**REVIEW**

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# Vertical distribution of bird migration between the Baltic Sea and the Sahara

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## Abstract

This review covers 40 years of migration studies of the Swiss Ornithological Institute with the tracking radar "Superfleder-maus". Since 1968, this pencil-beam radar was—according to its (military) capacities of surveillance and tracking—applied for two different tasks: (I) To record the intensity of migration at various heights (either based on densities recorded by conical scanning, or frequencies of passage recorded with fixed beams at various elevation angles); densities (birds $km^{-3}$) and frequencies (birds $km^{-1} h^{-1}$) are averages per height intervals of 200 m and do not refer to the position of single targets; they are suited to show average height distributions. (II) Tracking individual birds or flocks provides information on the exact position and flight behaviour of single targets over time. Part I: 16 (among 22) study sites with data from 1991 onwards are chosen to visualize and explain the vertical distribution of nocturnal bird migration according to regionally shaped environmental conditions in the Western Palaearctic and in the trade-wind zone. Average distributions at sites devoid of important orographic or persistent meteorological distortions usually show 20–30% of nocturnal migration in the lowest 200-m interval, 50% below 700 m above ground level (agl), and the 90% quantile reaching heights between 1400 and 2100 m agl. The remaining 10% of migrants are usually scattered up to about 4000 m above sea level (asl). The lower parts of migration are forced upwards when crossing mountain ridges and often remain high after such crossings; at subsequent observation points, migration is often high above ground. Particularly high altitudes prevail where wind conditions are improving with altitude, as e.g. during spring migration in the trade-wind zone. Part II deals with the seasonal and diurnal variation in the spatial distribution of particular bird targets. Birds were on average higher up at night compared to daytime and avoided flights close to the ground in hot desert areas. Highest flights were recorded during diurnal migration above desert areas. The highest 0.3% of the tracked birds were found between 3500 m and 4900 m asl at most sites, but at 5000–6870 m in spring migration of the Mediterranean and the trade-wind zone. The most extreme tracks were at altitudes between 4500 and 6600 m asl above the European mainland, and between 6000 and nearly 9000 m above the Balearic Islands and in the trade-wind zones. A concluding discussion deals with the reasons for generally low flight levels and the particular conditions and requirements of high-altitude migration. Flight conditions in the lower atmosphere deteriorate with altitude. Cost of climbing may impose additional restrictions (specifically for large non-passerines). Decreasing oxygen density imposes limits to high-altitude flight, and compensatory ventilation may induce increased water loss, if no physiological countermeasures are available. High flights are compulsory when crossing high mountain ranges and favoured when wind support increases with altitude. This is particularly true when long non-stop flights lay ahead, when turbulences and/or high temperatures at lower levels can be avoided, and possibly when time for homeward flights in spring can be minimized.

**Keywords** Quantification of bird migration · Pencil-beam radar · Fixed beam · Conical scanning · Vertical distribution · Altitude variation with location · Tracking radar · Temporal variation of altitude · Upper limit of migration

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## Zusammenfassung

### Höhenverteilung des Vogelzugs zwischen Ostsee und Sahara

Dieser Review umfasst 40 Jahre Vogelzugstudien der Schweizerischen Vogelwarte Sempach mit dem Zielfolgeradar „Superfledermaus". Seit 1968 wurde das für die (militärischen) Aufgaben Raumüberwachung und Zielverfolgung konzipierte Radargerät mit eng gebündeltem Strahl für zwei verschiedene Aufgaben eingesetzt: I) Um die Zugintensität auf verschiedenen Höhen zu registrieren (entweder Zugdichten, gemessen mit konisch rotierendem Strahl oder Zugfrequenzen, mit auf verschiedenen Elevationswinkeln fixiertem Radarstrahl); Dichten (Vögel km$^{-1}$) und Frequenzen (Vögel km$^{-1}$ h$^{-1}$) sind Mittelwerte für Höhenintervalle von 200 m und sagen nichts aus über die Position einzelner Radarziele; sie sind deshalb geeignet für die Darstellung mittlerer Höhenverteilungen. II) Die Verfolgung von Einzelvögeln oder Schwärmen liefert Informationen über die exakte Position und das Flugverhalten einzelner Radarziele im zeitlichen Verlauf. Teil I: Unter insgesamt 22 Beobachtungsorten wurden 16 mit Daten ab 1991 ausgewählt, um die Höhenverteilungen des nächtlichen Vogelzugs unter regional geprägten Umweltbedingungen in der Westlichen Paläarktis und in der Passatwind-Zone aufzuzeigen und zu erklären. Durchschnittliche Höhenverteilungen an Orten ohne wesentliche orographische oder persistierende meteorologische Verzerrungen zeigen normalerweise 20-30% des Nachtzuges im untersten 200-m-Intervall und 50% unter 700 m über Boden; das 90% Quantil erreicht Höhen zwischen 1400 und 2100 m ü.B. Die restlichen 10% sind üblicherweise verstreut bis zu Höhen von 4000 m ü.M. Beim Überqueren von Gebirgszügen wird die Untergrenze des Zuges angehoben und bleibt nach dem Flug über einen Kamm oft auf der erreichten Höhe. Aussergewöhnlich hohe Flugniveaus ergeben sich, wenn die Windbedingungen mit der Höhe zunehmend günstiger werden, wie etwa beim Frühlingszug in den Passatwindzonen. Teil II behandelt die saisonale und tageszeitliche Variation in der räumlichen Verteilung von einzeln verfolgten Vogelechos. Die Vögel flogen im Mittel nachts höher als am Tag und in der Sahara stärker vom Boden abgehoben als in Mitteleuropa. Die grössten Flughöhen wurden tagsüber in Wüstengebieten aufgezeichnet. Die höchsten 0.3% der verfolgten Vögel wurden an den meisten Orten zwischen 3500 m und 4900 m ü.M. gefunden, aber auf 5000-6870 m im Frühlingszug des Mittelmeergebiets und der Passatwindzonen. Extremwerte der Flughöhen waren über dem europäischen Festland 4500-6600 m ü.M. und über den Balearen und in den Passatwindzonen zwischen 6000 und beinahe 9000 m. Abschliessend werden die Ursachen für generell tiefen Zug sowie die speziellen Bedingungen und Anforderungen von hohem Zug diskutiert. Verschiedene Flugbedingungen werden in der unteren Atmosphäre mit zunehmender Höhe schlechter. Die Kosten des Aufsteigens bewirken zusätzliche Einschränkungen (speziell für grosse Nicht-Singvögel). Abnehmende Sauerstoffdichte setzt dem Zug in grosser Höhe Grenzen, und kompensatorische Steigerung der Atmung kann zu erhöhtem Wasserverlust führen, sofern die Vögel nicht über physiologische Gegenmassnahmen verfügen. Grosse Flughöhen werden durch Gebirge erzwungen und durch mit der Höhe zunehmende Windunterstützung begünstigt, insbesondere wenn lange Nonstop-Flüge bevorstehen, wenn Turbulenzen und/oder hohe Temperaturen auf geringen Höhen vermeidbar sind, und allenfalls, wenn mit der Höhe abnehmender Luftwiderstand erhöhte Fluggeschwindigkeit und damit Zeitminimierung ermöglicht.

## Introduction

### Radar measurements of height distributions

Eastwood (1967) provided a first summary on the application of radar to study height distributions of bird migration, starting in the early 1960s. Reported measurements were usually confined to heights between a few hundred meters above ground level (agl) and about 2500 m agl. Range limitations at low levels persisted in most studies for a long time (e.g. Blokpoel and Burton 1975; Jellmann 1979), while high-powered radars increasingly allowed the detection of migration at high altitudes (e.g. Richardson 1976; Williams et al. 1977).

Many recent radar studies—most of them environmental impact studies dealing with collision probability—used small marine radars (either off the shelf or improved to operate with a pencil-beam radar) in order to get estimates of height distributions (e.g. Harmata et al. 1999; Biebach et al. 2000; Hüppop et al. 2004, 2006; Desholm and Kahlert 2005; Desholm et al. 2006). However, these studies did not include echo identification and adequate consideration of the surveyed volume (see comments in Schmaljohann et al. 2007b, c, 2008b).

A different approach, namely the use of weather surveillance radars to obtain rough height information from large areas, etnitiated by Gauthreaux (1970) and Able (1970). This method experienced important revival and improvement in recent years, particularly due to cross-calibration with pencil-beam radar. Van Gasteren et al. (2008) concluded that weather radar reflectivity was (in spite of notable limitations) correlated with the measurements of the Swiss bird radar (see below), when integrated over altitude. Dokter et al. (2011) found that "weather radar can extract near real-time bird density altitude profiles that closely correspond

to the density profiles measured by dedicated bird radar." Kemp et al. (2013) applied such an operational weather radar to study the influence of weather on the flight altitudes of nocturnal bird migrants, but in these measurements, the information for the lowest 200 m over ground was still lacking.

In 1968, the Swiss Ornithological Institute obtained access to a powerful military pencil-beam radar. The support of the radar manufacturer and of various specialists (see acknowledgments) allowed avoiding many of the pitfalls related to the quantification of small animals and other objects in the airspace (cf. Beason et al. 2013). From the beginning, particular emphasis has been on exclusion of non-bird targets, covering low altitudes (down to 30 m agl), and considering the form of the radar beam to calculate numbers of echoes per unit of surveyed surface or volume (Bruderer 1971). In addition to the following paragraphs on methods, details of the development are given in Bruderer et al. (2012).

Most radar studies deal with the influence of meteorological factors on the intensity of bird migration (review by Richardson 1990), some recent studies with the co-variation of height distributions and atmospheric conditions (e.g. Liechti et al. 2000; Dokter et al. 2013; Kemp et al. 2013; La Sorte et al. 2015; Shamoun-Baranes et al. 2017). In contrast to these studies focusing on the influence of weather factors, we try to exclude short-term weather effects, by averaging height distributions over long periods in order to balance weather-induced modifications (part I of this study). Potential seasonal differences in weather conditions between sites are not accounted for.

Tracking of birds was used from the beginning of Swiss radar studies in 1968 to discriminate bird targets from others (Bruderer 1969) and to analyse their flight behaviour (e.g. Liechti and Bruderer 1995; Spaar 1997; Bruderer and Liechti 1998a; Bruderer 2017). In the present context wingbeat pattern and speed were used to exclude non-bird targets from the samples.

The aims of part I are (1) to present average height distributions of nocturnal bird migration at various sites in the western Palaearctic and the trade-wind zone, (2) to reveal the characteristics of the decline with height in nocturnal bird migration, (3) to visualize modifications of this quasi-exponential decrease according the environmental conditions at specific sites; this is to show similar modifications of bird migration according to similar environmental conditions. The aims of part II (making use of thousands of tracks from three climatically different regions) are (4) to reveal temporal variation of flight levels, (5) to estimate the upper limits of migration in various areas, (6) to discuss the reasons for generally low, but occasionally high migratory flights, and (7) the capacities of birds to fly at extreme altitudes.

# Part I: Average height distributions

## Methods and sites

### Measuring height distributions

The "Superfledermaus" used at the Swiss Ornithological Institute is an X-band fire control radar with 150-kW pulse power, 0.3-μs pulse length, and a nominal beam width of 2.2°. Pointing vertically upwards, it allowed detection of small passerines between about 150 and 4500 m agl (Bruderer and Joss 1969; Bruderer 1971). To overcome the limitation at low levels, the pencil-beam was not only aimed upwards, but additionally fixed at low elevation angles perpendicularly to the principal direction of migration, thus providing information down to about 30 m agl. A sensitivity time control (STC) was applied to eliminate small echoes (mostly small insects). Early recording of height distributions was based on visual echo counting on the range indicator of the radar or on film recording the Z-modulated R-scope (Bruderer 1971).

In 1991, recording of height distribution was modified by two innovations: To increase the surveyed volume (at the cost of somewhat reduced range), the pencil-beam radar was used in a conical scanning (SCAN) mode and data recording was computerized; in the analysis, the recordings from different elevations of the radar beam are integrated to provide average densities for height zones of 200 m (Bruderer et al. 1995a). Electronic recording allowed the application of a mathematically exact STC to compensate for the $R^{-4}$-dependence of echo size. As target identification could not be applied directly to the scans, these samples may comprise echoes of bats and large insects. The SCAN method does not provide information on the position of single targets, but average density of migration up to a height of about 4 km; the method was used with varying elevation angles as the standard method for quantitative recordings until about 2000. In spite of some unknown echoes included, the density indication is birds km$^{-3}$.

