for crosswinds. Over the years, weather conditions across spatial scales could likely explain between-year differences in migration intensities that cannot be explained by topography alone.

Flight directions

During spring migration, the flight directions generally point towards the northeast, which matches the preferred migration direction for the region. However, valleys substantially influenced the directional distribution and the directions themselves. In the Urseren Valley, birds were deviated towards the north, while in the Inn Valley, flight directions were heavily concentrated along the southwest to northeast axis of the valley. However, it was unexpected that the flight direction distribution in the Urseren Valley was larger than in the lowlands, as we hypothesized that the deviation would be largest in the lowlands, where migratory fluxes are not influenced by the local topography. Likely, this can be explained by the local topography:

the intersection of the two larger valley axes at the Urseren Valley radar site gives migrating birds the possibility to continue migration either towards the north, following the Reuss Valley, or towards east-northeast, crossing first the Oberalp Pass before following the Rhine Valley. The Urseren Valley additionally was the only location where a clear bimodality in flight directions was found, one prevailing group moving towards the north, and a minor second group moving southwest. At the radar location in the Urseren Valley, a strongly concentrated wind regularly blows from the Reuss Valley towards the southwest. This would explain the bimodality in such a way that birds exposed to this current are drifted towards the southwest. How these birds ultimately continue their journey cannot be inferred from the available radar data.

During autumn migration again, we found the lowest directional concentration in the Urseren Valley, especially during the day. We assume that contributing to this are nocturnal migrants that seek a site to stop over and refuel. It is likely that they relocate towards the lowlands in the north, where they find better food resources (Taylor et al., 2011; Woodworth et al., 2015). But as with spring migration, crosswinds at the valley intersection could be responsible for the greater dispersion in flight directions by causing birds to deviate from their original course through drift. At both Alpine sites, flight directions during day and night differed only marginally, but not so in the lowlands, where diurnal migrants flew more southwards, thus, less following the Alpine arc than nocturnal migrants. Because nocturnal migrants usually fly at higher altitudes (Bruderer et al., 2018), they can more easily recognize the Alps as a large structure. At the lowland site in Sempach this would result in a much earlier initiation of a circumvention of this geographical barrier for nocturnal migrants, while diurnal migrants likely would continue a southwestern course. A second explanation for this phenomenon could be attraction by light pollution, as the Swiss lowlands west of the radar site in Sempach are brightly illuminated compared to the relatively dark region south and southwest of Sempach. The high concentration of flight directions at the Inn Valley instead supports the hypotheses of channelling of migratory fluxes along valleys.

Between-site correlations

The correlation of peak migration events between our three radar sites was generally low compared to migratory fluxes along the lowlands, which have been shown to be highly consistent (Tschanz et al., 2019). This high consistency along the lowlands allows to accurately extrapolate migration intensities from one site to another. Our result suggests that it is not possible to accurately predict

migration intensity along Alpine valleys from lowland measurements solely.

The correlation of peak migration events between Alpine and lowland sites was generally lower during autumn, compared to spring migration. We assume that this phenomenon is caused by the prevailing regional weather conditions, which are less supporting for autumn-, than spring migration (Erni et al., 2005; Nussbaumer et al., 2022; Shamoun-Baranes et al., 2017). With conditions that are more challenging in autumn, weather can have a stronger local impact on migration intensity (Shamoun-Baranes et al., 2017). Frequent head- and crosswinds force migrating birds adapt flight directions and altitudes to optimize energy expenditure (Alerstam, 2011), which on a larger scale can result in a high likelihood of different routes (Werfeli et al., 2022). Ultimately, the lower consistency between lowland and Alpine sites is likely caused by the combined effect of wind and topography, which together form the main migratory fluxes (Aurbach et al., 2018).

However, the use of only three radar sites limits the power of these results and to gain greater confidence in these assumptions, more data is required. Furthermore, the effect of wind and topography across spatial scales remains rather poorly understood.

Implications for the conservation of migratory birds

Very high migration intensities, strong alignment of flight directions and flight direction distributions that depict the local valley topography demonstrate that Alpine valleys channel migratory fluxes and guide them across the Alps. During peak migration events, such as on October 3, 2019 (Fig. 2), migration intensities can be amplified, leading to exceptionally high MTR compared to the lowlands. Second, where valleys match the preferred migration direction, flight direction has a high concentration following the valley. The concentration of flight directions inside valleys may decrease considerably when it does not match or only partly matches the preferred migration direction, when there are intersecting valleys that offer alternative routes, or when birds are influenced by crosswinds that occur at valley intersections. Third, the relatively low correlation of peak migration events highlights that extrapolating migration intensity from the lowlands to the Alps is difficult and that forecasting peak migration events in the Alps might be prone to high uncertainty.

