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REVIEW

Topography and wind moulding directions of autumn migration between Europe and the West African savannas

Bruno Bruderer[1] · Dieter Peter[1]

Abstract

This review on autumn migratory directions is thought as a complement to an earlier overview on the vertical distribution of bird migration between the Baltic Sea and the Sahara (Bruderer at al. 2018): (1) A broad synopsis shows that nocturnal migration is generally SW-oriented above the western half of the European mainland, bending gradually southward above the western Sahara and shifting SE at the Sahara-Sahel transition. Important deviations of the SW stream occur along mountain ranges and coastlines. (2) Taking the Alps as a case example of such a leading-line reveals that the effect of the Alpine arc on migratory directions increases from E to W, becoming most prominent in Switzerland where the northern border and the main ridges of the Alps bend from WSW towards SSW. Thus, the migratory stream gets increasingly aligned with the course of the mountain range and reaches highest concentrations in the Swiss Lowlands. (3) Simultaneously recorded tracking radar data on nocturnal migration above Southern Germany and above the Swiss Lowlands show similar distributions of head ings, but different tracks (flight directions over ground). (4) Generally, a large proportion of the tracks above the rather flat country N of the Rhine is shifted towards S or SE by frequent westerly winds. This contrasts with barely drifting birds facing south-westerly headwinds canalized along the Jura Mountains in the Swiss Lowlands. (5) Tracks and headings under varying wind conditions above Southern Germany visualise different reactions to following vs opposing winds as well as to side winds from the right and left. (6) Radar-tracked night migrants above three different sites in south western Switzerland show their reactions to different topographical conditions which vary from moderate leading effects of the Jura Mountains at a lowland site, to extreme funnelling at an Alpine pass, and wide scatter when a large Alpine valley perpendicular to the principal SW-direction of migration is crossed. (7) Distinguishing between three height zones reveals that (a) the proportion of SSW migration increases with height; this besides a few birds drifting across the Jura Mountains; (b) at the Alpine pass, forward migration is canalised as a narrow stream and complemented by notable reverse movements, while the highest level (above the crests) is characterised by wide directional scatter including moderate southward drift; (c) the proportion of movements along the SE-NW leading Rhone Valley decreases with altitude, while the proportion of SW migration increases, and the distribution approximates that at the pass in the highest zone. (8) This information leads to ideas for continuative studies, particularly on reverse movements, drift and compensation in the Alps and their northern approach areas.

Keywords Migratory directions · Western Palaearctic · Southern Germany · Western Switzerland · Tracking radar · Leading-lines · Topography and wind · Tracks and headings

✉ Bruno Bruderer bruno.bruderer@vogelwarte.ch
[1] Swiss Ornithological Institute / Schweizerische Vogelwarte, Seerose 1, 6204 Sempach, Switzerland

Zusammenfassung

Topografie und Wind prägen die Richtungen des Vogelzugs zwischen Europa und den westafrikanischen Savannen.

Dieser Review über Zugrichtungen ist gedacht als Pendant zu einer früheren Übersicht über die Höhenverteilung des Vogelzugs zwischen Ostsee und Sahara (Bruderer et al. 2018): (1) Eine weit gefasste Synopsis zeigt, dass der nächtliche Vogelzug in der Westhälfte des europäischen Festlandes generell auf SW ausgerichtet ist, über der westlichen Sahara graduell südwärts dreht, und am SaharaSahel-Übergang südostwärts schwenkt. Bedeutende Abweichungen von der SW Richtung kommen vor entlang von Bergketten und Meeresküsten. (2) Die Alpen als Fallbeispiel eines solchen LeitlinienEffekts zeigen, dass der Einfluss des Alpenbogens von E nach W zunimmt, und besonders ausgeprägt wird, wo die Alpenketten in der Schweiz von WSW gegen SSW schwenken. Dort fällt der Zugverlauf zunehmend mit dem Verlauf der Gebirgsketten zusammen, was zu höchsten Zugkonzentrationen im Schweizerischen Mittelland führt. (3) Zeitgleich mit Zielfolgeradar erhobene Nachtzugdaten über Süddeutschland und dem Schweizerischen Mittelland zeigen ähnliche Eigenrichtungen, aber unterschiedliche Flugrichtungen (relativ zum Boden). (4) Generell werden über dem strukturarmen Gebiet nördlich des Rheins viele Vögel durch die häufigen westlichen Winde gegen S oder SE abgelenkt; dies im Gegensatz zu den Vögeln, die ohne wesentliche Drift gegen die entlang des JuraBogens kanalisierten südwestlichen Gegenwinde fliegen. (5) Flug- und Eigenrichtungen unter verschiedenen Windbedingungen über Süddeutschland veranschaulichen unterschiedliche Reaktionen auf Rücken- und Gegenwinde sowie auf Seitenwinde von links und rechts. (6) Mit Zielfolgeradar verfolgte Nachtzieher über drei topographisch verschiedenen Orten in der SW-Schweiz zeigen die Reaktionen von Zugvögeln auf unterschiedliche Bedingungen. Diese reichen von mässigem Leitlinieneinfluss der Jura-Ketten an einem Mittelland-Standort zu extremer Kanalisierung auf einem Alpenpass und breiter Richtungsstreuung beim Überqueren eines grossen, quer zur Hauptzugrichtung (SW) verlaufenden Tals. (7) Die Unterscheidung von drei Höhenbereichen zeigt (a) an der Tieflandstation mit der Höhe zunehmenden SSW-Zug neben wenigen über den Jura hinweg verdrifteten Vögeln; (b) auf dem Pass ist der Normalzug eng konzentriert; zusätzlich kommt erheblicher Umkehrzug vor; das höchste Intervall (über den Kämmen) ist charakterisiert durch erhöhte Richtungsstreuung, verbunden mit teilweiser südwärts Drift; (c) Flüge entlang des SE-NW orientierten Rhonetals nehmen mit der Höhe ab, während der SW-Zug zunimmt und die Richtungsverteilung im obersten Höhenbereich sich derjenigen auf dem Pass angleicht. (8) Diese Informationen führen zu Ideen für weiterführende Studien, insbesondere über Umkehrzug, Drift und Kompensation im Alpenraum und dem nördlichen Alpenvorland.

Introduction

The success of migratory movements depends on appropriate strategies adapted to a given environment. Innate programs with their temporal and spatial components and sufficient flexibility for adjustments in case of enduring environmental changes seem to be responsible for the large-scale flow of migration between Europe and Africa. In addition to endogenously controlled directions and time programmes, adult birds may make use of experience, while both young and adult birds will probably rely on behavioural rules, developed as adaptations to recurring en route features such as topography, refuelling possibilities, and atmospheric conditions (Bruderer 1997). Due to the complicated shape of Europe, birds are confronted with a broad variety of coastlines, and with potentially relevant sea crossings on their way to Africa, where directions may even change in the course of the night (Fortin et al. 1999). For passerine birds (making up the bulk of migration), feeding should be possible everywhere in Europe, albeit with varying refuelling rates (Erni et al. 2002, 2003). However, due to prevailing westerly winds in Europe, SW migrants are at a disadvantage compared to SE migrants; it seems that persistence of the SW flyway depends on refuelling possibilities before Sahara-crossing (Erni et al. 2005). In addition to the challenging coastlines, there are – in contrast to the N-S oriented mountain ranges in the Americas – several mountain chains across the migratory flyways in Europe, most prominent the Alps. It is plausible that the sequential obstacles of the Alps, the Mediterranean Sea, and the Sahara contribute to the persistence of directional preferences towards SW and SE instead of direct flights towards S. The origin of these basic flyways goes probably back to multiple colonisations of Europe from glacial refugia in the western and eastern Mediterranean during interglacial warming periods, including the actual one, which continues since the end of the last glaciation (Bruderer et al. 2008). Despite the problems with opposing winds, the principal direction of most nocturnal passerine migrants breeding W of 10° E is SW. Some species show a migratory divide between 10° and 20° E with eastern populations migrating SE. Further east (and particularly towards SE) the proportion of birds with southerly directions increases.

Nocturnal passerine migrants on the European SW flyway are obviously confronted with multiple challenges, such as coastlines and mountain ridges requiring decisions in favour of crossing or aligning, or opposing winds calling for trade-offs between strenuous attempts to maintain intended directions and varying possibilities of dealing with drift. In our review we will zoom in from a continentwide view of directions to the flow of migration around the Alps and to increasingly smaller areas with specific conditions to illustrate wind effects under differing orographic conditions:

(1) In a large-scale approach we visualize the general flow and regional deviations of nocturnal autumn migration over Europe based on observations with various types of radar, infrared, and moonwatching.

(2) Combining information from diverse sources about nocturnal migration in the region of the Alps, we illustrate multifaceted impacts of this well studied leading-line, varying e.g. with the approach angle of the migrants towards the northern border of the mountain range, and according to the general wind regime.

(3) A first regional study with simultaneous tracking radar observations in southern Germany and the Swiss Lowlands indicates that night migrants moving above a faint relief to the North of the Rhine seem to have more difficulties to maintain their preferred SW-direction under westerly winds than those advancing close to the mountain ranges of the Alps and the Jura.

(4) In a second regional study we compare the distributions of tracks, headings, and wind directions from two complete (but different) autumn seasons in the area of Nuremberg and in the Swiss Lowlands, thus testing the differences between orographically different sites for larger samples.