From 2000 onwards, SCAN was increasingly complemented and finally replaced by a new fixed-beam (FB) method. This method was used with the original tracking radar but also with smaller equipment. A fully automatized unit was developed and operated at various sites across Europe since 2007 (Bruderer et al. 2012; https://swiss-birdradar.com/birdscan-mt.html). In contrast to the SCAN method, the FB method counts the number of targets crossing the radar beam [i.e. the frequency of migration or migration traffic rate (MTR), measured as birds km$^{-1}$ h$^{-1}$]. Due to a new receiver system and optimized electronic data recording, the FB range was increased to 5 km for small passerines, and to 6 or 7 km for larger, particularly continuously flapping

birds (Schmaljohann et al. 2008b). Quantification of passage starts with the application of an STC excluding all the echoes that would not be visible beyond a 3-km range (i.e. most insects). Permanent ground echoes are eliminated by clutter masks. The remaining echoes are "filtered" according to radar cross-section (RCS) and echo signature. The filter program was trained by expert-classified targets and thus retains not only single birds with clear wingbeat pattern but also soaring birds and loose flocks (Zaugg et al. 2008). Large and particularly dense flocks (in daytime) as well as some other unidentifiable bird echoes may be excluded from the samples, with the consequence that "counting birds only" will lead to a reduction of valid targets. Exclusion of small birds may increase with distance because (1) the amplitude of echo signatures declines at extreme distances, (2) the increase of the radar pulse volume with distance may result in unidentifiable multi-target echoes. Similar to the SCAN method, the FB method integrates measurement of various elevation angles, thus providing no positions of single targets.

To compare the results of the two methods (SCAN and FB), we present the data as proportional distributions of targets per height bin of 200 m. Densities and frequencies are only given as an indication for all heights together, accepting that the FB method provides lower absolute numbers than the SCAN method, and that for the SCAN method, the units are targets or birds km$^{-3}$, and for the FB method, birds km$^{-1}$ h$^{-1}$.

In addition to the quantitative difference between SCAN and FB methods, the data differ with respect to wind effects: FB measures the frequency of passage (i.e. the "success of migration"), which depends on the ground speed ($V_g$) of the birds; thus, the passage frequency is increased when the birds are flying with the wind, and reduced when flying against the wind. SCAN measurements show the density of migration (or "migratory activity"), which is not sensitive to wind.

We analyse only data from 1991 onwards: SCAN data (bold and italicized in Table 1, open circles in Fig. 1) and FB data (bold in Table 1, dots in Fig. 1). The distributions are restricted to heights between about 30 and 4000 m agl, and to nocturnal migration (between 21 and 04 h). They show average vertical profiles of migratory intensity plus the corresponding 50 and 90% quantiles for long periods of spring or autumn migration. Bootstrap 95% confidence intervals were calculated based on 1000 bootstrap replicates from the daily vertical profiles.

### Study sites 1975–2004

Table 1 and Fig. 1 show the study sites used from 1975 till 2004 as well as the study periods, the number of measurements (n) per site, the measuring method (FB and SCAN data), and, additionally, some characteristic heights (agl) and altitudes (asl) of bird flight. In the case of FB and SCAN data, one measurement is a complete, usually hourly

**Table 1** Radar sites, observation periods, number of measurements (n) per type of radar data, altitudes (a asl), height (h agl), and characteristic values of high migration

| Site Nr. | Sitename, year, season (country) | Coordinates | Altitude of site | Period | FB (n) | SCAN (n) | FB h 90% (m agl) | SCAN h 90% (m agl) | Tracks (n) | h 90% tracks (m agl) | a 99.7% tracks (m asl) | max a (m asl) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Rügen 2005 autumn (D) | 54° 23' N / 13° 09' E | 20 | 8 Sep - 22 Oct | | | | | 3308 | 1490 | 3326 | 6659 |
| 2 | Fehmarn 2009/2010 spring (D) | 54° 30' N / 11° 14' E | 5 | 19 Feb - 6 Jun | 1552 | | 1931 | | 32043 | 2078 | 4363 | 5856 |
| 2 | Fehmarn 2009/2010 autumn (D) | 54° 30' N / 11° 14' E | 5 | 13 Aug - 16 Nov | 1570 | | 2034 | | 17758 | 1683 | 4183 | 5619 |
| 3 | De Bilt 2007 autumn (NL) | 52° 08' N / 5° 17' E | 10 | 18 Aug -16 Sep | 246 | 533 | 1425 | 1297 | 5998 | 1755 | 4168 | 6626 |
| 4 | Trappes 2008 spring (F) | 48° 35' N / 1° 31' E | 30 | 8 Mar - 7 May | 524 | | 2139 | | 11630 | 2210 | 4912 | 5894 |
| 5 | Wideumont 2007 autumn (B) | 50° 02' N / 5° 26' E | 577 | 18 Sep - 22 Oct | 280 | 615 | 1466 | 1772 | 11028 | 1845 | 3916 | 5782 |
| 6 | Stuttgart/Ohmden 1987 autumn (D) | 48° 39' N / 9° 32' E | 380 | 27 Sep - 9 Oct | | 55 | | 1491 | 2361 | 1955 | 3545 | 4443 |
| 7 | Nürnberg/Lehrberg 1987 autumn (D) | 49° 20' N / 10° 31' E | 450 | 1 Aug - 30 Oct | | 279 | | 1829 | 11396 | 1940 | 3623 | 4605 |
| 8 | Möggingen 2008 autumn (D) | 47° 46' N / 9° 00' E | 424 | 12 Aug - 6 Nov | 754 | | 1728 | | | | | |
| 9 | Haidershofen 2013 autumn (AUT) | 48° 05' N / 14° 31' E | 364 | 21 Aug - 13 Nov | 756 | | 1761 | | | | | |
| 10 | Kappelen 1988 autumn (CH) | 47° 05' N / 7° 15' E | 442 | 17 Aug - 28 Oct | | | | | 7497 | 2089 | 3899 | 4957 |
| 11 | St. Gotthard 2010 autumn (CH) | 46° 33' N / 8° 35' E | 2140 | 3 Sept - 18 Oct | 648 | | 1573 | | | | | |
| 12 | Planachaux 2007 autumn (CH) | 46° 10' N / 6° 50' E | 1677 | 6 Aug - 29 Oct | 704 | | 1403 | | | | | |
| 13 | Col de la Croix 1988 autumn (CH) | 46° 20' N / 7° 08' E | 1718 | 1 Aug - 9 Oct | | | | | 8332 | 1655 | 4479 | 5197 |
| 14 | Hahnenmoospass 1975 autumn (CH) | 46° 27' N / 7° 29' E | 1930 | 27 Jul - 11 Sep | | | | | 5456 | 1855 | 4889 | 5394 |
| 15 | Messina 2006 spring (I) | 38° 14' N / 15° 39' E | 100 | 29 Mar - 15 May | 351 | | 2226 | | 12191 | 1910 | 2619 | 4456 |
| 15 | Messina 2010 autumn (I) | 38° 13' N / 15° 40' E | 310 | 6 Sep - 9 Nov | 507 | | 2083 | | | | | |
| 16 | Vélez-Málaga 1996 autumn (E) | 36° 44' N / 4° 35' W | 20 | 15 Aug - 24 Oct | | 1108 | | 2404 | 29866 | 1985 | 3603 | 5286 |
| 16 | Vélez-Málaga 1997 spring (E) | 36° 44' N / 4° 35' W | 20 | 22 Mar - 26 May | | 1540 | | 2177 | 30353 | 2425 | 4290 | 6137 |
| 17 | Mallorca 1997 spring (E) | 39° 22' N / 3° 04' E | 10 | 24 Mar - 26 May | | 1354 | | 1632 | 24085 | 2480 | 4956 | 7852 |
| 17 | Mallorca 1996 autumn (E) | 39° 22' N / 3° 04' E | 10 | 5 Aug - 24 Oct | | | | | 24182 | 2140 | 3710 | 6231 |
| 18 | Sede Boqer 1991 autumn (IL) | 30° 52' N / 34° 47' E | 470 | 19 Sep - 31 Oct | | 177 | | 1081 | 11609 | 1780 | 4082 | 5256 |
| 18 | Sede Boqer 1992 spring (IL) | 30° 52' N / 34° 47' E | 470 | 30 Mar - 30 Apr | | 139 | | 2333 | 9443 | 2340 | 6871 | 8963 |
| 19 | Arava/Hazeva 1991 autumn (IL) | 30° 49' N / 35° 15' E | -160 | 9 Sep - 31 Oct | | 241 | | 2162 | 11964 | 2210 | 4899 | 6948 |
| 19 | Arava/Hazeva 1992 spring (IL) | 30° 49' N / 35° 15' E | -160 | 1 Mar - 20 May | | 377 | | 3240 | 19045 | 2375 | 4116 | 6158 |
| 20 | Ouadâne 2003 autumn (RIM) | 20° 56' N / 11°35' W | 410 | 24 Aug - 25 Oct | 492 | | 1994 | | 12912 | 2185 | 4145 | 6049 |
| 20 | Ouadâne 2003 spring (RIM) | 20° 56' N / 11°35' W | 410 | 6 Mar - 15 May | | | | | 27627 | 3045 | 4947 | 6594 |
| 20 | Ouadâne 2004 spring (RIM) | 20° 56' N / 11°35' W | 410 | 15 Mar - 10 May | 429 | | 3573 | | 11657 | 3035 | 5479 | 6625 |
| 21 | Bir Amrâne 2004 spring (RIM) | 22° 47' N / 8° 43' E | 272 | 03 Apr - 25 Apr | 193 | | 3540 | | | | | |
| 22 | Mohammed Lemna 2003 autumn (RIM) | 18° 35' N / 8° 38' E | 338 | 19 Sep - 30 Sep | 94 | | 3014 | | | | | |

Particularly high values brown, extreme values red

Numbers of sites according to Fig. 1

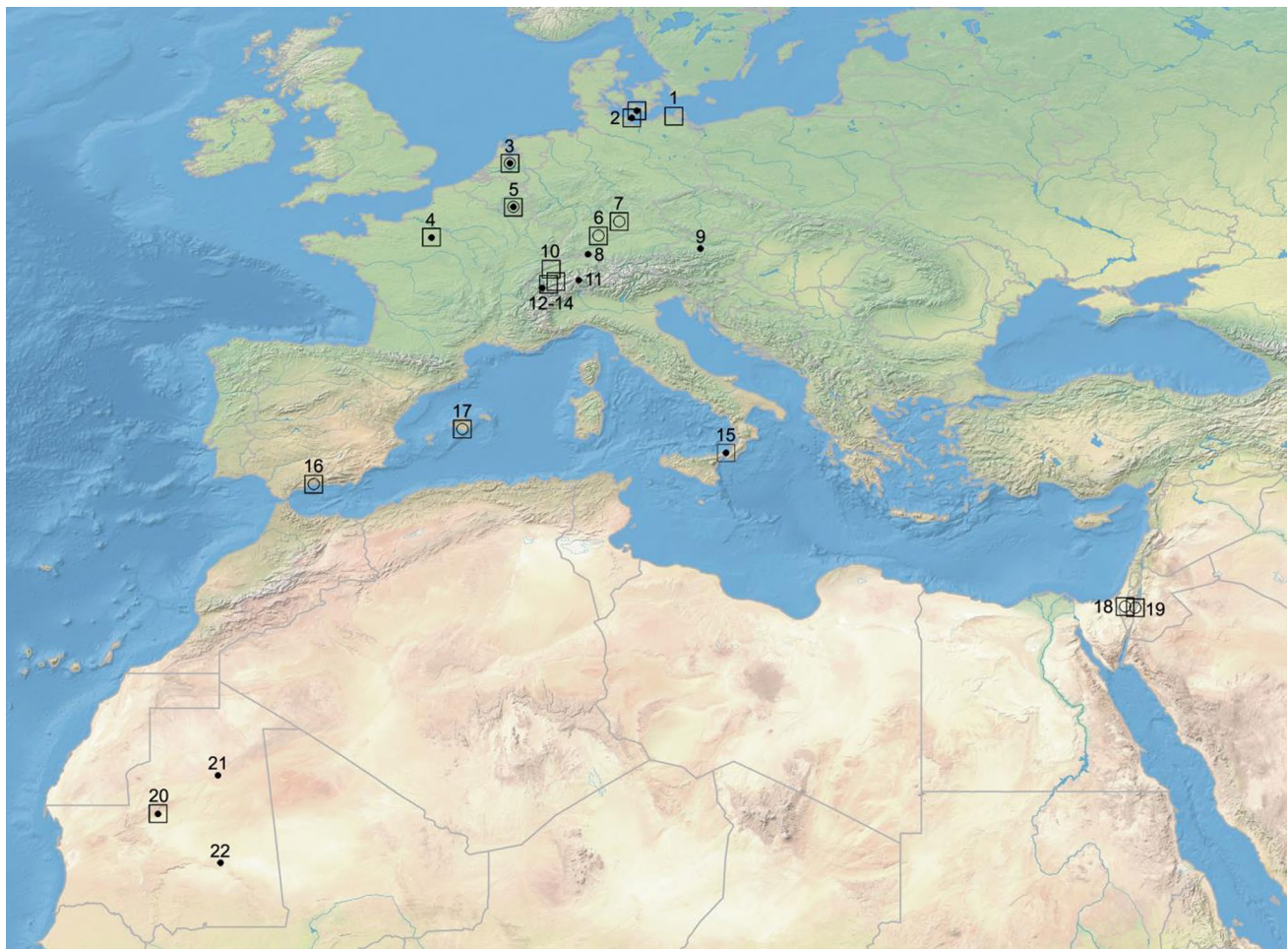*FB* fixed-beam, *SCAN* scanning, *ht* height agl, *a* altitude asl