Our findings have implications for migratory bird conservation, especially the expansion of wind energy. When evaluating potential sites for constructing new wind farms, conservation efforts have primarily aimed to protect potential habitats of particularly high-risk species, such as

the bearded vulture (Bundesamt für Raumentwicklung ARE, 2020; Liechti et al., 2013). However, wind farms also threaten the safe passage of migratory passerines, as shown by a case study in the Jura mountains (Aschwanden et al., 2018; Aschwanden & Liechti, 2016). Twenty to twenty five percent of nocturnally migrating passerines fly below 250 m AGL, well in reach of the rotor blades of most wind turbines (Bruderer et al., 2018). Migrating passerines fly even closer to the ground in poor visibility (Hamer et al., 2021; Kreienbühl, 1954) and when searching for suitable stopover sites in the early morning hours (Briedis et al., 2020). The channelling of migratory fluxes along valleys has implications for the placement of wind turbines. Our findings suggest that turbines placed in a valley or on a mountain pass pose a high risk for migratory birds, especially when the valley's orientation matches the preferred northeast to southwest migration direction. Despite a weaker concentration of flight directions, migratory birds still occur in very high densities in valleys whose axis does not match the preferred migration direction or at locations where valleys intersect. For either topographic situation, an individual assessment is necessary to find locations with relatively low bird densities. Micro-siting options (May et al., 2015), e.g., the removal of high-risk turbines, have shown to be effective at preventing collisions at specific sites (Drewitt & Langston, 2008), but could be avoided by carefully assessing migration behaviour on site, prior to wind turbine construction. Post-construction, May et al. (2015) propose passive and active measures to reduce the potential threat to migratory birds. A passive measure is to improve the visibility of wind turbines to birds (May et al., 2015). An active measure is to temporarily shut down wind turbines during peak migration nights (Aschwanden et al., 2018). Shutting down wind turbines is expensive and requires detailed information about expected migration intensities, which can be retrieved through on-site monitoring or forecasting by extrapolating migration intensities from other sites. Research considers forecasting migration intensities, especially peak migration events, an essential step for bird conservation (Aurbach, 2021; Horton et al., 2021; Kranstauber et al., 2022; Van Doren & Horton, 2018). However, migration flows in the Alps are highly uncertain (Fig. 5) and monitoring at lowland sites poorly predicts peak migration events in Alpine valleys. Instead, we recommend on-site monitoring of migration intensities as a proven, effective tool for the coordination of timed shutdowns of wind turbines during peak migration events. Wind turbine shutdowns should aim at protecting the passage of at least 50% of the seasonal migration traffic (Horton et al., 2021). For our study sites, this would result in a total of 22 action nights in autumn and 15 in spring (Fig. 4). During these, extreme migration intensities often last just a few hours of

the night. Therefore, on-site monitoring with real-time coordination of wind turbine shutdowns could reduce the number of hours when wind turbines stand still (Horton et al., 2021). In addition, the data collected at wind farms could help improve peak migration forecasting in and around the Alps, benefitting researchers, concerned stakeholders of energy companies and the migratory birds alike.

Conclusion

Migratory birds frequently use valleys as passages through the Alps. These valleys channel migratory fluxes on a relatively narrow path, amplifying migration traffic rates compared to the lowlands. Our results challenge the thesis put forward in the past that most birds avoid crossing the Alps. Current plans to expand wind energy pose a potential threat to migratory birds, especially on routes along Alpine valleys and across passes with high migration rates. Migration intensities are less correlated between Alpine sites than along the lowlands, speaking against extrapolating and predicting peak migration events from the lowlands to the Alps. Instead, we call for local monitoring to coordinate shutdowns of critically placed wind turbines to prevent high numbers of collision victims. We recommend avoiding planning new wind turbines in mountain valleys, especially in those aligned with the preferred direction of migration, and on the associated mountain passes, or only consider such constructions if accompanied by appropriate active and passive protection measures.

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Author contributions

SH, FL, PR and RW conceived the ideas and designed the methodology; BS and FL designed the field study and organized the data collection; SH analysed the data; SH, BS, FL, and PR led the writing of the Manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Conflict of interest

The authors of this article declare no conflict of interest, financial or otherwise.

Data sharing

The data and scripts will be provided upon acceptance or on request.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Demonstration of how we selected the migration seasons based on the average daily MTR and daily directional concentration (resultant vector length of flight directions). The grey curve shows the index we calculated (normalized MTR multiplied by directional concentration). The black dashed line marks the mean value of the index for each year, which was used as a threshold to separate between migratory and non-migratory periods. Days outside of any migration season are displayed in blue, and days labelled as either spring or autumn season are displayed in yellow.

Figure S2. Expected migration intensity as modelled by the GAM. The panels show the expected migration intensities for Sempach (left) the Urseren Valley (middle) and the Inn Valley (right). Each panel shows the day of the year on the *x*-axis and the hour of the day on the *y*-axis. The tiles of the plot are coloured to display the modelled expected MTR. The legend on the bottom right of each panel shows how the colours relate to MTR.

Figure S3. Yearly between-site correlations of daily mean MTR. The *y*-axis shows Spearman's correlation coefficient (ρ) as dots, with error bars indicating the 95% confidence intervals. The colours denote the site combinations, yellow for Sempach to Inn Valley, red for Sempach to Urseren Valley and blue for Inn Valley to Urseren Valley.

Figure S4. Yearly between-site correlations of daily residuals of measured MTR from modelled expected MTR. The *y*-axis shows Spearman's correlation coefficient (ρ) as dots, with error bars indicating the 95% confidence intervals. The colours denote the site combinations, yellow for Sempach to Inn Valley, red for Sempach to Urseren Valley and blue for Inn Valley to Urseren Valley.