(5) In a third step, the data set of Nuremberg was used to compare the distributions of tracks and headings in two height zones under different wind conditions (weak and strong winds along and across the axis of undisturbed migration) to provide an idea of reactions to characteristic wind situation and stimulate ideas for further studies.

(6) In order to visualize the influence of local topography under average wind conditions we compare the distribution of all tracks and headings recorded throughout a complete autumn season at three different sites in southwestern Switzerland (in the Lowlands, at an Alpine pass, and in a large valley across the main flow of migration).

(7) By distinguishing three height zones above these three sites we expect to see decreasing effects of topography with height and increasing difference between tracks and headings due to growing wind force. We hypothesize that birds flying above the neighbouring mountains would suffer some drift under the frequent westerly winds; this, however, to a much lower extent than above the less structured relief in southern Germany.

Methods, sites, and data

We used the tracking radar “Superfledermaus” which can be positioned at specifically chosen sites and has been applied for the study of bird migration since 1968 continuously (Bruderer 1971, Bloch et al. 1981, Bruderer et al. 2012, Bruderer 2020). At various locations along the western European flyway, we measured the spatial distribution of migrating birds which provides information on the variation of migratory intensities and on height preferences of the migrants. We also tracked single targets (birds and pilot balloons) which inform about the adjustments of the vertical distribution of migrants in relation to wind conditions (Bruderer & Steidinger 1972, Bruderer et al. 2018). In the present study we deal with the directional behaviour of tracked birds.

The flight paths of radar-tracked birds provide the direction of the targets relative to the ground (track or flight direction), their groundspeed, vertical speed, and height above ground level (agl). The wind data measured by pilot balloons allow calculating the headings (direction of the body axis) and airspeeds of single birds. The general rule was that radar operators sampled similar numbers of bird echoes in the height intervals 0-1000, 1000-2000, and > 2000 m above the radar station. Thus, the numbers of targets sampled at different heights do not represent the height distribution of birds. Nevertheless, low numbers of tracks in a certain height interval reflect the difficulty of the operators to find targets, and thus indicate extremely low intensity of migration. The polar coordinates of the tracked objects (birds or pilot balloons) provided by the radar at intervals of 1 sec were digitized, transformed into Cartesian coordinates, and averaged over 20 sec. These averages were used to calculate individual flight direction and heading, height above radar, groundspeed, and airspeed as well as vertical speed in a personal computer, where all the data were stored.

For detailed studies at particular sites, birds tracked between 20 h and 05 h were included in the standard analysis (provided their airspeed V_a was > 5 and < 25 m/s, and their vertical speed V_z > -5 and < 3 m/s). Whenever possible, the wind-measurement at midnight was used for the calculation of headings and airspeeds of all night migrants. In the rare cases when this measurement was lacking, the wind data of the nearest evening or morning pilot balloon was used. For altitudinal comparisons, we used three height zones (over flat country roughly up to 1500 m, 1500-2500, and > 2500 m asl, i.e. above sea level); in mountain areas we compared height zones a) well below the neighbouring mountains, b) at the height of the main crests (comprising a few 100 m above and below) and c) above the neighbouring mountains. For certain comparisons with data sets from flat areas we used only two height zones from mountain areas, excluding narrow zones around the mountain crests.

Besides the large-scale studies (points 1 and 2 in the introduction), the following specific radar sites provided particular data sets: (A) For a regional comparison between southern Germany and the Swiss Lowlands we used simultaneously (31 August until 22 September 1987) recorded tracking radar data from the area of Nuremberg (Lehrberg 10° 31’ E / 49°29’ N, 450 m asl,), near Regensburg (Painten 11° 48’ E / 48° 59’ N, 540 m asl) and Payerne in the Swiss Lowlands (6° 57’ E / 46° 49’ N, 490 m asl). (B) For a comparison of the flight behaviour of nocturnal migrants under varying wind conditions we used the data of a complete autumn season at Lehrberg near Nuremberg (1 Aug – 30 Oct 1987). (C) To study the influence of local topography on the flight behaviour of nocturnal migrants we installed radar stations at three locations with distinct orographic conditions in western Switzerland: 1) *Kappelen* near Aarberg (7°15’29.8” E / 47°03’12” N, 442 m asl, 17 Aug – 28 Oct 1988) some 20 km NW of Bern; 2) *Col de la Croix*, a pass in the westernmost part of the Bernese Alps (7°07’56.4” E / 46°19’56” N, 1718 m asl, 1 Aug – 9 Oct 1988); 3) *Monthey* (6°57’39.6” E / 46°16’26.3” N, 390 m asl, 7 Aug – 8 Oct 1988), on the bottom of the SE–NW leading Rhone-Valley, 15 km SE of the eastern end of Lake Geneva.

The basic direction (BD) is the mean vector of the tracks recorded in a specific area under minimal wind influence (Bruderer & Liechti 1990). As BD may differ between altitudes, we defined it for two or three height zones above each radar site, using the track directions of all individuals flying in weak following winds (wind speed = V_w < 5 m/s) or in opposing and side-winds with speeds V_w < 3 m/s.

Additional data used for overviews at a continentwide scale and in the general region of the Alps are partly based on other methods such as weather surveillance radar (WSR) air traffic surveillance radar, marine radar, infrared (IR), and moon-watching. Publications describing these methods and resulting knowledge are specified in Annex 1 and 2.

Background, results and findings

Large-scale directions and deviations

Pleistocene contractions and inter-glacial expansions of the distribution ranges of many bird species (e.g. Bruderer et al. 2008, Ponti et al. 2020) provided a general basis for the development of migratory movements between breeding and non-breeding ranges. This general basis is moulded by evolutionary processes according to environmental conditions continuously up to now. Radar, infrared, and moonwatch observations illustrate the result of this optimization (Fig. 1): Directions of nocturnal migration above central and western Europe are generally centred around SW (i.e. roughly perpendicular to the retreating front-line of the last Pleistocene glaciation). Important deviations occur along mountain ranges and coastlines. In the northern half of the European mainland (mainly northern Germany and Poland) environmental conditions induce mainly deflections towards WSW, while in southwestern Europe the coasts promote rather southerly directions. In north-western Morocco migrants continue with SW movements, while directions in Mauritania shift gradually towards S or SSE and "switch" to SE at the transition to the Sahel savannas. The pattern seems to be governed by the spatial distribution of landmasses and their coasts, additionally by mountain ranges, most pronounced along the northern border of the Alps, but also along the western Carpathians and the Spanish Cordilleras. The abrupt directional shift at the southern edge of the Sahara indicates that habitat-change may be a relevant additional cue. In the eastern Mediterranean, directions are mainly southward, except some deviations around islands and along the Gulf of Suez.

The idea that topographical features such as mountain ranges, large valleys or coastlines may influence the routes of migratory birds in the sense of leading-lines has a long tradition (e.g. Palmén 1876, Göldi 1914, Geyr von Schweppenburg 1933, Toschi 1939, Schüz 1971). Birds approaching mountain areas across their intended route should evaluate the risks and costs of crossing or circumventing these obstacles. Considering that on average 50% of the migrants flying over relatively flat European regions are below 700 m agl (above ground level), at some sites even below 500 m (Bruderer et al. 2018), it is obvious that notable parts of the migrants have either to climb or to fly a detour at mountains higher than 700 m above the surrounding terrain (Aurbach et al. 2018).

Autumn migration in the region of the Alps

The influence of the Alps on migrating birds has been discussed since the beginning of the 20th century (Fatio 1905, Göldi 1914, Sutter 1955, Vuilleumier 1963, Bruderer and Winkler 1976). Radar observations and moon-watching campaigns documented important funnelling of nocturnal autumn migration along the arc of the Swiss Alps, resulting in average migration traffic rates of 4000 birds/km/h in the Swiss Lowlands or 2 million birds passing between the Jura and the Alps in nights with favourable weather conditions (Liechti et al. 1996a)[1]. Tracking radar studies along the pre-Alps revealed that birds approaching the Alps at low levels often prefer to fly along the flanks of the first ridges instead of climbing; birds approaching above the mountains in fair weather tend to continue with unchanged directions or undergo partial drift with westerly winds (Bruderer 1981, Liechti and Bruderer 1986, Bruderer and Jenni 1988). The question, why drift is much weaker in the Swiss

[1] This in comparison to average migration traffic rates above southern Germany with 1000-2000 birds/km/h

Lowlands compared to southern Germany (Bruderer and Jenni 1990), will be approached in the two following chapters comparing the two regions again.

In eastern Austria most nocturnal autumn migrants maintain their SSW directions to cross the Alps which they encounter at an angle of roughly 60°; this large angle seems to induce no important concentration of migration at the northern border of the eastern Alps (Aschwanden et al. 2020, Rössler and Schauer 2014, dashed blue line in Fig. 2). Further on along the northern border of the Alps from Austria towards Switzerland, the approach angle decreases to about 40° in eastern Switzerland and to 10° near Geneva, because the border as well as the highest ridges of the Alps shift from roughly 245° (in the eastern half of Switzerland) to 230° and eventually 220° (in the western half). Migration accumulates increasingly due to continuous arrival of migrants from NNE and increasing alignment with the course of the SW-bending Alps. The concentration is further increased when birds are drifting southward with the frequent westerly winds in the approach area. These are also the situations when important numbers of birds are moving through SW-leading valleys and passes (pink lines in Fig. 2).