**Fig. 1** Geographical location of the radar stations used for the present study. Stations with tracking data (providing data on the temporal variation of vertical distributions) are shown as open squares, SCAN data by open circles, and FB data by dots (two or three signatures combined in case of combined methods applied at a site). Details of the sites are presented in Tables 1 and 2

measurement comprising all elevations of the radar beam (example in Bruderer et al. 1995a). Each of these complete measurements contains hundreds or thousands of echoes recorded at various elevation angles.

## Results

Table 2 classifies the observation sites chosen for Figs. 2, 3, 4, 5, and 6 according to geography and environmental conditions, adding references to publications describing the features of the selected sites. The main parameters for comparison are the height intervals with highest intensity of migration as well as the 50 and 90% quantiles of the vertical distribution. Comparison between locations differing in altitude is facilitated by scales above ground (agl) and sea level (asl). Figures 2, 3, 4, 5, and 6 cover nocturnal migration only (21–04 h).

The colour gradient among the "green" sites of Table 2 leads from northern coastal areas to increasingly hilly inland

areas. Fehmarn at the coast of the Baltic Sea (Fig. 2a, b) covers complete spring and autumn seasons. During both seasons, about ¼ of nocturnal migration was in the lowest 200 m; both distributions are similar, in spite of frequent westerly winds that might be expected to favour lower flights in autumn than in spring. At De Bilt (NE of Utrecht, Fig. 2c) more than 35% of early autumn migrants were concentrated in the lowest 200 m. In the second half of the autumn, migration was very intense in the hilly area of the Ardennes (Wideumont, Fig. 2e) but less concentrated in the lowest 200 m than in the coastal areas; nearly equal intensity of migration in the second height interval (200–400 m) induced a relatively low 50% quantile, and high frequencies between 400 and 800 m led to a low 90% quantile. At Trappes (Fig. 2d), with birds flying towards the lights of Paris, migratory intensity was even more reduced in the lowest intervals than above the Ardennes, leading to relatively high values of the 50 and 90% quantiles. The distribution derived from a complete autumn season at Haidershofen/A (20 km

**Table 2** Classification of radar sites (Figs. 2, 3, 4, 5, and 6) according to geographical region and environmental conditions

| Site Nr. | Fig Nr. | Name | Region | Conditions | References |
|---|---|---|---|---|---|
| 2 | Fig 2a | Fehmarn, autumn | Baltic coast | flat lowlands at coast | Bruderer et al. 2012 |
| 2 | Fig 2b | Fehmarn, spring | Baltic coast | flat lowlands at coast | Bruderer et al. 2012 |
| 3 | Fig 2c | De Bilt, autumn | central Netherlands | flat lowlands close to coast | Dokter et al. 2011 |
| 4 | Fig 2d | Trappes, spring | Paris area | heavily built-over lowland | Dokter et al. 2011 |
| 5 | Fig 2e | Wideumont, autumn | Ardennes | hilly country | Dokter et al. 2011 |
| 8 | Fig 3a | Möggingen, autumn | NE-entrance to Swiss Lowlands | hilly courntry 30 km N of the Alpine border | Bruderer et al. 2012 |
| 9 | Fig 3b | Haidershofen, autumn | S edge of Danube Valley SW of Linz | flat area 15 km N of the Alpine border | |
| 11 | Fig 3c | St. Gotthard, autumn | central Swiss Alps | Alpine pass with previous mountain-crossing | Bruderer et al. 2012 |
| 12 | Fig 3d | Planachaux, autumn | western Swiss Alps | Alpine pass with previous mountain-crossing | Komenda-Zehnder et al. 2010 |
| 15 | Fig 4a | Strait of Messina, spring | southern tip of Italy | coast with take-off in mountain area | Bruderer et al. 2012 |
| 15 | Fig 4b | Strait of Messina, autumn | southern tip of Italy | coast with previous mountain-crossing | Bruderer et al. 2012 |
| 16 | Fig 4d | Vélez-Málaga, autumn | southern coast of Spain | coast with partial approoch across mountains | Bruderer and Liechti 1998a |
| 16 | Fig 4c | Vélez-Málaga, spring | southern coast of Spain | coast after sea-crossing | Bruderer and Liechti 1998a; Meyer et al. 2003 |
| 17 | Fig 4e | Mallorca, spring | Balearic islands | coast after long sea-crossing | Bruderer and Liechti 1998a |
| 18 | Fig 5c | Sede Boqer, autumn | Negev Higlands (southern Israel) | trade-wind, above elevated area | Liechti and Bruderer 1995; Bruderer et al. 2000 |
| 19 | Fig 5a | Hazewa, autumn | Arava Valley (southern Israel) | trade-wind, after mountain-crossing | Liechti and Bruderer 1995; Bruderer et al. 2000 |
| 20 | Fig 6a | Ouadâne, autumn | central Mauritania | trade-wind, above hot desert close to oasis | Liechti and Schmaljohann. 2007; Schmaljohann. et al. 2009 |
| 19 | Fig 5b | Hazewa, spring | Arava Valley (southern Israel) | anti-trades above depression | Liechti and Bruderer 1995; Bruderer et al. 2000 |
| 18 | Fig 5d | Sede Boqer, spring | Negev Higlands (southern Israel) | anti-trades above elevated area | Liechti and Bruderer 1995; Bruderer et al. 2000 |
| 20 | Fig 6b | Ouadâne, spring | central Mauritania | anti-trades above hot desert close to oasis | Liechti and Schmaljohann 2007a,b; Schmaljohann et al. 2009 |
| 21 | Fig 6d | Bir Amrâne, spring | north-eastern Mauritania | anti-trades above hot plain desert | Schmaljohann et al. 2009; Salewski et al. 2010 |
| 22 | Fig 6c | Mohammed Lemna, autumn | south-eastern Mauritania | strange autumn distribution above plain desert | Liechti and Schmaljohann 2007a,b; Schmaljohann et al. 2009 |

References indicate publications with description of the sites

Green: flat coastal lowlands (light green) to hilly inland areas (increasingly darker), brown: sites with previous mountain-crossing (Alpine and Mediterranean), blue: Mediterranean sites with migrants arriving from the sea, yellow: sites in the trade-wind zones (Israel with brownish tinge, Sahara plain yellow)

SW of Linz, Fig. 3b) may be seen as typical for relatively flat lowlands along the northern border of the Alps, showing a gradual decrease of migratory intensity with height up to 4000 m agl. The situation at Möggingen/D (western end of Lake Constance) differs from Haidershofen in so far that arriving migrants had to cross the neighbouring hills of the Bodanrück (about 200 m higher than the radar site) before reaching the radar site; notable parts of them flew in the two height intervals above the lowest one.

The "brown" and "light brown" site groups of Table 2 comprise areas where the migrants had to cross mountain ranges before reaching the radar stations, two of them in the Alps, three at the Mediterranean Sea. The two stations at Alpine passes (Fig. 3c, d) are themselves high above sea level: The radar station of St. Gotthard is at 2140 m asl (slightly higher than the pass), and Planachaux is at 1677 m asl (zero level in Fig. 3d, 246 m lower and 4.5 km NE of Col de Bretolet). At Planachaux, negative elevation angles allowed observations down to − 300 m below the site across the valley: About 15% of the birds climbed along the valley towards Col de Bretolet (CB in Fig. 3d, at 1923 m asl). Most migrants arrived, however, at flight levels of 200–800 m higher than the pass to be crossed 4.5 km further to the SW, the mode of the distribution was nearly 500 m higher than the pass. At St. Gotthard, the mode of the distribution was about 700 m higher than the pass; most birds flew between 600 and 800 m agl. At both Alpine sites, the mode was much

higher agl than at the "green" sites; the 90% quantile, however, was lower than at most lowland sites (except Wideumont). On the other hand, these values were much higher above sea level (2300 and 3100 for Planachaux, 2800 and 3700 for St. Gotthard) than at all other European stations. Migration was compressed in a narrower height zone than at lowland stations.