Reactions to winds in flat and mountainous regions

Simultaneous observations

Simultaneous tracking radar studies for three autumn weeks at two sites in southern Germany (near Nuremberg and near Regensburg) and one in the Swiss Lowlands (Payerne, to the SE of Lake Neuchâtel) showed nearly matching directional distributions of headings at all sites, but considerable differences in the distribution of tracks (Fig. 3). The birds seemed to head towards similar intermediate destinations but reacted differently to winds: Near Nuremberg about half of the tracked birds maintained south-westerly directions, obviously being able to compensate side-winds. The other half of the tracked birds moved mainly towards the SE-sector, indicating important deviation by W-winds. Near Regensburg winds were practically always from WNW and W (shifted about 20° clockwise in comparison to winds at Nuremberg, and thus comprising stronger side-wind components): The distribution of tracks showed a lower proportion of SW-migrants than near Nuremberg and – in addition to a SEcohort – an equally important cohort moving southward. In the Swiss Lowlands winds tend to be canalized in this large valley, particularly along the mountain ranges of the Jura. Fig. 3 shows a difference between the available (general) wind directions (scattered around 230°) and those measured for each tracked bird (and thus preferred by the birds, these concentrated around 240°): It seems that the birds preferred direct headwinds (240°) to winds with a 10-20° lateral component. The direct headwinds induced an increased scatter of tracks, but no pronounced deviation of the average distribution, and only a small proportion of SE movements.

Long-term observations during two different seasons

The radar sites at Nuremberg and Kappelen are perfectly suited to visualize the effects of varying wind conditions on the directional behaviour of nocturnal bird migrants depending on topography; Nuremberg is a site with minimal influence of topography, Kappelen has a prominent mountain range nearby.

General wind conditions (Fig. 4) were dominated by westerly winds at Nuremberg, at low levels scattered between 240° and 320°, and complemented by a small proportion of winds from SE (120140°). At levels above 1500 m asl winds came mainly from a narrow WNW-sector (260-290°). Headings were spread in a sector of about ±30° around 230° (corresponding to low-level BD) at both flight levels, slightly more dispersed at low levels. Tracks were extremely scattered between W and ESE at low levels, with a dominating WSW-cohort and a smaller SE-cohort. Astonishingly, the scatter of tracks was much smaller above 1500 m asl with one cohort roughly corresponding to the headings (and centred around upper-level BD); a smaller off-course drifting cohort and was spread across a wide sector around SSE.

At Kappelen, winds were canalized along the mountain range of the Jura even above the ridges. For birds flying below the crests (< 1400 m asl) there were practically no side-winds, and even above the ridges side-wind components were small. Therefore, tracks and headings of autumn migrants were concentrated in a narrow sector around 240° (along the axis of prevailing winds) at low levels. At flight levels > 1500 m asl one cohort of tracks was still centred around 240°, while a second cohort of birds had crossed the Jura mountains with tracks and headings around 200-210°. BD above 1500 m seems to represent an average of the two cohorts. Active mountain-crossing (with similar headings and tracks) represents a behaviour that differs from birds drifting towards S or SE off their headings in southern Germany.

The basic direction as an indication of desired directions

The similarity of average heading distributions in Fig. 3 and 4 may prompt us to believe, that headings represent the intermediate goal directions of the birds. However, headings vary under the influence of side-winds (Fig. 5), because the birds try to compensate deviations by heading into the wind. Therefore, Bruderer and Liechti (1990) suggested that track directions under least wind influence provide a better indication the birds' desired directions than headings. Therefore, they defined the term "basic direction" (BD) as the prevailing track direction in a particular area under least wind influence. Astonishingly, this basic direction showed a slight counter-clockwise shift with altitude above southern Germany (roughly 230° for low flying birds, while varying around 218° for birds > 1000 m above radar or ~ 1500 m asl). Birds seemed to compensate small side-wind components under weak following winds and even under very weak opposing winds, maintaining BD by heading into the wind. As the capacity of the birds for compensation is limited, partial drift increased with wind speed. With further enhancement of wind force some of the birds shifted their body axis southward; thus, resulting in over-proportional S- and SE-ward deviations.

Bruderer and Jenni (1990) suggested that the altitudinal shift in BD might (according to birds caught in the Swiss Lowlands and on Alpine passes) be due to an increased proportion of birds from northern populations flying at high altitudes, well prepared for mountain-crossing with high energy reserves, pointed wings, and southerly directions. They also visualised for a wide range of radar stations in southern Germany and Switzerland a) relatively constant heading distributions contrasting with wind-governed track distributions to the N of the Rhine, b) scattered, but not deflected tracks under westerly winds in the Swiss Lowlands, suggesting that the winds funnelled between the Jura and the Alps are more or less direct headwinds, thus lacking important side-wind components, c) the lack of an altitudinal shift in track directions above the eastern part of the Swiss Lowlands contrasting with important altitudinal southward shifts close to mountain ridges of the pre-Alps along or across the principal direction of migration.

Reactions to varying wind conditions in flat country

To provide an idea of the birds' reactions to varying winds we present the distributions of tracks and headings within two height zones under weak and strong winds from four sectors above the Nuremberg radar (Fig. 5). – Under *weak following winds* tracks around 230° are prominent at both altitudes. At low altitudes this is close to the basic direction BD; scattered headings indicate that the birds try to maintain BD by compensating small side-wind components. At the higher level, a second cohort with tracks towards 210° is added; the two cohorts result in a BD of ~ 216°. Two prominent peaks of headings towards 210° and 240° support the idea of two different populations. The peak towards 240° indicates compensation of winds from the N. With *strong following winds* the two peaks of tracks towards 230° and 210° are maintained in the upper height zone, while in the lower zone tracks are scattered ± 20° around BD, and some birds move towards 260° with easterly winds. – Under *weak opposing winds*, tracks at low levels are more scattered than under following winds and slightly deviated (220° and 250°). Higher up, headings are mainly centred around 230°, while tracks show two modes (at 220° and 240°). *Strong winds from WSW* induce pronounced drift towards SE, at high flight levels from normal headings (around 230°); at low levels most headings are S of BD, indicating that some of the birds did not only give up compensation, but shifted their heading southward. – *Weak side-winds from the right* induce increased compensation efforts in both height zones with headings between 220° and 260°; this results in two peaks of tracks at 210° and 240° at low levels, and somewhat more drift higher up; small numbers of SSE oriented movements occur. In *strong side-winds from the right*, practically all the tracks are deviated towards S or even SE from headings at low levels centred around 240250° (but scattered between 220° and 300°), and somewhat more concentrated headings spread around 230-240° higher up. – With *winds from the left* deviations are less pronounced. Under weak winds two heading components stand out at both flight levels: a) normal headings towards 230° and 240°, b) more prominent, compensating headings towards 210-220°. This results in a) tracks scattered broadly around BD at low and high levels, b) important deviations towards 250°, particularly at low levels. Under *strong winds from the left* partial compensation results in moderately deviated tracks, most of them remaining within the SW sector (mainly between 240° and 260°), thus less deviated than those in winds from the right.

Influence of local topography

Three sites with different topography

The radar sites Kappelen, Col de la Croix and Monthey provided simultaneously recorded data on the flight behaviour of nocturnal migrants at three topographically differing sites in southwestern Switzerland. Fig. 6 shows the position of the three sites (each indicated by a red point) in relation to the relief, with the Jura Mountains along the north-western edge of the Swiss Lowlands and the Alps to the SE. The site-specific tracks and headings of the migrants are summarized over all heights and the complete season, arranged relative to a cross which indicates the centre of the directional distribution. Compared with the reference station in the Swiss Lowlands (Kappelen), directions at Col de la Croix were extremely concentrated along the high ridges of the Bernese Alps, with a notable part of movements in directly opposite directions. The birds at Monthey showed a wide scatter around principal directions between 210° and 240°; in addition to this main migratory stream there were two competing cohorts tending up and down the Rhone Valley. Differences between tracks and headings were much smaller at all Swiss sites than in southern Germany.

Three flight levels per site

Fig. 7 visualises the variation of flight directions and headings within three height zones above the three radar stations in the Swiss Lowlands, at an Alpine Pass, and in the lower Rhone Valley. The sitespecific height zones comprised birds well below the local mountain ridges, at the height of the ridges (some 100 m above and below), and well above the neighbouring crests.

The *Kappelen* station (442 m asl) was situated 8 km SE of the Jura foothills, where the mountain tops 13-15 km to the NW of the radar site reach 1300-1500 m asl. Low flying birds were therefore protected against winds from W and NW, and winds as well as the birds tended to follow the large valley of the Swiss Lowlands bordered to the NW by the arc of the Jura Mountains. At the height of the mountain ridges, tracks and headings of the main migratory stream were slightly shifted (from 240° at the lowest level) towards 230°. In addition, notable migration arrived across the Jura Mountains with directions around 210°, and some birds were drifting SE. Above the mountains, headings towards 230-240° still prevailed, while the proportion of tracks towards 200-220° was increased; the difference between tracks and headings indicates a notable proportion of partially drifting birds.

The *Col de la Croix* radar station (1718 m asl) was ~ 1 km to the NNE of the pass and 58 m lower than its culmination. The birds arriving at the pass from NE were confronted with the massive ridge of Les Diablerets. The peak closest to the radar (3.5 km to the SE) reaches 2788 m asl. From this point the ridge descends gradually over 2 km towards WSW, eventually sloping down to the Rhone Valley. The mountains bordering Col de la Croix to the NW maintain altitudes of about 1800-2000 m asl (only about 100-300 m above the radar) over a distance of 5 km from the radar towards WSW, before declining to the Rhone Valley. Extremely funnelled migration with directions towards 230° and 240° and movements in exactly opposite directions were characteristic for this Alpine Pass. At the height of the mountain ridges the spread of directions, particularly of (drift-compensating) headings were increased; reverse directions were prominent. At the highest flight level, the scatter of headings and tracks was even wider than at the other sites, while the principal directions still followed the neighbouring mountain ridges. A conspicuous component (visible also at the medium level) was represented by directions towards 280-290°, roughly towards two villages (Leysin and Cergnat/Le Sépey, possibly attracting birds by their lights).

The *Monthey* station (390 m asl) was situated ~ 1 km off the western border of the Rhone Valley and nearly 5 km from its eastern border. The narrow entrance to Val d'Illiez (the SW-oriented valley leading to Col de Bretolet) is 3 km SSW of the point where the radar was positioned. The bottom of the Rhone-Valley is 4-5 km wide towards NW; towards SE it narrows to a width of 1 km at a distance of 5 km with mountain peaks reaching roughly 3000 m asl at a distance of 11 km to both sides. Track directions at low levels were mainly oriented towards the entrance of Val d'Illiez and showed pronounced branches up and down the Rhone Valley. At the height of the neighbouring mountains, birds could see the main course of Val d'Illiez; this attractive direction coincided with the main directions at Col de la Croix; the proportion of flights up and down the Rhone Valley as well as towards the narrow entrance of Val d'Illiez diminished. Above the crests, tracks and headings resembled those at Col de la Croix (with less drift towards southerly directions, but some reverse movements).

Earlier studies on an Alpine pass

At the Hahnenmoos pass in the eastern part of the Bernese Alps the canalisation of the migrants is less strict than at Col de la Croix, because the high ridges to the S are more than 7 km away from the pass and towards SW the migrants have a wide choice of directions. Despite these broad possibilities, migratory directions were concentrated towards 240° and 230° with winds from NE (following) and SE (from left). Opposing winds and particularly winds from NW (right) led to increased scatter towards S and SSE. According to the frequency of winds, the number of birds tracked with opposing winds was roughly four times higher than with winds from each of the other sectors (Bruderer 1978). – A more detailed analysis of the data set from the Alpine pass (Bloch et al. 1981) differentiated three height zones: While movements at low levels were adjusted to local topography, migration above the neighbouring mountain ridges (> 3000 m asl) was shifted towards SSW (220°-200°) under following winds and side winds from the right (NW), thus deviating considerably from the directions at low levels at the pass and prevailing directions in the Swiss Lowlands. With the (dominating) opposing winds from SW, forward migration at low levels was spread around 230° and 250°, while deviated movements were broadly scattered mainly between 50° and 120° (thus including wider scatter but less reverse migration than at Col de la Croix); at altitudes higher than the neighbouring ridges, reverse movements further diminished in favour of SE and southward flights (i.e. drift instead of reverse migration).

Wind drift and compensation capacity

Liechti (1993) analysed the same data set of migration near Nuremberg that is used in our present study. He analysed and visualized the distribution of tracks and headings under various wind conditions, and presented a model calculating the degree of side-wind compensation at altitudes below 1000 m agl as well as higher up: Low flying birds were able to compensate completely for side-wind components reaching about 20% of their own airspeed (i.e. about 2.4 m/s = 8.6 km/h); higher wind speeds allowed only partial compensation. Compensation decreased with height, lowering to 14% of airspeed at heights of 1000-2000 m, and to 7% at heights > 2000 m agl. Nocturnal migrants seemed to compensate drift mainly according to wind direction and not according to wind speed. Birds flying higher than 1000 m agl maintained headings compensating for winds below 1000 m agl. Increasing proportions of southerly flight directions above 1000 m agl are not only due to wind, but also to more southerly headings of birds. Particularly under strong headwinds (> 10 m/s from SW) southerly headings of many birds result in tracks towards SE or even E. If the birds use the angular velocity of landmarks to estimate the angle between heading and track, as suggested by Liechti (2006), this compensation capacity will decrease with increasing flight level, particularly in areas with no prominent topographical structures.

The airspeed of birds is an important reference parameter, when considering variation of flight directions with wind. The capacity for drift compensation depends on airspeed. The definition of this reference is, however, tricky, because airspeeds vary not only with bird species, but also with windspeed, and increase with altitude (Bruderer 1971, Schmaljohann and Liechti 2009). At an Alpine Pass the average speed of passerines was 12.6 m/s or 45.4 km/h, but considerable variation according to winds: with opposing winds average speed was about 50 km/h; under following winds, large passerines reduced their airspeed to about 45 km/h, small passerines to ~ 36 km/h) (Bloch et al. 1981). The proportion of passerines during September and October is usually 90-98% of all migrants in southern Germany (Bruderer and Liechti 1998) as well as in the Swiss Lowlands (Bruderer 1971). An all-over average of 45 km/h or 12.5 m/s may be a reasonable value for average airspeed of nocturnal autumn migration over central Europe. With opposing winds close to the birds' average airspeed, the birds may increase their airspeed by about 20%, and reduce it with following winds (Bruderer 1971).

Liechti (1995), applying Pennycuicks (1989) calculation manual, chose a Garden Warbler *Sylvia borin* as a model bird, and arrived at theoretical reference speed of 10.5 m/s (~ 38 km/h), representing maximum range speed V_{mr} at sea level and zero wind. As autumn migrants in central Europa are usually confronted with opposing winds and fly considerably higher than sea level, it is understandable that average speeds measured under field conditions in autumn are higher than the theoretical speed.

Following winds provide optimal conditions by increasing ground speed and thus the speed of migration, while allowing the birds to reduce their airspeed from maximum range speed towards minimum power speed (Pennycuick 1975). In following winds, the scatter of track directions is reduced (by sheer mechanical concentration). Opposing winds reduce ground speed, induce increased power consumption due to augmenting air speed, and physically increase the scatter of tracks. Side winds induce deviation from the intended direction to an intermediate goal, if birds do not or cannot compensate for occurring drift.

Discussion and prospects

Detailed radar, infrared, and moon-watch data collected over decennia from aeras all over Europe and northern Africa combined with recent data of the European weather radar network provide a unique opportunity to integrate continentwide directional information on bird migration across scales and time.

Large-scale pattern and approach to the Alps

The general pattern of nocturnal bird migration revealed by a European weather radar network (Nilsson et al. 2019) was a motivation to complement this stimulating overview by information from other sources, providing a more detailed and geographically extended picture of migratory directions. Deviations from general migratory directions become obvious along coastlines, at mountain ranges and at the transition from the Sahara to the Sahel savannas. New radar data from Aksakovo (Bulgaria) corroborate the moon-watching data integrated in Fig. 1 with an average direction of nocturnal autumn migration (200°) roughly parallel to the neighbouring Black Sea coast (Michev et al. 2020). In the region of the Alps the information of Fig. 1 is very dense; readers not familiar with the topography of the areas may need to consult the original publications or summaries of particular areas presented by Bruderer (2017, pp. 50 and 100-115). Light-level geolocators do not show small scale deviations of directions; but even with this limitation various topography-related deviation may become visible, e.g. Spanish, Bulgarian, and Swedish Great Reed Warblers that seem to have changed direction when leaving the European continent towards Africa, and similarly on their return flights in spring (Koleček et al. 2016); Swedish Wheatears suggesting massive changes of directions in the area of the Carpathians along the northern borders of Hungary and the Czech Republic or an individual changing from a SEflight along the Adriatic coast of Italy to a track aiming towards the western Sahara, another one from Italy via Sicily to Tunis (Arlt et al. 2015). The directional shift at the Sahara/Sahel transition (habitat change in a flat landscape) was confirmed by tracking Common Redstarts with geolocators (Kristensen et al 2013). The possibility that migrants may visually recognise and react to seasonally appropriate habitats was supported by experiments with red knots (Kok et al. 2020).

An important new aspect of autumn migration towards the Alps is the difference in crossing behaviour of nocturnal migrants approaching the Alps in eastern Austria compared to Switzerland (Rössler and Schauer 2014). Besides the fact that the eastern part of the Alps in Austria is less high than the western part in Switzerland, the large approach angle of roughly 60° in eastern Austria seems to favour crossing instead of deviation, while the arc of the Alps bends increasingly southward in Switzerland, resulting in a reduction of the approach angle from initially about 40° to eventually 10° along the Swiss Lowlands. The effect of the Alps as a leading-line seems to increase with the decrease of the approach angle, thus confirming a general suggestion of Schüz (1971) about leading-lines.

Decreasing compensation with height above ground?

If visual cues on the ground are used to detect wind drift, we expect corrections to winds aloft to decrease with the visibility of landmarks, and thus with height above ground (Liechti 1993, 2006). Pronounced drift with frequent westerly winds above rather flat landscape (in southern Germany) contrasting with compensated drift along and above mountain ranges supports this view. However, we must consider that mountain ridges (as e.g. the Jura) are not only a prominent leading-line for the birds, but also for the winds. The winds are canalized by the Jura Mountains, and thus comprise reduced side-wind components. Forthcoming studies should aim at quantifying the influence of increasing wind speed from different sectors at various sites and altitudes on the tracks and headings of nocturnal migrants.