Mediterranean stations with previous mountain crossing ("light brown" in Table 2) show the same effect as at the Alpine passes: Autumn migration at the Strait of Messina (Fig. 4b) demonstrates extreme influence of previously crossed mountains. The radar station was located 4 km to the E of Villa San Giovanni and 2 km to the S of the northern coast (310 m asl, measurements reaching down to nearly sea level). Autumn migrants approached the radar station mainly from the NE and ENE (40–60°). Most of them had been crossing mountain ridges and highlands reaching 600–1000 m asl a few kilometres to the NE of the radar. Due to this particular topography, practically all birds were recorded above 600 m agl and 900 m asl, with the maximum intensity of migration at 800–1000 m agl. The 50% quantile reached nearly 1200 m agl, and the 90% quantile 2000 m agl (equalling 2300 m asl). In spring 2006 (Fig. 4a), the radar station was located at the western-most corner of Calabria, at the edge of Villa San Giovanni (100 m asl). Nocturnal migration approached the radar station mainly from the SW, i.e. from the central, mountainous parts of
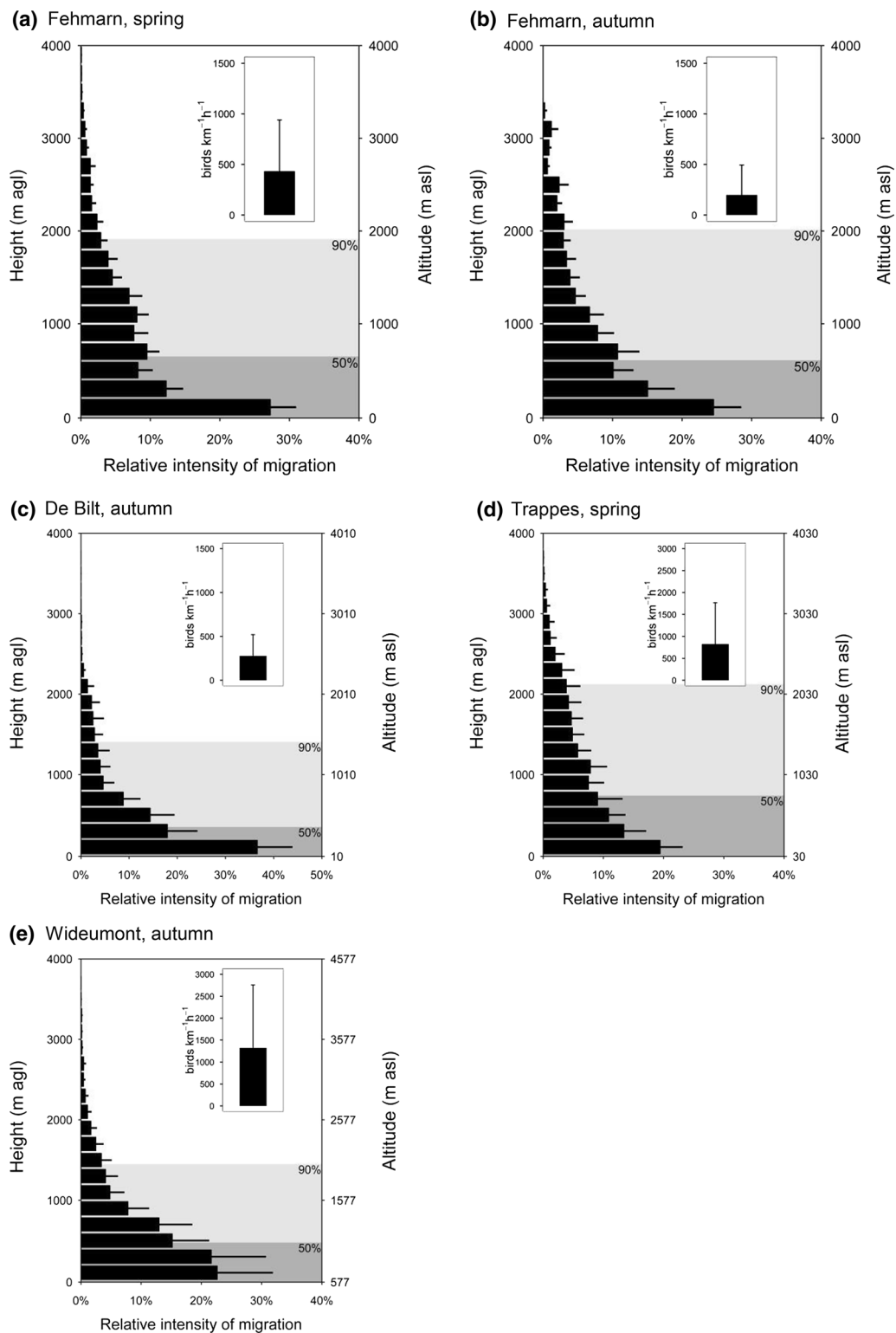
**Fig. 2** Proportional vertical distribution of nocturnal bird migration (agl and asl) to the north and northwest of central Europe. Sites 2–5 according to Fig. 1 and Table 1 (height bins of 200 m with the upper limit of the 95% confidence interval). Fixed-beam (FB) measurements at the Baltic coast: **a** Fehmarn/D (19 Feb–29 May 2009, 8 Mar–6 June 2010), **b** Fehmarn/D (13 Aug–16 Nov 2009, 14 Aug–15 Nov 2010), and near the Atlantic coast: **c** De Bilt/NL (18 Aug–16 Sep 2007), **d** Trappes/F (8 Mar–7 May 2008), and **e** Wideumont/B (18 Sep–22 Oct 2007). The insets indicate the total migration traffic rate (MTR; birds $km^{-1} h^{-1}$)
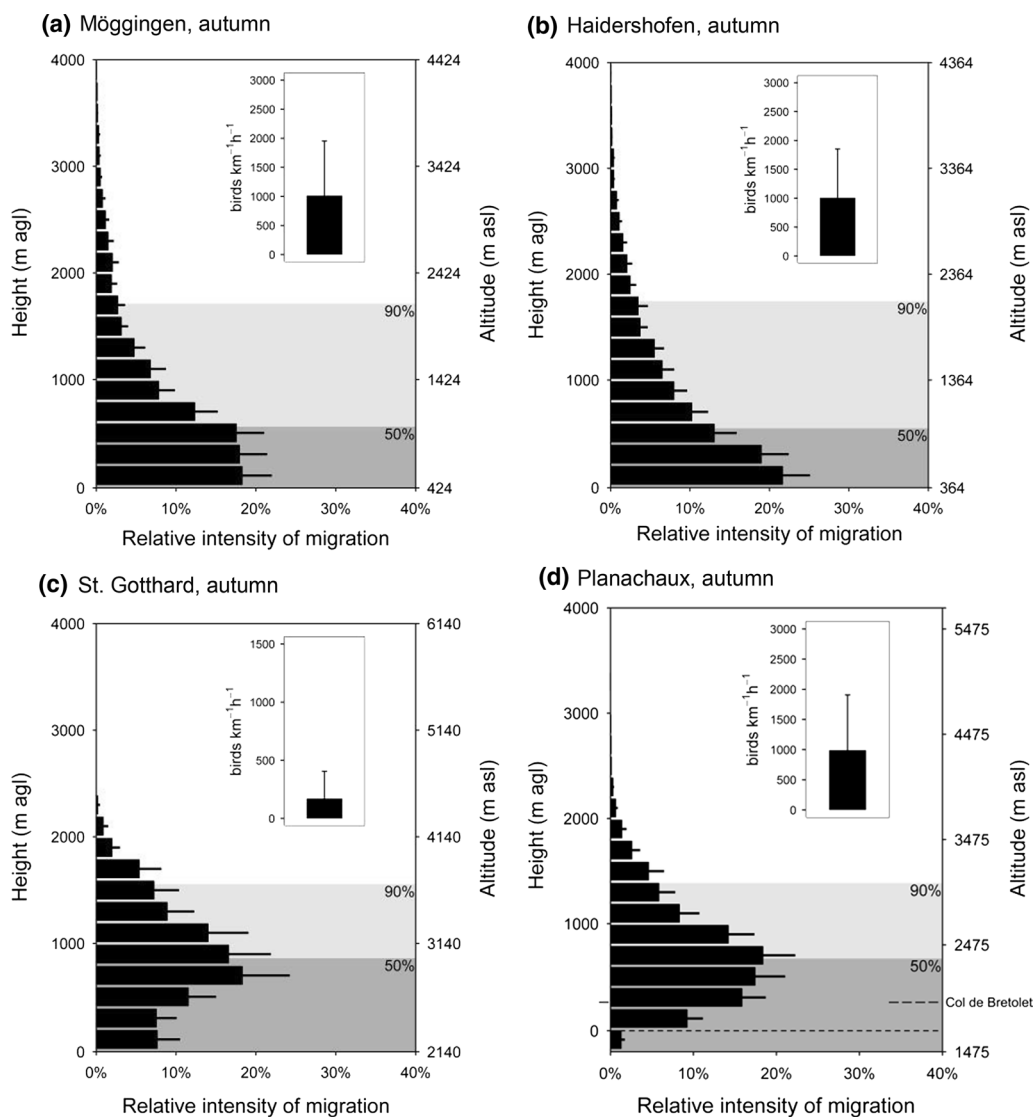
**Fig. 3** Proportional vertical distribution of nocturnal bird migration (agl and asl) in central Europe, sites 8, 9, 11 and 12 (height bins of 200 m with the upper limit of the 95% confidence interval): **a** Fixed-beam (FB) measurements near Möggingen/D at the Lake of Constance (12 Aug–6 Nov 2008), **b** Haidershofen/A (21 Aug–13 Nov 2013), and at two Alpine passes: **c** St. Gotthard/CH (3 Sept–18 Oct 2010), **d** Planachaux/CH next to Col de Bretolet (6 Aug–29 Oct 2007, CB = elevation of Col de Bretolet, dashed line = elevation of radar site). The insets indicate total MTR (birds km$^{-1}$ h$^{-1}$)

Sicily. Passerines from Tunisia are probably all resting on Sicily before continuing towards Calabria. According to the varied topography in the departure and approach areas, the vertical distribution was widely scattered across the whole span from 0 to 2000 m, decreasing up to 3000 m (the limit of analysed quantitative data at this site). The distribution of autumn migration at Vélez-Málaga (Fig. 4d) was due to intense departures in the coastal area to the E of the radar station, followed throughout the night by birds having crossed mountain areas between 800 and 2000 m asl; late at night and towards morning directions shifted progressively towards the W, with birds increasingly intending to land

along the coast (Bruderer and Liechti 1998a, Nievergelt et al. 1999). This combined effect of take-off or landing in coastal areas, besides crossing mountain areas at night, resulted in a distribution similar to the spring distribution at the Strait of Messina (the 50% quantiles reaching 1200 m, and 90% quantiles reached 2200 and 2400 m, respectively).

The "blue" sites are radar stations where the migrants arrived from the sea, i.e. without any topographical distortions. Due to the lack of obstacles in the approach areas at Vélez-Málaga (Fig. 4c) and Mallorca (Fig. 4e), the distributions were similar to Fehmarn (Fig. 2a, b), with the highest intensity in the lowest interval, and quasi-exponential decrease

**Fig. 4** Proportional vertical distribution of nocturnal bird migration (agl and asl) in the central and western Mediterranean. Sites 15–17 (height bins of 200 m with the upper limit of the 95% confidence interval): Fixed-beam (FB) measurement at the Strait of Messina/I (**a** 29 Mar–15 May 2006 and **b** 6 Sep–9 Nov 2010). SCAN measurements at the south coast of Spain: **c** Vélez-Málaga/E (22 Mar–26 May 1997), **d** Vélez-Málaga/E (15 Aug–24 Oct 1996), and on the Balearic Islands **e** Mallorca/E (24 Mar–26 May 1997). The insets indicate total bird density (birds km$^{-3}$) in the case of SCAN measurements, and total MTR (birds km$^{-1}$ h$^{-1}$), respectively
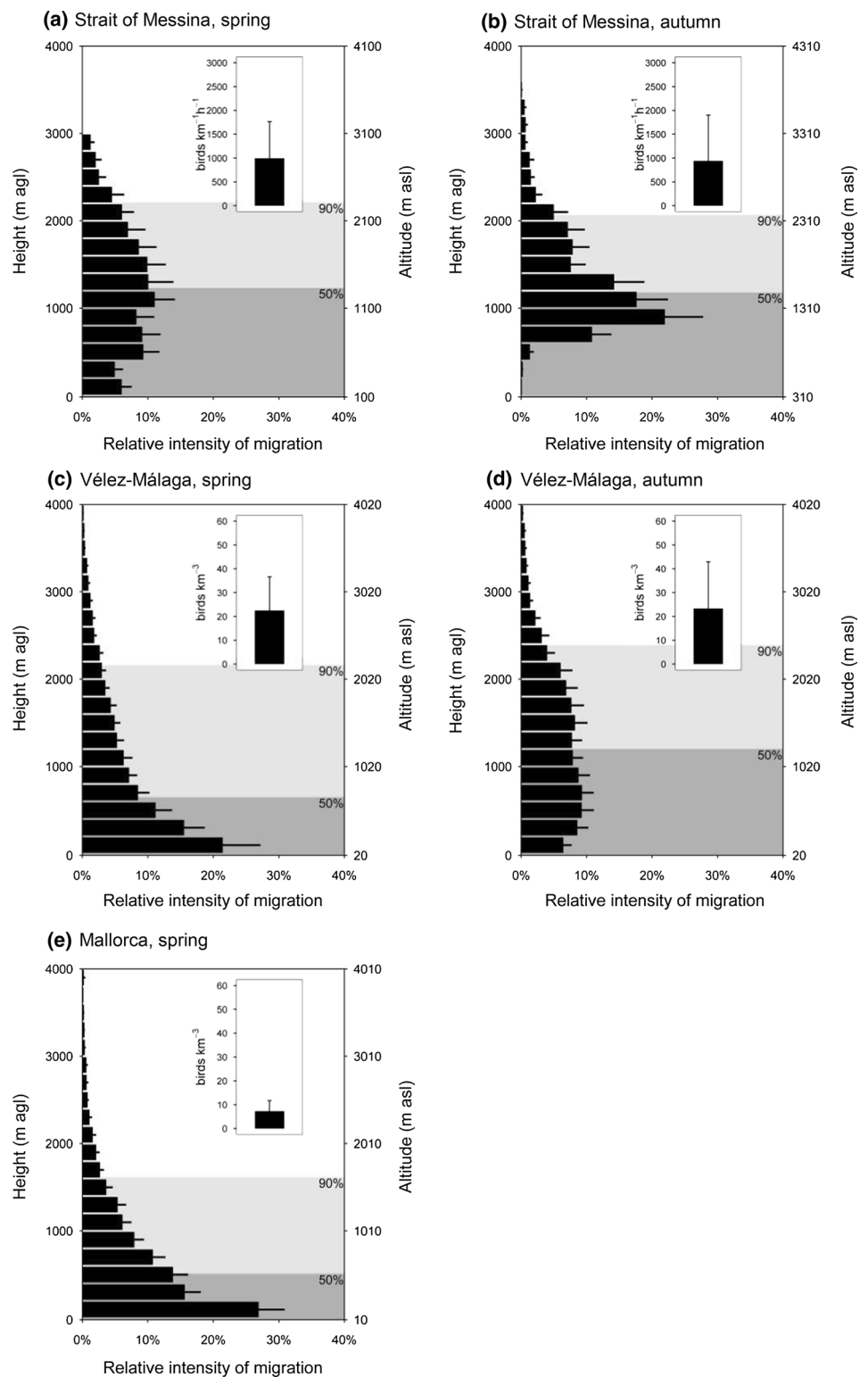


up to nearly 4000 m. At Vélez-Málaga, 50% of the birds were below 650 m, and 90% were below 2200 m agl (and asl). These quantiles were lower on Balearic Island (Fig. 4e), and more birds flew in the lowest interval (due to increased landing tendencies on the island after a very long sea crossing).