Different directional behaviour according to topography

Above the rather flat area near Nuremberg, wind distributions are centred around W or even WNW, while winds in the western Swiss lowlands are canalized along the mountain ranges of the Jura, i.e. in narrow sectors around WSW (and ENE) in both height zones. The distributions of tracks and headings are more concentrated and nearly coincide at low levels along the Jura Mountains; above the mountain ridges, a SSW-oriented (mountain-crossing) cohort is added to the tracks. Near Nuremberg, broad scatter of headings indicates a wide range of behaviour ranging from compensation to tolerated drift; this results in tracks scattered across the complete southern half of the wind rose at low levels. Higher up, the scatter of tracks and headings (as well as winds) is reduced, but the contrast to the birds migrating along the Jura Mountains is obvious in both height zones. A quantitative analysis of the birds' reactions to increasing winds from all sectors of the wind rose should show, whether similar winds (even with rare occurrence) would cause similar behaviour of the migrants, or alternatively, that migrants close to a prominent leading line are better at compensating similar side-wind effects.

Variation of directions in mountainous terrain

Including complete seasons and all altitudes at three sites in western Switzerland reveals no obvious difference in the principal directions of migration; the site-specific movements seem to be part of the same migratory stream. There are, however, topography-related differences in the lowest hight zone, diminishing with height: At Col de la Croix, the low-level concentration of directions is compulsory, while along the Jura there is no barrier hampering S and SE movements; at Monthey, flights up and down the Rhone Valley are inviting at all flight levels. – Above the crests, frequent westerly winds induce a slight anti-clockwise shift of track directions, most prominent for birds crossing the Jura Mountains. Such directional shifts due to mountain-crossing are even more pronounced at the first ridges of the pre-Alps (Liechti and Bruderer 1986).

A special feature of night migration at Col de la Croix are tracks and headings towards 280-290° at medium and high flight levels. We suspect that visual attraction by the villages Leysin and Cergnat/Le Sépey may be responsible for these particular directions. Attraction by light is a well-known phenomenon (e.g. Posch et al. 2010) and has also been described for special cases in the Alps by Bruderer (2017). High proportions of deviated (including reverse) movements had also been observed at the Hahnenmoos pass further east in the Bernese Alps, particularly with opposing winds. Quantification of the conditions favouring such unseasonal movements is envisaged.

At Monthey, directions below the height of the neighbouring mountain crests are extremely scattered, while directions above the ridges resemble those at Col de la Croix. Considering that migrants having crossed a pass or a mountain ridge do usually maintain their flight level (Bruderer et al. 2018), we may assume that birds flying below the ridges are not deviated parts of the main migratory flow from Col de la Croix, but migration along the Rhone Valley. The complex behaviour at Monthey will be analysed in forthcoming studies.

Altitudinal shift of directions was even more pronounced along the border of the pre-Alps, thus contrasting with the Swiss Lowlands, where no important change of directions with altitude was observed (Bruderer 1981). – Liechti and Bruderer (1986) summarised previous radar observations on bird migration in Switzerland: Birds arriving at the first pre-Alpine ridges below the crests seem to optimise their behaviour by a trade-off between minimum climb, minimum deviation, and avoiding strong headwinds; alignment with topography increases with decreasing deviation of the ridges from preferred migratory directions. This behaviour leads to the well-known concentrations of migration in SW-leading valleys (pink dashed lines in Fig. 2). Birds arriving at flight levels higher than the ridges across their preferred direction tend to maintain the same directions as above the Lowlands during fair weather with weak or following winds. However, with the frequent westerly winds the birds are exposed to drift, increasing with height and wind force. On average, this leads to an important southward shift of directions with altitude at all sites close to pre-Alpine ridges crossing normal autumn directions of migration.

Conclusions and prospects

In southern Germany, the southward shift of the basic directions with height seems to be a consequence of a cohort of birds from northern populations joining the general stream of migration. Extreme deviations from basic direction in strong westerly winds contrasting with moderate deviation by winds from SE (left) call for a quantification of wind effects. To the south of the Jura, a mountaincrossing cohort becomes increasingly prominent with height. At Col de la Croix southward movements above the mountains are less pronounced than at the Jura, and nearly lacking at the Monthey site. The complex conditions in the Rhone Valley are a challenging subject for a detailed analysis.

With respect to directional shifts according to wind conditions, we deduce the following hypotheses: Birds avoid drift towards the right of their basic direction to a higher degree than towards the left. Following winds are better compensated than opposing winds. In opposing winds, birds try to compensate side-wind components as long as wind speed is less than the bird's airspeed. With increasing wind speed, tracks become either increasingly scattered or the birds get drifted. Headings may indicate (a) constant efforts for compensation resulting in decreasing success of compensation with increasing wind, (b) drift-tolerance without compensation, (c) partial alignment of headings with wind directions, (d) down-wind flights. Expecting increasing drift effects high above topographical reference points, we will test these predictions by quantifying wind effects for two different height zones above topographically differing sites.

Generally, the outcome of this broad comparison of data derived with various methods from wide parts of Europe and North Africa opens new perspectives to think about (1) the evolution of this migration system in connection with changes in the meteorological and climatological environment, (2) consequences for conservation of bird migration in the region, (3) integration with additional data derived from sources such as synoptic weather information, ringing data, and citizen science, (4) detailed analyses based on individual tracking data and local weather parameters.

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Author contributions BB designed the study and wrote the article; DP managed the radar data bank, selected the required data sets, prepared the graphics, and commented the text.

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Figures

Fig. 1 Migratory directions of nocturnal autumn migration between Europe and Africa on a map in Mercator projection with a 10°-grid. The sources of the selected data are: European Weather Radar network (Nilsson et al. 2019), surveillance radar in Switzerland (Baumgartner and Bruderer 1985), near Beja in Portugal and at Gibraltar (Hilgerloh 1988, 1989), old marine radars (Adams 1962, Casement 1966), tracking radar (Bruderer 1975, 1981, Bruderer and Jenni 1988, Bruderer and Liechti 1998, 1990, Liechti et al. 2012), moon-watch operations in the area of the Alps (Liechti et al. 1996a, b, Rössler and Schauer 2014), in the area around the western edge of the Pyrenees and the SW-corner of Portugal (Wallraff and Kiepenheuer 1963, summary in Rivera and Bruderer 1998), in Italy and the south-eastern half of Spain (Bruderer and Liechti 1999, Trösch et al. 2005), along the Atlantic coast of northern Morocco (Hilgerloh et al. 2006, Trösch et al. 2005), in south-eastern Europe (Bateson and Nisbet 1961, Zehthindjiev and Liechti 2003), in Egypt (Kiepenheuer and Linsenmair 1965, Biebach et al. 1991). Infrared observations from various points along the Mediterranean coasts from southernmost France to southernmost Spain, one point also inland at the western edge of the Spanish Cordilleras (Rivera and Bruderer 1998), another series from southern Mauritania (Liechti et al. 2003). For summaries of observations in the Mediterranean and in the area of the Alps see Bruderer (2017, p. 103-115). For details on the original publications see

Annex 1.

Fig. 2 Nocturnal bird migration in the region of the Alps. This is a summarizing interpretation of available information on directions and intensities. Red arrows starting at the upper edge of the frame indicate the longrange migratory directions over Central Europe, their extensions show how the birds continue in fair weather with following winds at high altitudes. Southward pointing arrows (pink) represent southward drifting migration; their continuation is indicated by movements zig-zagging through some large valleys providing crossing possibilities at moderate flight altitudes protected against adverse winds. The mass of birds approaching the Alps and the Jura from NE are indicated by blue arrows, concentrations following the highest ridges of the Alps by a green line. Yellow lines suggest movements circumventing the Alps to the East. The publications used for this interpretation are presented in Annex 2.

Fig. 3 a) Distribution of tracks (bold black lines) and headings (thin red lines) for nocturnal migration (20-05 h) above Lehrberg/Nuremberg (D), Painten/Regensburg (D), and Payerne (CH) (31 August till 22 September 1987). **b)** Distribution of the wind directions measured per tracked bird (bold lines) and general wind directions = means per 200 m intervals up to 1200 m above each radar station (thin lines) for the same sites, periods and times.