The "yellow" clusters in Table 2 comprise data from the trade-wind zones of Israel and the Sahara (Figs. 5, 6). The sites in Israel (with a brownish tinge) show situations with additional influence of topography, particularly in autumn:
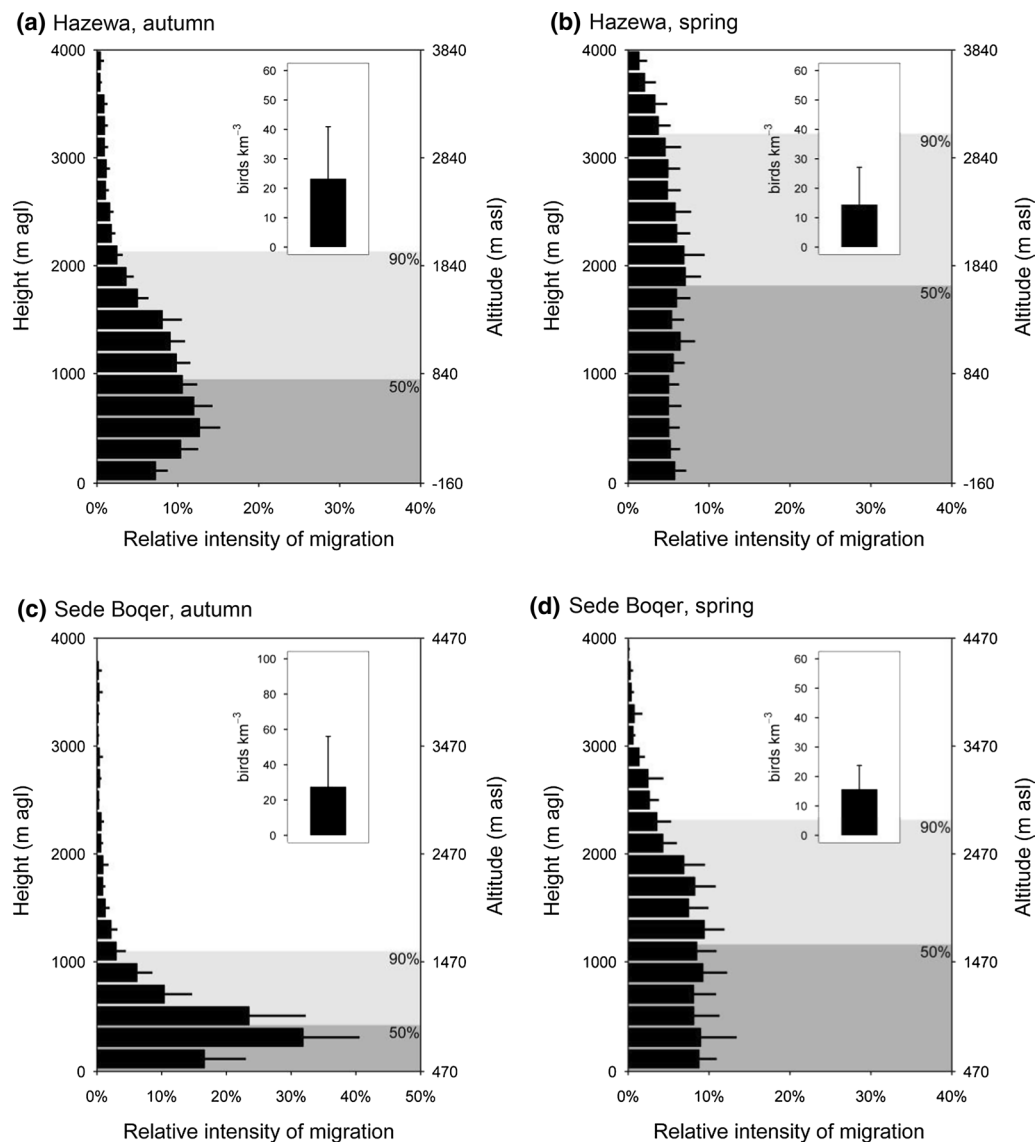
**Fig. 5** Proportional vertical distribution of nocturnal bird migration (agl and asl) in the eastern Mediterranean (southern Israel, sites 18 and 19; height bins of 200 m with the upper limit of the 95% confidence interval): SCAN measurements in the Arava Valley (**a** Hazewa/ IL, 9 Sep–31 Oct 1991, **b** 1 Mar–20 May 1992) and on the Negev Highlands (**c** Sede Boqer/IL, 19 Sep–31 Oct 1991, **d** 30 Mar–30 Apr 1992). The insets indicate total bird density (birds km$^{-3}$)

The distribution of autumn migrants arriving at Hazewa (in the depression of the Arava Valley, Fig. 5a) may be considered as a compromise between the trade-winds favouring migration at low altitudes and the arrival across elevated areas (e.g. the nearby Negev Highland at about 500 m asl, and the Jordanian mountains at > 1000 m. At Sede Boqer (on the Negev Highlands 470 m asl, Fig. 5c), migration was "compressed" in a narrow height interval, the lower parts of migration forced upwards by topography, the upper parts limited by increasing antitrades above 1500 m asl.

Spring migration in Israel (Fig. 5b, d) and in the Sahara (Fig. 6b, d) demonstrate consistently the influence of increasing wind support with altitude; in Israel, this is less pronounced than in the Sahara; on the Negev Highlands (Fig. 5d, Sede Boqer), this is less than in the Arava Valley (Fig. 5b, Hazewa). Spring migration in the Sahara seems to take place at higher levels above the plain desert (Fig. 6d, Bir Amrâne) than close to an oasis (Fig. 6b, Ouadâne). The autumn data from Mohammed Lemna comprise a challenge, because they do not conform with the idea that autumn migration in the trade-wind zone is mainly concentrated at levels below the antitrades (i.e. below about 1500–1800 m asl; Bruderer et al. 1995b). The percentage of (the very low number of) birds was equal below and above 1800 m agl.
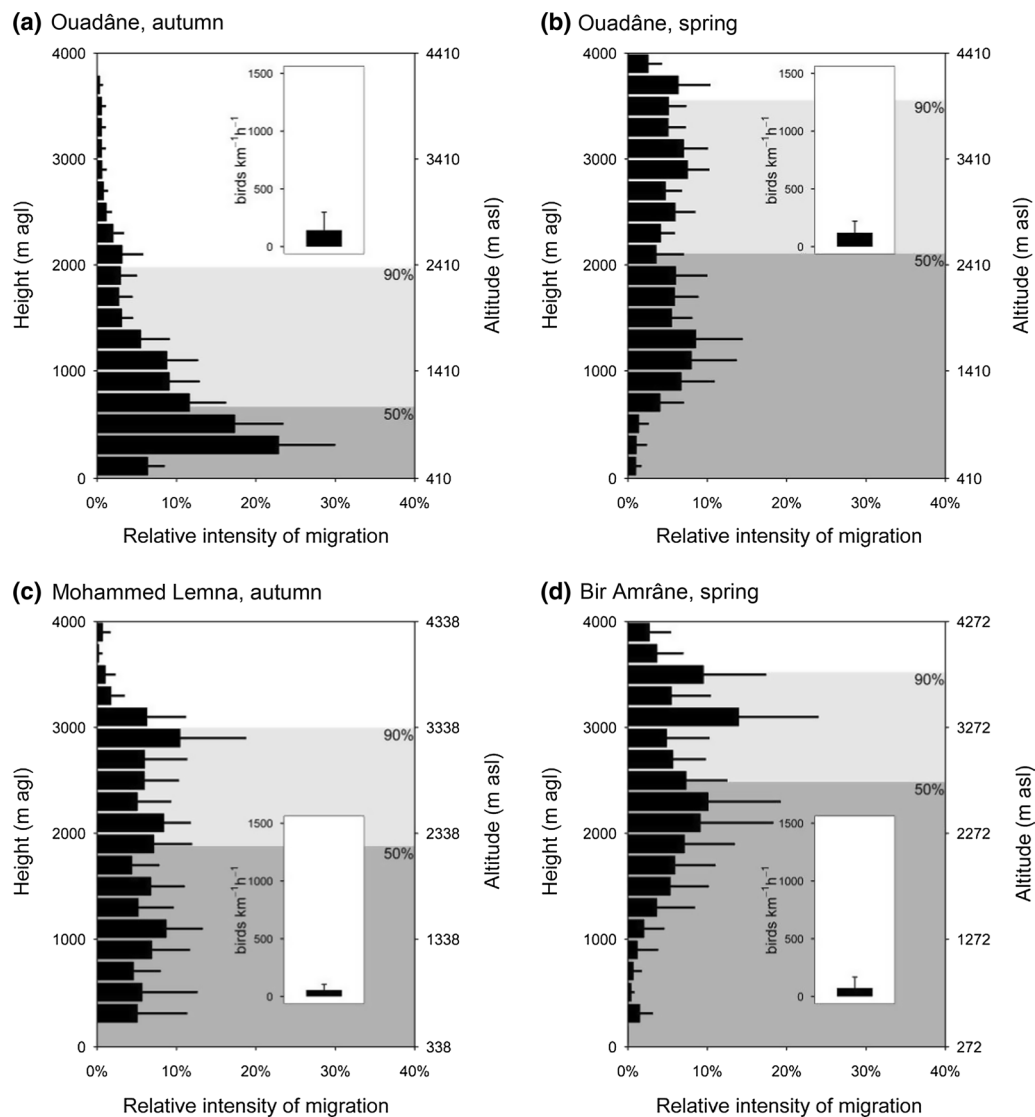
**Fig. 6** Proportional vertical distribution of nocturnal bird migration (agl and asl) in the western Sahara, sites 20–22 (height bins of 200 m with the upper limit of the 95% confidence interval): Fixed-beam (FB) measurements in Mauritania: at an oasis (**a** Ouadâne/RIM, 24 Aug–25 Oct 2003), (**b** Ouadâne, 15 Mar–10 May 2004), in the plain desert (**c** Mohammed Lemna/RIM, 19–30 Sep 2003), and (**d** Bir Amrâne/RIM 3–25 Apr 2004). The insets indicate total MTR (birds km$^{-1}$ h$^{-1}$)

## Discussion

Our data allow for the first time to compare average vertical distributions of nocturnal bird migration from a wide range of sites in the European-African migration system, and to explain variation by topographic or persistent meteorological features of the respective sites. Variable weather influences are, to a high degree, balanced over relatively long observation periods. Nocturnal migration is particularly suited for such comparisons, because it comprises large numbers of singly flying birds, while in daytime, the number of targets is reduced due to flocking. Examples for the comparison of day and night are available in Bruderer and Liechti (2004) and Bruderer et al. (2012). Variation of height distributions with weather conditions was documented, e.g. by Bruderer (1971), Blokpoel and Burton (1975), Bruderer et al. (1995b), Bruderer and Liechti (1998b), and Kemp et al. (2013).

In temperate zones devoid of major orographic elevations, the average altitudinal distribution of bird migration was, in most cases, characterized by roughly 20–30% of nocturnal migrants flying in the lowest 200 m agl, 50% below 700 m, and 90% below 2100 m agl. In temperate Europe, autumn migrants may be prone to fly particularly low, because prevailing westerly winds increasing with altitude make low

flights energetically profitable (e.g. Shamoun-Baranes et al. 2017). In spring, the migrants may fly higher than in autumn because they often profit from following southwesterly winds. Bruderer (1971, pp. 136/137) showed that nocturnal spring migrants in the Swiss Lowlands flew higher in clear nights compared to cloudy and particularly rainy conditions. In undisturbed weather, the height distribution of spring migrants was influenced by the altitudinal profile of winds, with distinct layers of intense bird migration at altitudes with optimal winds. These findings were recently confirmed by a statistical analysis of long-term data gathered by C-band Doppler radar in the Netherlands (Dokter et al. 2013). Combined radar and visual observations in the Netherlands showed that under conditions with strong opposing winds, diurnal migrants did not only concentrate at low altitudes, but often flew in the lowest few meters over ground, many of them below the reach of radar detection (Buurma 2002). Nocturnal migrants do, however, avoid the lowest few meters over ground as Komenda-Zehnder et al. (2010) showed by radar, and Bellrose (1971) found "no evidence of birds migrating at night below 100 ft agl" during his aircraft searches.