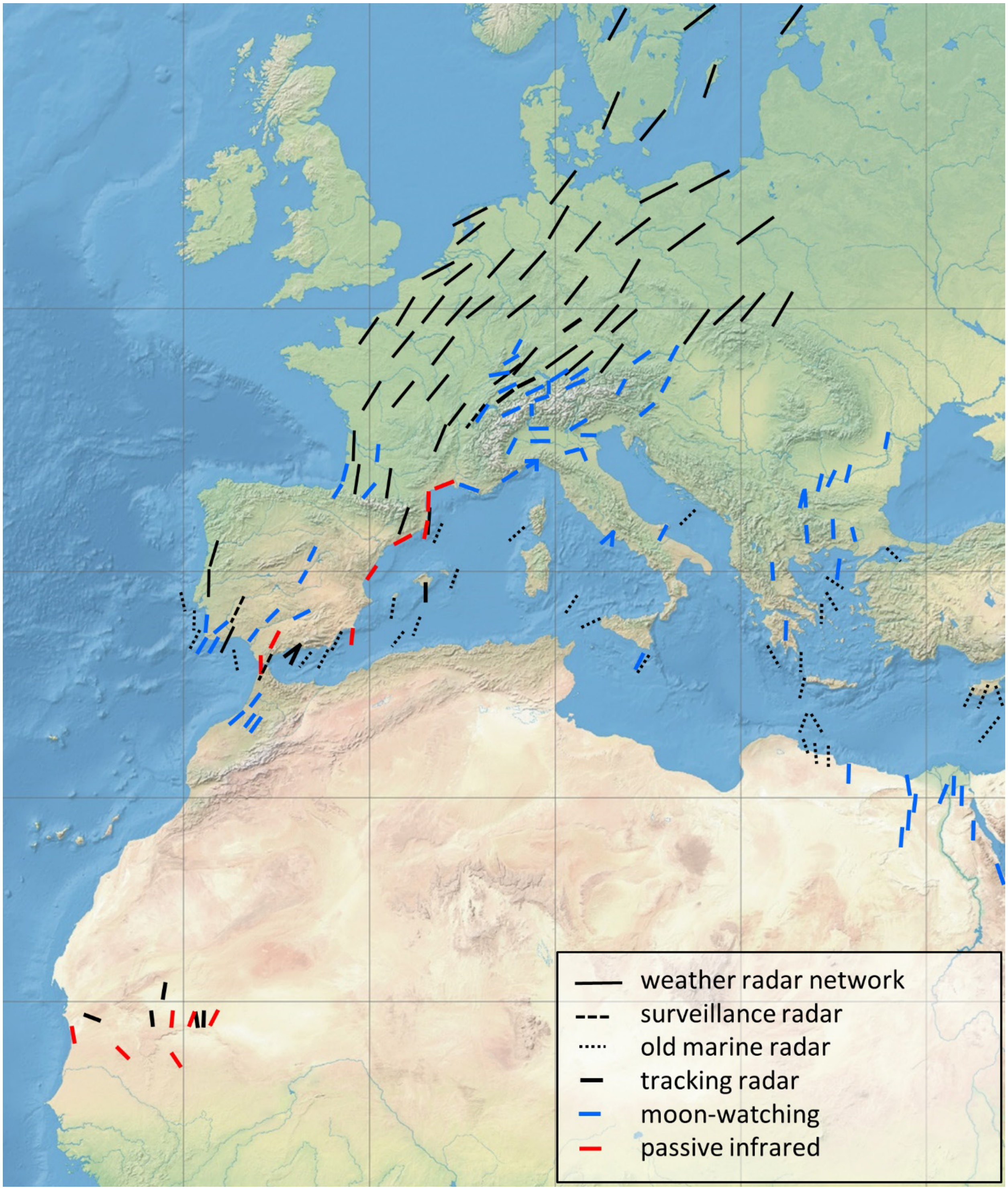
Fig. 4 Directional distribution (in classes of 10°) of tracks (bold black), headings (fine red), and winds (shaded blue) for two flight levels at Nuremberg and Kappelen. The limit of the height zone included (right) and sample size (left) is indicated at the upper edge of each graph. The basic direction per site and height is indicated as a dashed line.

Fig. 5 Distribution of tracks (black), headings (red), and wind directions (shaded pale blue for weak winds < 5 m/s and dark blue for strong winds ≥ 5 m/s) within two height zones and (> 1500 and < 1500 m asl) above Lehrberg near Nuremberg. The wind-sectors (following, opposing, from right and left) are chosen relative to the basic direction of migration (BD: dotted line in the SW-sector) defined for the two height zones. Black crosses mark the centre of the distributions. Sample size in the left upper corner of each graph.

Fig. 6 Relief-map of south-western Switzerland (Federal Office of Topography swisstopo) showing the border of Switzerland with a green line, the main rivers and lakes (Geneva, Neuchâtel, Biel, Morat) and superimposed the locations of three radar sites (red points) with the distribution of flight directions (black) and headings (red) of all the nocturnal migrants tracked between 20 and 05 h, averaged over the whole season and all altitudes (in 10°-classes); the centre of the directional distributions is indicated by a cross. The three radar sites are (from N to S): Kappelen close to the SE flank of the Jura mountains (n = 5515), Col de la Croix, the western-most pass in the Bernese Alps (n = 7256), and Monthey in the Rhone Valley (n = 5036).

Fig. 7 Comparison of the directional distribution (in 10°-classes) of tracks and headings from three height intervals at the same radar stations as in Fig. 5. Height intervals comprise (from bottom to top) birds flying below the neighbouring mountain ridges, within the range of the crests, and well above the crests.

Fig 1



weather radar network
surveillance radar
old marine radar
tracking radar
moon-watching
passive infrared