Comparison with other radar measurements is often problematic, because the coverage of either low or high altitudes as well as the exclusion of non-bird echoes may be insufficient in many studies, and allowance for changes in detection probability with distance is rare (Schmaljohann et al. 2007c, b; Beason et al. 2013). Available data from relatively flat areas in the temperate zone do, however (within the given methodological limitations), support the notion of most intense migration at low levels and pronounced decrease with height (e.g. Bellrose 1971; Blokpoel and Burton 1975; Jellmann 1979; Hüppop et al. 2006; Kemp et al. 2013; Fijn et al. 2015).

Direct comparisons of our bird radar measurements at De Bilt, Wideumont, and Trappes with a network of C-band weather radars showed reasonable correlation between the vertical density profiles of the bird radars and the height-integrated weather radar measurements (Dokter et al. 2011). Kemp et al. (2013) applied the C-band Doppler radar at De Bilt to analyse the influence of weather on the flight altitudes of nocturnal migration. Using only nights with relatively strong migration, they found the highest birds close to 4000 m agl and a slow increase of bird densities downwards from this upper limit. At 2000 m, the 90% quantile was reached, and the 50% quantile at about 600 m. Both of these values would be some 100–200 m lower down if the lowest interval (lacking in these measurements) would contain 20–30% of all birds. Neglecting the lowest height bin, these results are similar to most of our measurements devoid of orographic or atmospheric distortions.

Vertical distributions differing from this general picture occur at sites where the birds had to cross mountain ridges before reaching the radar station. At such sites, the lower height bins contained only few birds. This effect was already visible at Möggingen (Fig. 3a), but most pronounced at Alpine passes, where migration was much higher than the elevation of the passes would require: At St. Gotthard, birds arriving on a straight course from the NE crossed mountain ranges 500–1000 m higher than the pass within the last 1–30 km. At Planachaux, the mountains to both sides of the valley are about 800 m higher than the radar site, similar to mountain ranges crossed some 35 km before (i.e. less than 1 h of flight).

Another feature of migration at Alpine passes is that height distributions are vertically compressed, because the upper limit of migration climbs less than its lower limit is forced upwards by topography. The radar positioned at Planachaux next to Col de Bretolet (Fig. 3d) showed that at least 85% of the nocturnal migrants flew higher than the pass already 4.5 km before reaching the passage; only 2.5% flew within the lowest interval of −100 to −300 m below the level of the radar (but still high above the valley bottom). In daytime, about 40% of the birds climbed for crossing the pass, and more than 10% flew below the level of the radar (Komenda-Zehnder et al. 2010).

Autumn migration at the Spanish coast as well as spring and autumn migration at the Strait of Messina confirm the effect of previously crossed mountains. On the other hand, spring arrivals across the sea (at Málaga and Mallorca) show that without any obstacles in the approach areas, height distributions are similar to the northern stations without orographic particularities.

In the trade-wind zone, autumn migration is most intense in the north-easterly winds below about 1500–1800 m asl. At Ouadâne, 50% of nocturnal migrants were below 600 m, with the mode of the distribution around 300 m agl, similar to measurements in the Egyptian Sahara (Klaassen and Biebach 2000). This rule was abandoned at Mohamed Lemna, where weak autumn migration was scattered over heights of 400–3200 m agl (750 m to 3550 m asl). Speculating about the reasons for this unexpected behaviour, we hypothesize that the larger the distance of desert crossing, and the more extreme the desert conditions below, the more the migrants might be prepared to climb to altitudes providing better convective cooling and possibly reduced turbulence; thus, overriding to a certain extent the normally dominating effect of winds (Liechti and Schmaljohann 2007a; Schmaljohann et al. 2009).

Spring migrants in Mauritania tended to climb above the trade-wind layer with seasonally opposing winds. High-altitude migration (mainly 3000–6000 m asl) was also recorded by Richardson (1976) and by Williams et al. (1977) in the trade-wind area of the Caribbean.

## Part II: Temporal variation and extreme heights

### Methods and sites

#### Tracking selected targets

In contrast to the averaged distributions of radar targets of the previous part, tracking data provide information on the exact positions of specific targets (besides direction, speed, height, and wing-beat pattern of these targets). Pilot balloons were tracked three to four times per day to obtain information of winds at the relevant heights. During the wind measurements as well as during FB and SCAN measurements, tracking was not possible, as the same radar was used for all these tasks. In the present context, the measured heights of tracked birds (identified visually or according to their echo signature) are used to demonstrate seasonal and diurnal variation in the height of bird migration.

The method was applied since the beginning of tracking studies with the "Superfledermaus" radar (Bruderer 1971; Bruderer and Steidinger 1972). Originally, it was based on visual detection of echoes on the available radar screens (R-scope = range indicator in the frequent situations with many bird targets; RHI = range-height indicator with the beam scanning vertically and horizontally for scattered targets during weak diurnal migration or at high altitudes). The operator selected a target and started automatic tracking that was continued over 90 s in the early studies, and reduced down to 20 s in recent studies. During limited times of diurnal migration, the operators tried to obtain visual information on tracked targets. Selection of low-flying targets in the approach sector increased the probability of target identification and tracking until identification increased the time needed per record. From 2004 onwards, tracking was increasingly automatized, first at night, later also in daytime when no visual target identification was intended: The radar was steered by a computer program to search targets over a limited time at various heights (similar to a human operator, but avoiding human bias). Only targets that could be identified as individual birds or flocks of birds (either visually in a telescope mounted parallel to the radar beam or according to their echo signature) are considered for the present analysis.

With respect to the temporal and spatial distribution of the tracked targets, some limitations have to be considered: A preference for high targets may favour the acquisition of high-flying birds, while the declining quality of echo signatures at distances beyond about the 3.5-km range reduces the number of identifiable targets at high altitude. Variation along the time axis is also, to a certain extent, influenced by the radar operators, particularly when visual identification (requiring longer than usual tracking at low heights) is

intended in diurnal migration. A bias that goes in the opposite direction is that the proportion of tracked targets compared to available targets gets reduced with increasing target abundance (e.g. at night) due to the time needed to record a track. When targets are scarce (e.g. in daytime), the operators are always able to find a target; this may result in an over-estimation of diurnal migration. The method provides a fair idea of diurnal variation in migratory flight altitudes and the highest flights per site. The method is unique in providing the exact position of bird echoes in time and space, thus contrasting to methods that derive average migration intensities from a combination of several measurements.

In the present study we implement electronically recorded tracking data of the "Superfledermaus" radar. Such data are available from 1975 onwards (italicised in Table 1, open squares in Fig. 1). The data are presented in the form of box-and-whisker plots, the seasonal data with colours for day and night and three colour intensities for sample sizes. Table 3 provides 90% bootstrap confidence intervals for the complete season's samples. An example visualizing the distribution of all the data points of mean altitude per tracked bird echo is given in Bruderer and Peter (2017).

### Results

#### Day-to-day variation of height

Figures 7 and 8 show the vertical distribution of tracked birds over time for selected 30-day periods. The radar sites of Fig. 7 are at sea level (altitude equals height), Ouadâne (Fig. 8) is 410 m asl.

Fehmarn (Fig. 7a) shows late autumn migration, starting with moderate flight levels and numbers of tracked birds in early October. From mid-October onwards, altitudes and numbers of birds were lower in most nights (probably a consequence of generally declining migration combined with increasingly bad weather). Typically reduced numbers (and also partly reduced flight altitudes) are caused by the passage of weather fronts over Denmark, e.g. on October 7 and 12, and particularly from October 23 till 26.

At De Bilt (Fig. 7b, mid-August till mid-September), flight levels as well as the number of tracked birds were higher than at Fehmarn (later in the season and further NE; Table 3). The missing observations are caused by rain. During occasional bad-weather days some unexpectedly high-flying birds had been recorded.

Vélez-Málaga (Fig. 7c): The sequence shows spring migration arriving from the Mediterranean Sea at relatively high altitudes (with medians around 848 m agl in daytime and around 967 m at night; Table 3) and high intensities throughout. Diurnal intensities were increased by the arrival of nocturnal migrants that flew above the sea at daybreak,

**Fig. 7** Seasonal course of migration along European coasts (sites 2, 3 and 16) based on the mean height of tracked birds for day and night; the boxes represent 50% of the observations, the horizontal bar is the median, the whiskers are drawn until the last observation within 1.5 times the interquartile range from the box, and circles are observations beyond this range; shading of colours indicates sample size: **a** Fehmarn/D (5 Oct–4 Nov 2009; *n* = 3159); **b** De Bilt/NL (17 Aug–16 Sep 2007; *n* = 5960); **c** Vélez-Málaga/E (9 Apr–9 May 1997; *n* = 14,728)



**(a)** Fehmarn, autumn

**(b)** De Bilt, autumn

**(c)** Vélez-Málaga, spring
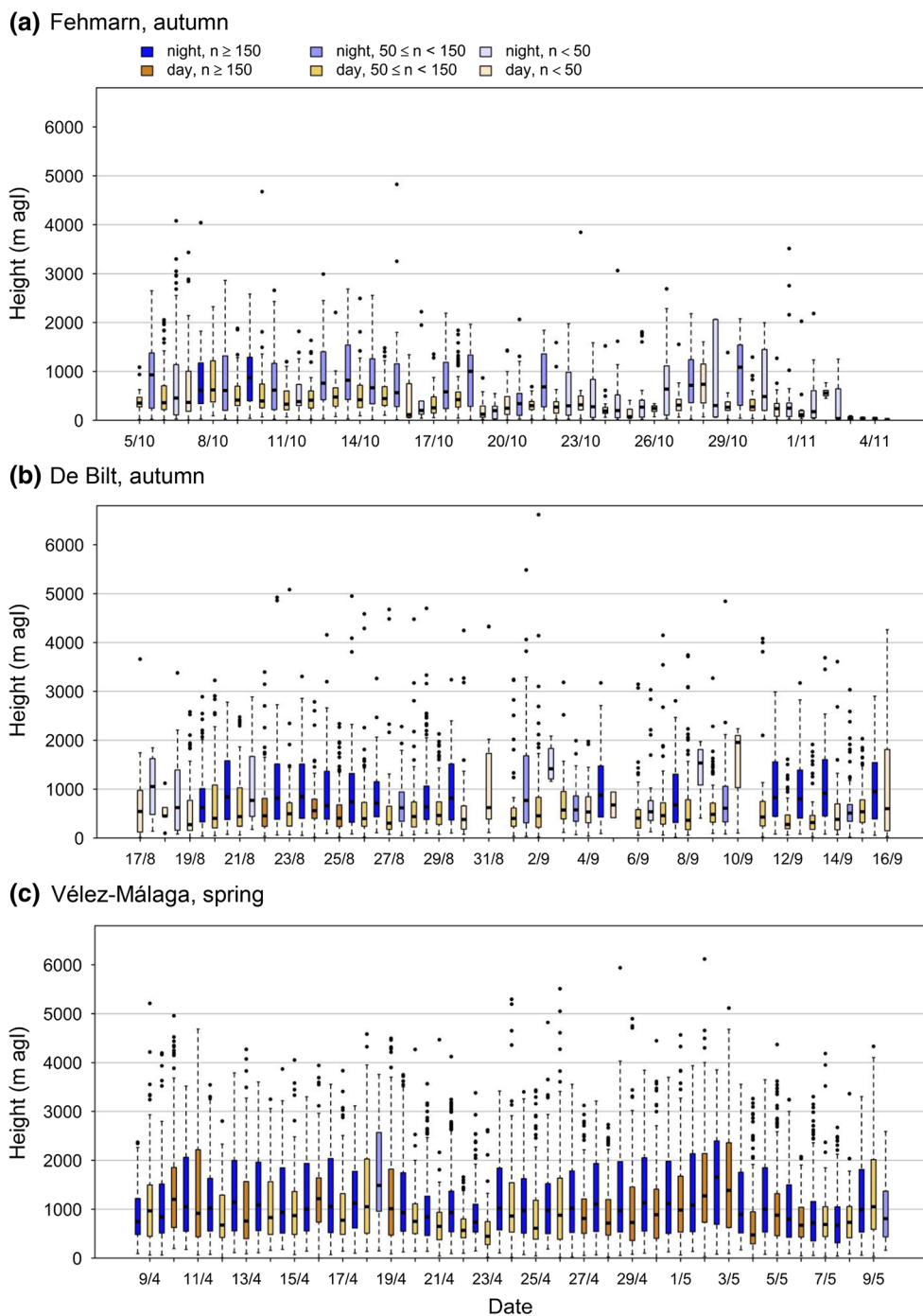
but also by swallows, swifts, and raptors arriving throughout the day.

During autumn migration at Ouadâne (Fig. 8a, Table 3), the median heights as well as the 25% quantiles of migration were higher than during (undisturbed) spring migration in the Mediterranean (Fig. 8b, Table 3), while the 75% quantiles as well as the upper tails of the height distributions were lower due to increasing influence of the antitrades at high altitudes. The lower tails of the height distributions were higher above ground, indicating avoidance of the hottest air

layers close to the desert surface. In October, the height and intensity of migration decreased. This was at least partially due to inclement weather: From October 1 till 3, a sandstorm approaching from NE passed the area; winds reached speeds of 95 km h at ground level and yellow dust reduced visibility to less than 1 km. On October 16, a bad weather front approached again from the north, reducing visible diurnal migration to nearly zero in the morning of October 19. The following days until the end of the observations on 24 October were characterized by intermittent showers and

**Table 3** Three quantiles of heights with 95% bootstrap confidence intervals

| Figure and site | 25% Quantile | Median | 75% Quantile |
|---|---|---|---|
| Figure 7a Fehmarn night | 260 (241–279) | 609 (549–674) | 1262 (1219–1308) |
| Figure 7a Fehmarn day | 206 (194–220) | 345 (332–365) | 556 (536–586) |
| Figure 7b De Bilt night | 386 (374–398) | 727 (700–755) | 1404 (1357–1464) |
| Figure 7b De Bilt day | 238 (226–251) | 438 (416–459) | 758 (724–792) |
| Figure 7c Vélez-Mâlaga night | 521 (511–532) | 967 (943–991) | 1756 (1721–1792) |
| Figure 7c Vélez-Mâlaga day | 455 (442–472) | 848 (822–875) | 1481 (1437–1528 |
| Figure 8a Ouadâne autumn night | 744 (733–757) | 1142 (1124–1158) | *1652 (1636–1672)* |
| Figure 8a Ouadâne autumn day | 541 (529–562) | 884 (860–1158) | *1373 (1348–1409)* |
| Figure 8b Ouadâne spring night | 1298 (1275–1318) | 1890 (1869–1914) | 2532 (2511–2552) |
| Figure 8b Ouadâne spring day | 981 (953–1010) | 1772 (1715–1828) | 2788 (2732–2840) |

Sites of Figs. 7 and 8 arranged according to increasing height of migration (the only exceptions, in italics, are the 75% quantiles in autumn at Ouadâne)

extremely weak diurnal migration (a result of the Intertropical Convergence Zone reaching exceptionally far N in 2003).

During spring migration at Ouadâne (Fig. 8b), the lowest birds flew even more than in autumn off the ground, particularly at night. In daytime, the number of birds tracked at low levels was increased due to the operators aiming at species identification. The medians were concentrated around 1890 m agl at night, and around 1772 m in daytime, with the

75% quantiles reaching 2532 m at night and the very high value of 2788 m in daytime (Table 3). Nearly all the birds at extreme heights had been observed in daytime. Variation in the height distributions was mainly caused by variation in the vertical wind profile (Liechti and Schmaljohann 2007a, b ; Schmaljohann et al. 2009).

The common feature of all these distributions is the alternation between relatively high nocturnal and generally lower

**Fig. 8** Seasonal course of migration in the Mauritanian Sahara (site 20) based on the mean height (agl) of tracked birds for day and night; for interpretation of box-and-whisker plots, see Fig. 7; shading of colours indicates sample size: **a** Ouadâne/RIM (19 Sep–19 Oct 2003; *n* = 6822), **b** Ouadâne/RIM (11 Apr–11 May 2003; *n* = 14,464). Altitudes (asl) are 410 m higher than indicated by the scale on the ordinate



**(a)** Ouadâne, autumn

**(b)** Ouadâne, spring
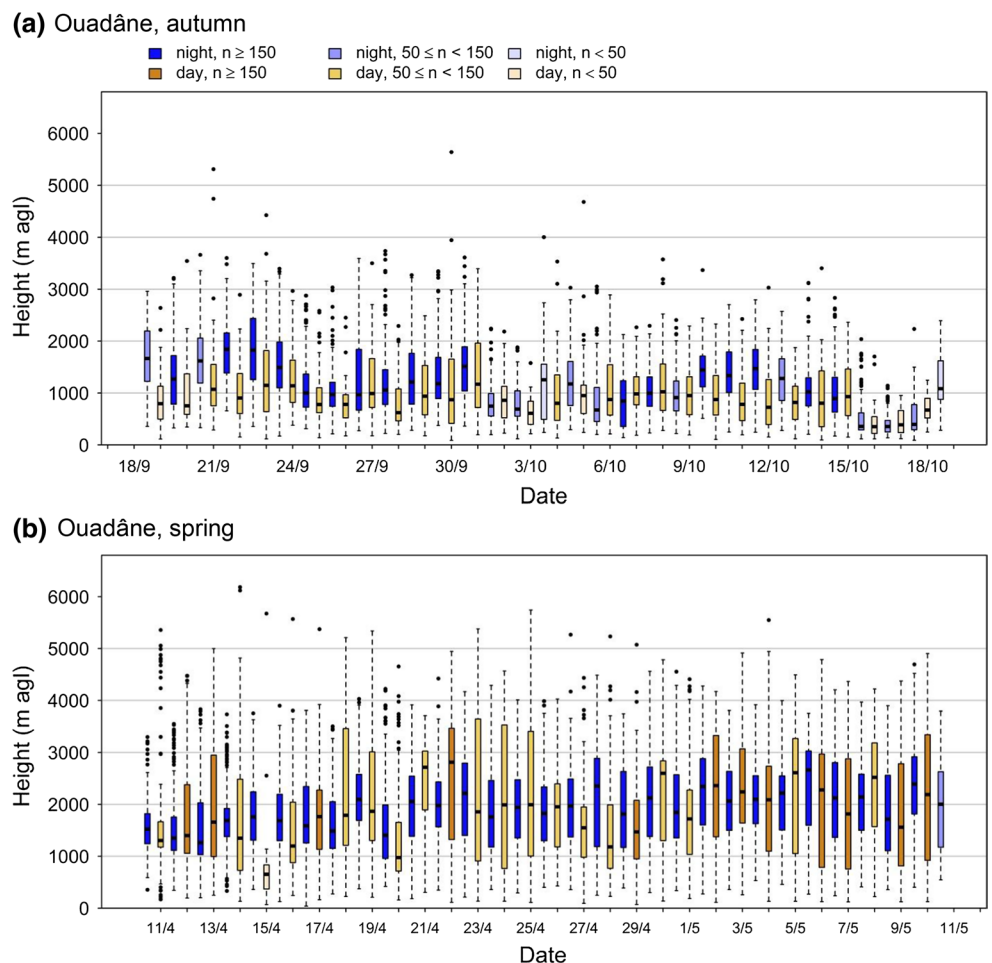
diurnal migration. The highest migrants at all sites (except Fehmarn) had, however, been recorded in daytime. Table 3 is arranged according to increasing heights. The only deviant in this sequence is the 75% quantile in autumn migration at Ouadâne, where opposing antitrades reduce high migration. Figure 8a, b demonstrate the differential effect of trade winds and antitrades on autumn and spring migration in the Sahara. The highest spring flights were observed during morning in the trade-wind zone over the Negev Highlands (Israel), where considerable numbers of mainly wading birds climbed to altitudes of 5000 and almost 9000 m asl in favourably directed low-level jet streams, instead of landing in inhospitable areas (Table 1; Liechti and Schaller 1999).

### Diurnal variation of altitudes

As in the case of seasonal migration, the diurnal course of migration is visualized in the form of box-and-whisker plots (Fig. 9). These are based on superimposed tracking data of 10 subsequent days for 3 regions. An example of data with a point for each tracked bird is available in Bruderer and Peter (2017).

The diurnal course of migration in late August at De Bilt (Fig. 9a) was characterized by lower numbers of tracks during daytime compared to night; the medians of tracks below 500 m from 09 till 17 h, slightly increasing heights before sunset, pronounced increase from sunset till 23 h (medians reaching 800 m), and slight decrease till 05 h. Between 05 and 06 h (i.e. around sunrise), the number of tracks decreased (partly due to the wind measurement), while height increased, possibly as a sort of dawn ascent. Between 06 and 09 h, medians were slightly above 500 m, and from 09 h until late afternoon, they were around 300 m agl. All the characteristic values of the distribution were higher at night than in daytime. Birds above 3000 m occurred between 17 h in the evening and 9 h in the morning.

The characteristics of diurnal height variation in late spring at Vélez-Málaga (Fig. 9b) are: Relatively low numbers of tracked birds throughout the afternoon with most medians at heights of 600–800 m; beginning of nocturnal migration after sunset (interval of 21–22 h), the median reaching 1200 m towards 23 h. From 23 until 06 h, heights of medians varying between 800 and 1200 m, relatively low before and around sunrise, higher in the interval after sunrise higher (08–09 h, with small sample size due to the morning wind measurement taking place at this time). Diurnal migrants arrived during the morning from the sea at similar heights as nocturnal migrants and still in relatively high numbers. Between 04 and 08 h, birds above 3000 m tended to disappear; migrants flying even higher than at night were tracked between 08 and 12 h, with some even in the afternoon. These birds may be interpreted as migrants continuing

from the Sahara across the Mediterranean Sea and the mountain ranges of the Cordilleras, climbing to high altitudes in daytime.

Nocturnal spring migrants at Ouadâne (Fig. 9c) avoided the lowest 300–400 m; the lowest diurnal migrants were tracked as low as 100 m agl (due to operators aiming at species identification). In the afternoon, the number of tracks was low and median heights varied around 1000 m, considerably lower than at night and in the morning, in spite of some high flyers between 4000 and 5000 m. A particular phenomenon of spring migration (observed over long periods at Ouadâne after the evening wind measurement, see Bruderer and Peter 2017) was an aggregation of diurnal migrants at heights between 2500 and 3500 m before and around sunset. This enormous concentration was followed by a gap at high levels and massive departure, represented by extreme densities of tracked birds between 500 and 1300 m (Bruderer and Peter 2017), here shown by the 50% box reaching from 700 to 2100 m. After this departure phase, the tracked birds moved upwards continuously until 22 h. After 22 h, the median height slightly decreased, levelling off around 2000 m with most birds flying between 1500 and 2700 m until 05 h. After 05 h, the median moved downward by about 500 m until the time around sunrise (~06:10 h). In the interval between 07 and 08 h, the number of tracked birds was reduced due to the morning wind measurement, but migration moved upwards again to reach medians above 2000 m and 75% quantiles even higher than at night. While the median started moving downwards in the interval from 11 to 12 h, the upper limit of migration tended to rise. The highest birds were observed during the afternoon, while the bulk of migrants was tracked below 2000 m between 13 and 18 h.

The diurnal course of migration over Ouadâne indicates that notable numbers of nocturnal spring migrants extend their flights far into the day, reaching highest altitudes around noon. In addition to wading birds with practically no refuelling possibilities in the desert, this behaviour may also include passerines when these are favoured by tailwinds, and/or suitable resting sites are restricted under extreme desert conditions (Schmaljohann et al. 2007a, b; Adamík et al. 2016).

### The upper limit of migration

The highest birds tracked are used to estimate the upper limit of migration. Altitudes asl are used because for the upper limit of migration, heights above ground level are less important than the reference to sea level.