Fig 2

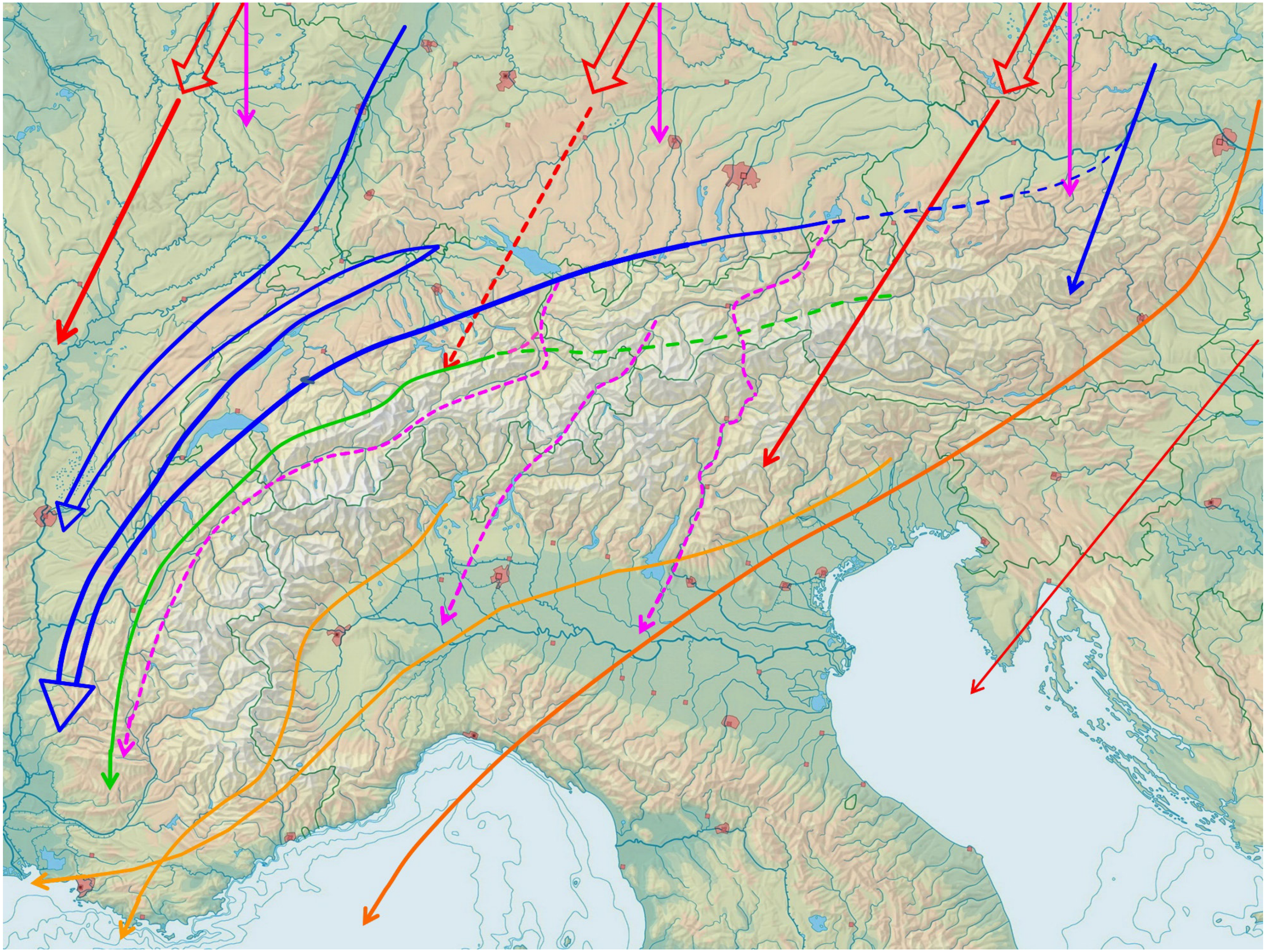


Fig 3

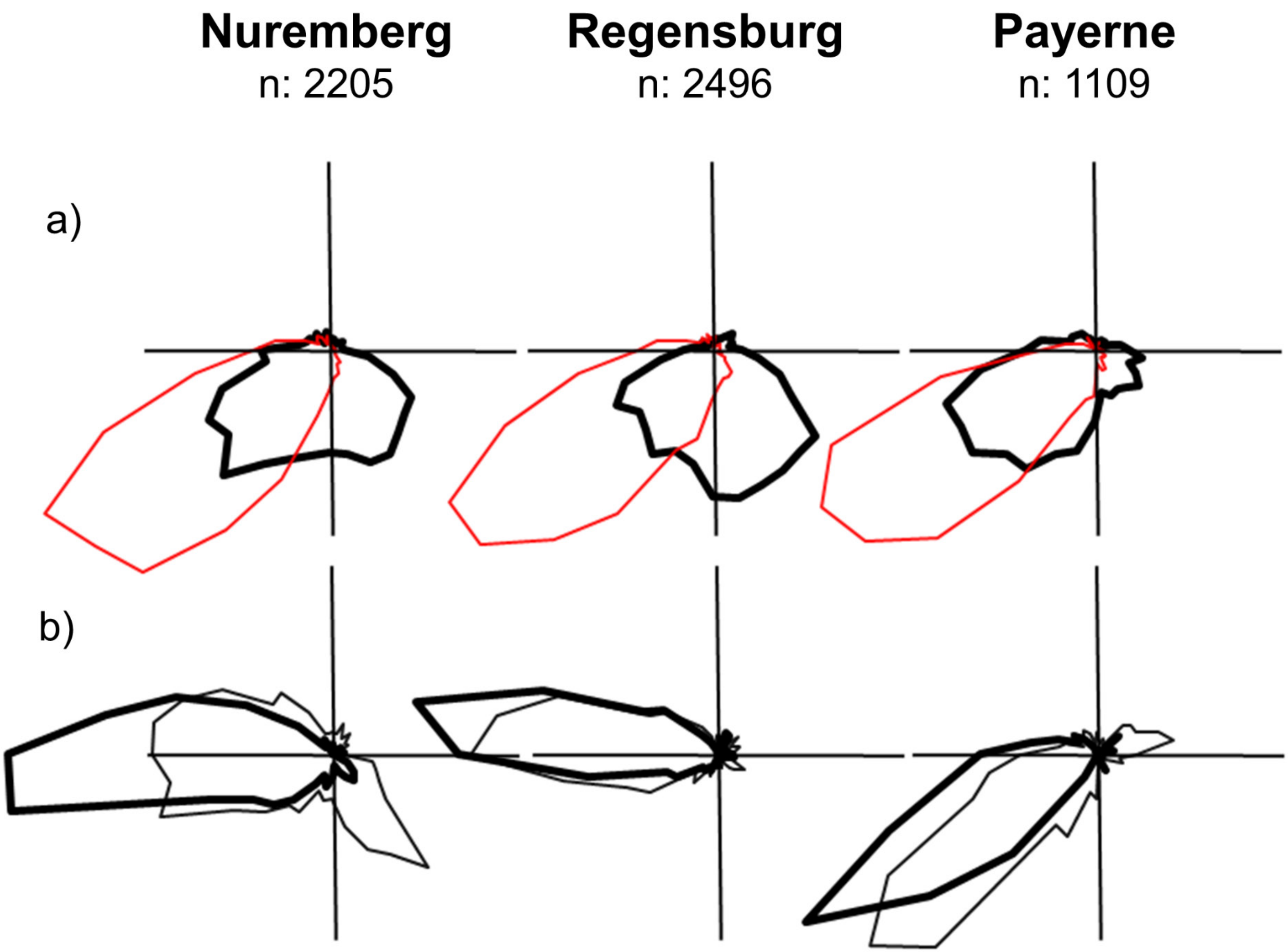


Fig 4

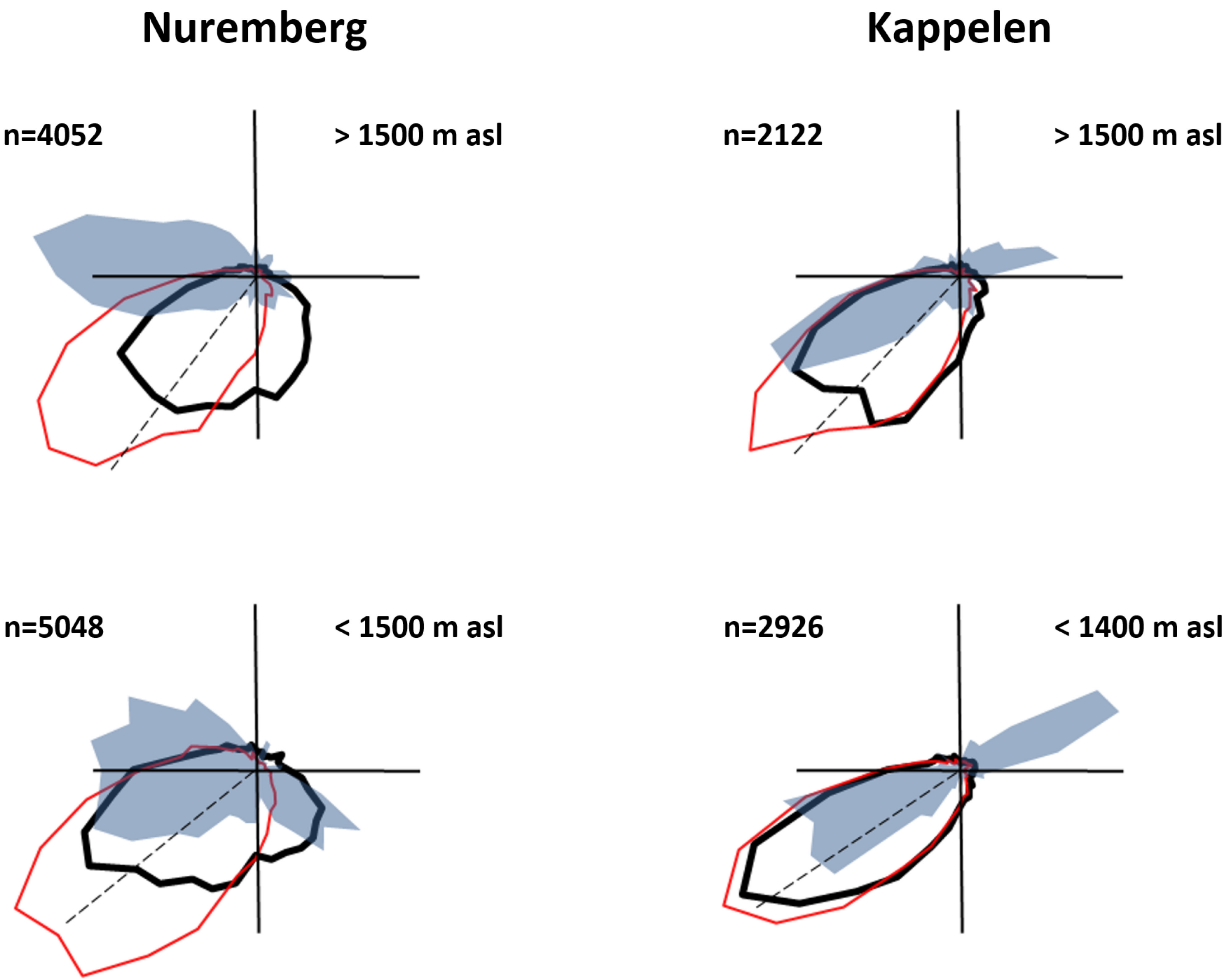

Nuremberg
Kappelen
n=4052
> 1500 m asl
n=2122
> 1500 m asl
n=5048
< 1500 m asl
n=2926
< 1400 m asl

Fig 5

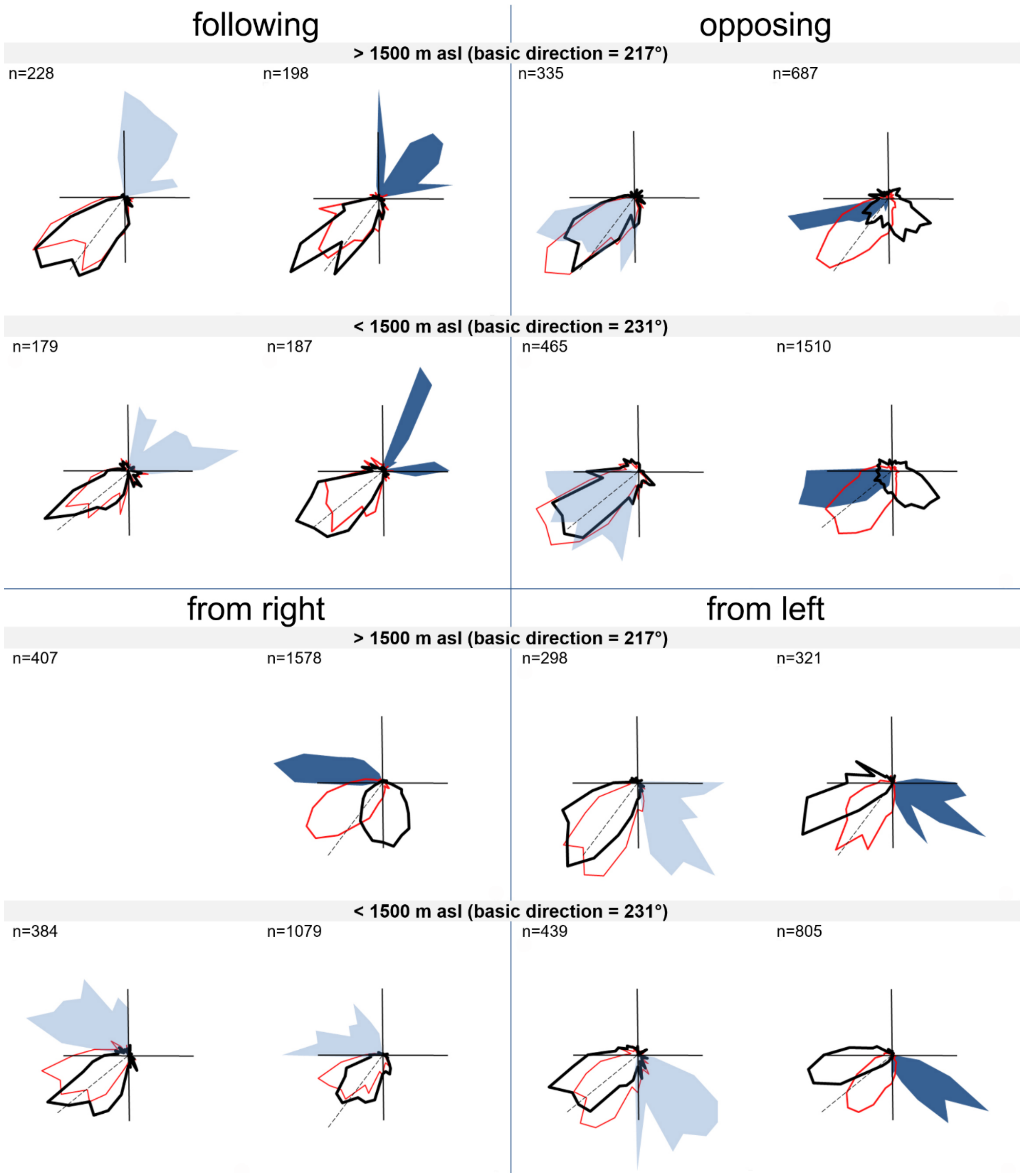

following
opposing
> 1500 m asl (basic direction = 217°)
n=228
n=198
n=335
n=687
< 1500 m asl (basic direction = 231°)
n=179
n=187
n=465
n=1510
from right
from left
> 1500 m asl (basic direction = 217°)
n=407
n=1578
n=298
n=321
< 1500 m asl (basic direction = 231°)
n=384
n=1079
n=439
n=805

Fig 6

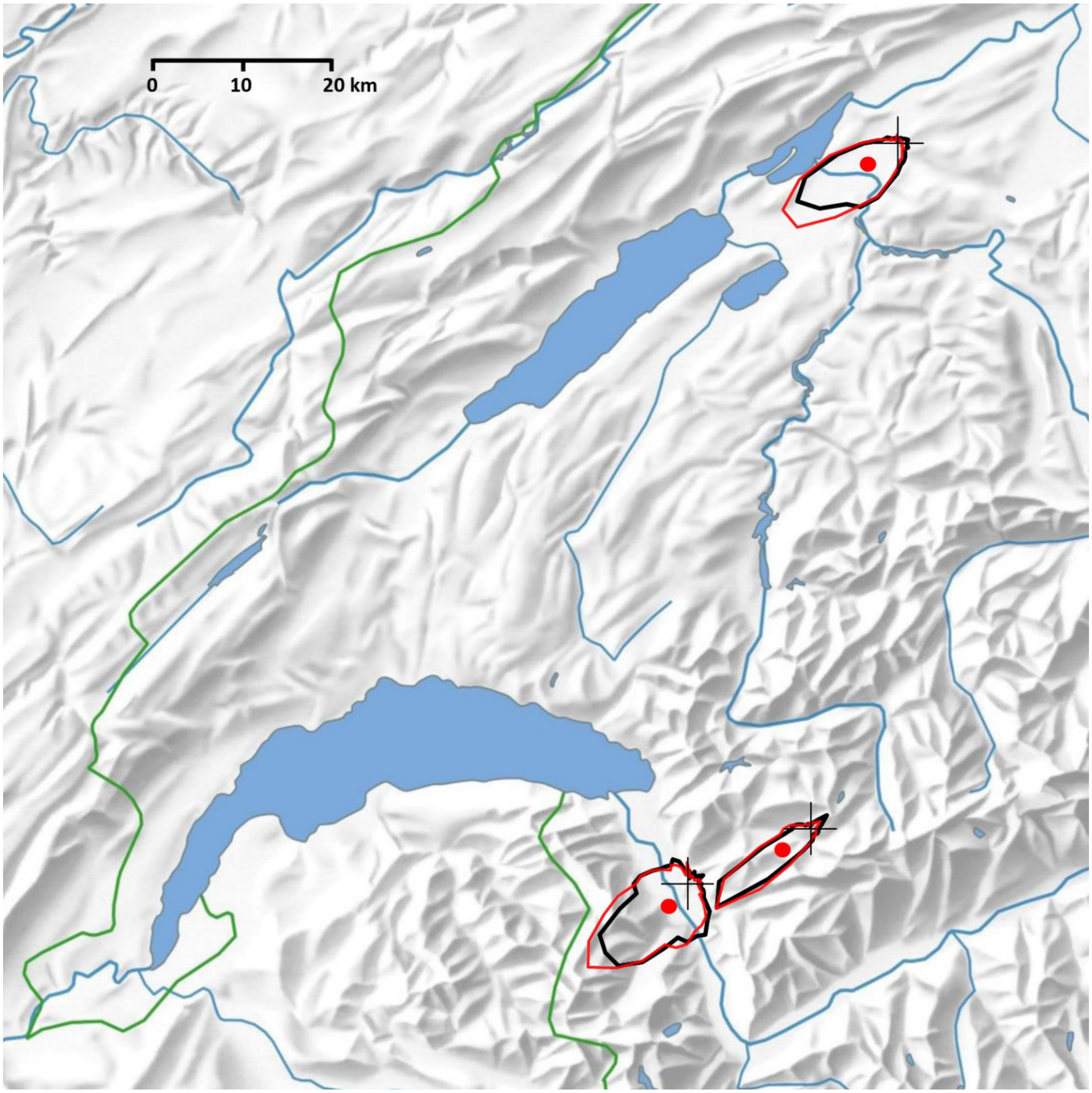
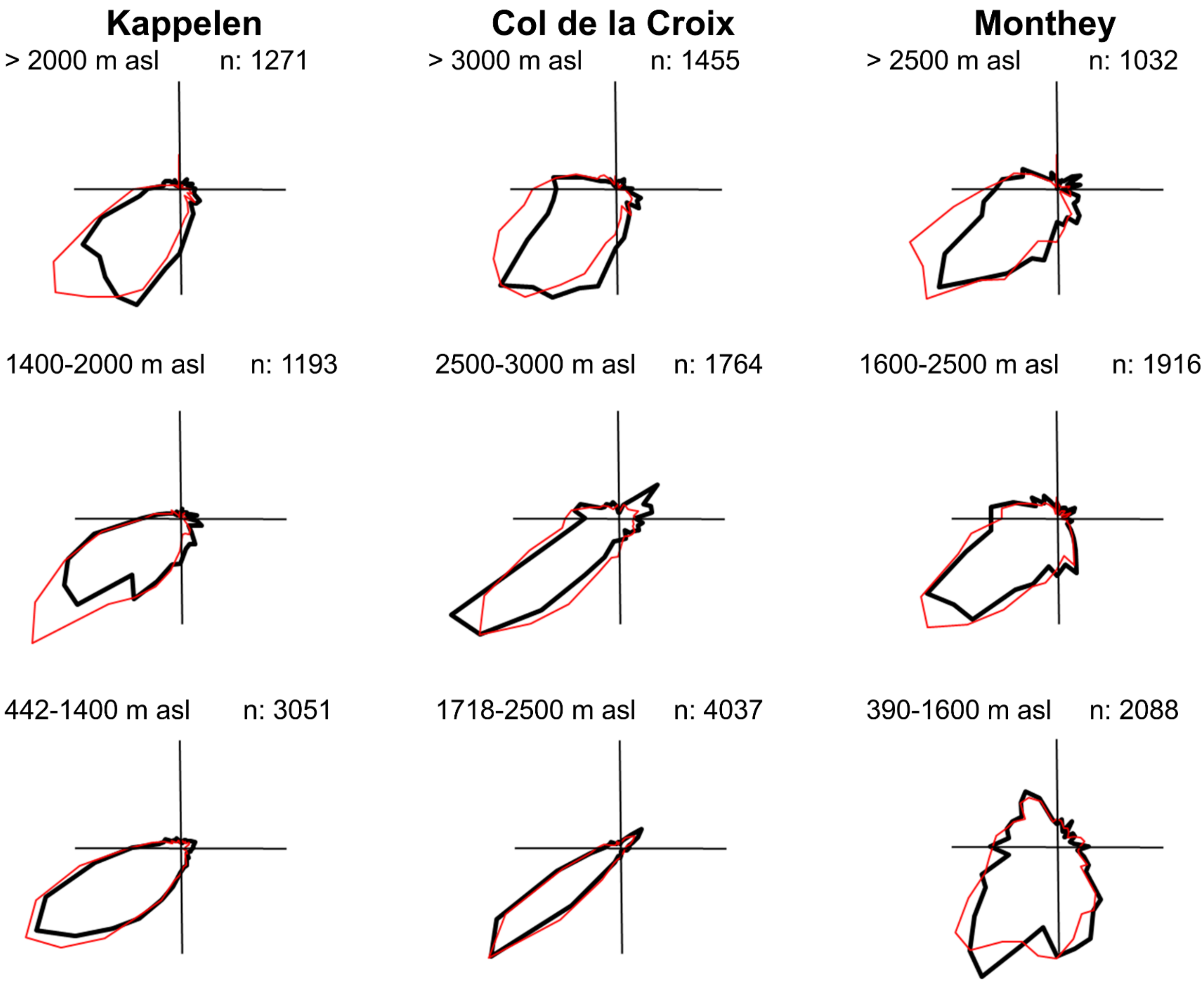


Fig 7



Kappelen
Col de la Croix
Monthey
> 2000 m asl n: 1271
> 3000 m asl n: 1455
> 2500 m asl n: 1032
1400-2000 m asl n: 1193
2500-3000 m asl n: 1764
1600-2500 m asl n: 1916
442-1400 m asl n: 3051
1718-2500 m asl n: 4037
390-1600 m asl n: 2088