The 99.7% quantile tracks in Table 1 indicate the altitude above which the highest 0.3% of identified birds had been found

**Fig. 9** Diurnal course of migration in three regions (sites 3, 16 and 20). Data of 10 days are pooled for 24 h per site; for interpretation of box-and-whisker plots, see Fig. 7; the sample size for light grey boxes is ≤ 100, and for dark boxes, it is > 100: **a** north-western Europe (De Bilt/NL, 19–29 Aug 2007; *n* = 2903 tracks); **b** western Mediterranean (Vélez-Málaga/E, 27 Apr–7 May 1997; *n* = 5225 tracks); **c** western Sahara (Ouadâne/RIM, 2–14 May 2003; 6253 tracks). The ordinate indicates heights (agl); at De Bilt and Vélez-Málaga, this is equal to altitude (asl); at Ouadâne, altitudes are 410 m higher than indicated by the scale



**(a)** De Bilt, autumn

**(b)** Vélez-Málaga, spring

**(c)** Ouadâne, spring
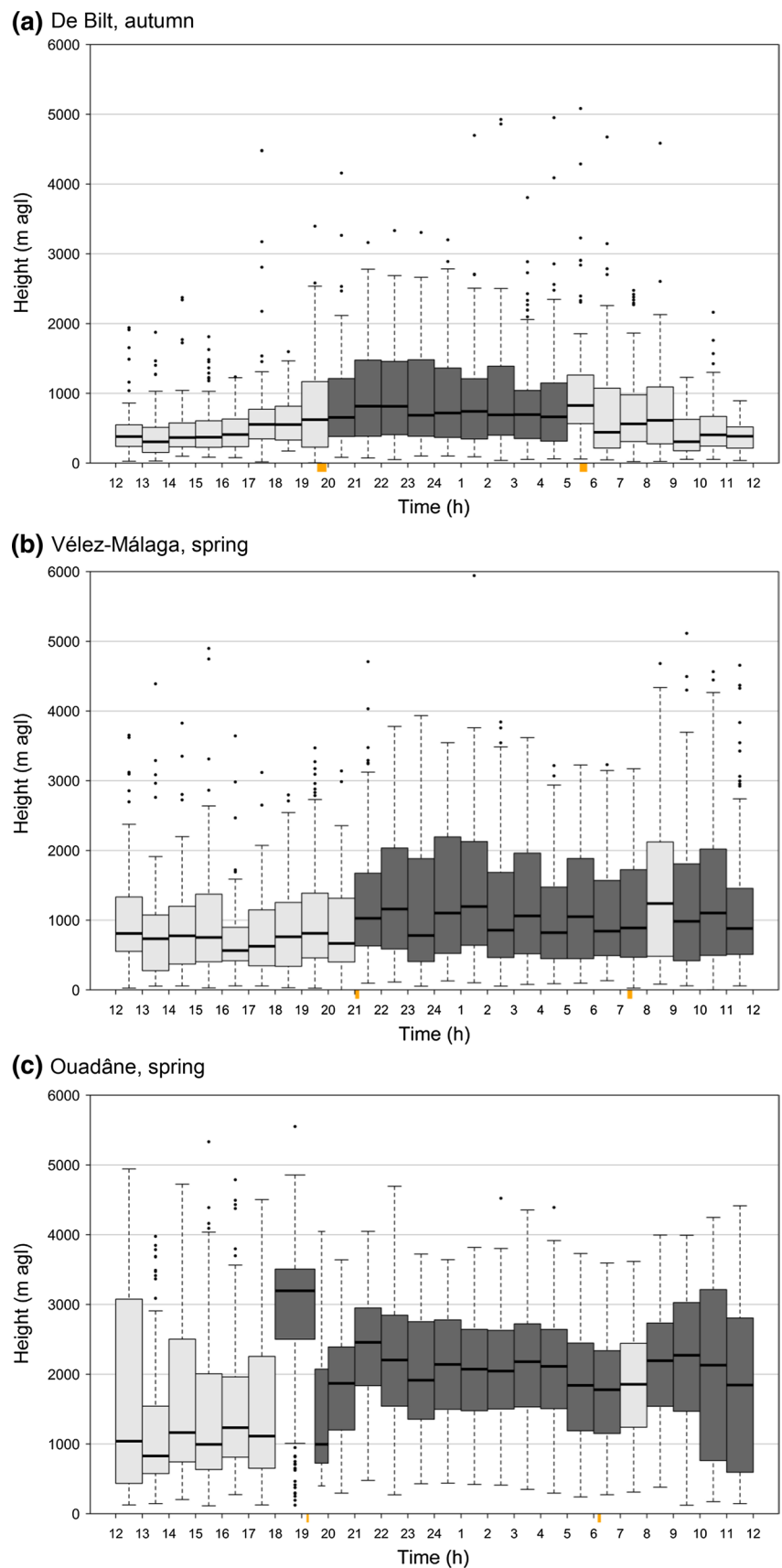
per site. This relatively low number of birds (10–100 individuals according to sample size) depends to a certain extent on the searching intensity of the operators at work. These quantiles reached, in most cases, altitudes between 3500 and 4900 m. Lower altitudes are due to limited interest for high-altitude migration during applied studies at the respective sites (Rügen and Messina). Higher altitudes occurred in spring migration, particularly in the Mediterranean and the trade-wind zones: nearly 5000 m up to 5500 m at Mallorca and in the western Sahara, and even 6870 m on the Negev Highlands.

The highest migrants were tracked at altitudes between about 4500 and 6600 m above the European mainland, and between 6000 and nearly 9000 m above the Balearic Islands and in the trade-wind zones: The highest autumn migrant was above the Arava Valley (Hazeva, 6948 m), and the highest spring migrants were above Mallorca (7852 m) and above the Negev Highlands (Sede Boqer, 8963 m).

## General discussion on flight altitudes

### Advantages of flying low

Besides avoiding lowest flight levels to prevent collisions with obstacles on the ground at night, or when rising above the hottest air layers over subtropical deserts, nocturnal migration shows a pronounced decrease with height, leaving 50% of the birds below 700 m agl, as long as the lower parts of migration had not been pushed upwards by previously crossed mountains or by persistent unfavourable winds at low levels. Thus, "normal migration" is rather low.

Flying in the lower parts of the troposphere has advantages: Drift avoidance is easier with a good view of the ground. The angular speed of landmarks seen by a bird decreases rapidly with increasing height (Liechti 2006). As wind force usually increases with altitude, drift itself is prone to increase accordingly. Flying low facilitates finding suitable resting sites. Remaining below frontal clouds helps avoiding lack of vision and in-cloud turbulences; in case of precipitation, it favours rapid landing. With low stratus clouds, birds are often concentrated just below or above these low-turbulence layers; remaining below facilitates maintaining tracks relative to landscape features, while impeding stellar orientation; flying above the fog hampers drift compensation. Kemp et al. (2013) emphasized that in the temperate zone, nocturnal migrants do usually not climb to altitudes with the best winds, but remain at the lowest levels with acceptable wind conditions. On the other hand, Bruderer (1971) found that under anticyclonic conditions, spring migrants in central Europe adjusted their flight levels mainly to the distribution of winds, concentrating at altitudes with best wind profit. This was corroborated (at least partially) by Dokter et al. (2013) who stated that under certain synoptic conditions, birds may efficiently cross regions with opposing surface wind by choosing a higher flight altitude with more favourable wind, thus leading to the formation of distinct migration layers at varying altitude up to 3 km.

Remaining at low levels reduces the cost of climbing. As the costs of climbing in continuously flapping birds are correlated with body size (Hedenström and Alerstam 1992), large flapping flyers may be expected to fly lower than small ones. Such differences had been observed by Green (2004), with lower flight levels of migrating geese compared with waders. This draws attention to the fact that the species involved may influence vertical distributions. Our data are dominated by passerines. The proportion of continuously flapping waders and waterbirds is below 6% in nocturnal migration over the inland areas of Europe (Bruderer 1971); it is probably higher along the northern and north-western coasts of Europe. Early autumn migration above the European mainland comprises mainly small trans-Sahara migrants, while later in the season, larger thrushes may prevail among the passerines, and heavier waterfowl over smaller waders.

While the general reasons in favour of low flight levels probably apply for all birds, some questions may be raised with respect to the cost of climbing in passerines. Long-distance migrants among passerines are small and therefore privileged with lower climbing costs than larger birds. Additionally, their relatively large wings produce more lift than needed for horizontal flight and more drag than desirable for rapid flight. By intermittently flapping their wings, they reduce profile drag periodically close to zero, while proceeding on a ballistic trajectory with closed wings. With this bounding flight, they increase horizontal speed and avoid excessive lift (Bruderer and Boldt 2001). On the other hand, climbing is easy and inexpensive for intermittently flapping birds, because they can vary their vertical speed by just varying the relative duration of flapping and pausing (Renevey 1981; Bruderer et al. 2010). When starting for migration, their climb rates are so high and take-off phases so short, that climbing birds are rarely tracked by radar (Bruderer et al. 1995b). Similarly, towards the end of nocturnal migration, the landing phase is very short. In some cases on the island of Mallorca as well as in the Negev Highlands at Sede Boqer, it was possible to see birds tracked by radar, diving nearly vertically downwards in the early morning from heights of 1000 m and more, showing up in the telescope mounted parallel to the radar antenna a few 100 m above ground, and opening their wings some meters above ground like a skylark after its song-flight (own unpublished observations).

In addition to the mechanical limitations of generating power for climbing (at least in large migrants), birds might prefer low flight levels to avoid increased evaporative water loss at high altitudes (Klaassen 2004). Model calculations

by Carmi et al. (1992), Carmi and Pinshow (1995), and by Klaassen (1995) suggest that small trans-Sahara migrants tending to reduce water loss should prefer altitudes below roughly 1000 m due to ventilation increasing with the altitudinal decrease of air density and oxygen partial pressure. Klaassen (1996) emphasizes that the rate of water loss will increase with altitude mainly due to increased pulmonary flow associated with reduced oxygen pressure, and suggests that water stress may be an important determinant of migratory behaviour (Klaassen 2004). The models predicting low flight levels in favour of water economy are, however, challenged by radar observations of flight altitudes in the trade-wind zones of Israel (Bruderer et al. 1995b; Liechti et al. 2000) and in the western Sahara (Liechti and Schmaljohann 2007a; Schmaljohann et al. 2009): Spring migrants prefer high flight levels (above the north-easterly trade winds), while water stress as predicted by the above-mentioned models seemed to play a minor role. Temperature decreasing with altitude may also favour high flights in spring. But our autumn data confirm that wind is the most important factor determining altitudes of migration in the trade-wind zone: Over the Sahara, nocturnal autumn migrants fly at low levels, tolerating extremely low humidity and high temperatures far beyond expected limits, but profiting from favourable trade-winds (Schmaljohann et al. 2008a).

## Why do some birds fly higher than "normal" migrants?

The highest identified migrants tracked in spring migration above the deserts of Israel (Bruderer 1994; Liechti and Schaller 1999) and above the Sahara (Schmaljohann et al. 2008c) comprised herons, gulls, terns, waders, and probably also ibises and ducks. These birds would usually not find suitable resting sites in the desert and will, therefore, be prone to fly non-stop across the deserts, at least in favourable winds. For such long journeys—including flights during the hottest parts of the day—climbing to high altitudes might be cost-efficient even for large birds, because high above the deserts they would profit from convective cooling, lack of turbulences, and higher speeds due to reduced air density. In addition, they may be able to recuperate part of the climbing cost by slowly descending towards the end of the journey (this is in contrast to steeply descending passerines).

The theoretical speed of maximum range ($V_{mr}$) increases by about 5% per kilometre of height due to decreasing air density. The air speed of tracked birds increased even by 10% (Bruderer 1971; Schmaljohann and Liechti 2009). To reach these higher speeds and to compensate reduced lift in thin air, small passerines increase their wingbeat frequency by about 1.1 Hz per kilometre altitude (Schmaljohann and Liechti 2009). Increased speed provides a possibility for

time minimization, while energy-wise, high flights provide no advantage (Pennycuick 2008) unless they are favoured by wind support. Birds tracked above 3000 m asl at the radar stations of the present study had significantly higher average ground speeds than air speeds, indicating pronounced selection for wind support. This was most pronounced during spring migration in the trade-wind zone, but also above the western Mediterranean Sea, suggesting time minimization on return flights towards the breeding grounds (Bruderer and Peter 2017).

## Why can birds fly at high altitudes?

Extremely efficient cardiovascular and respiratory systems enable even non-migratory species to survive at altitudes with very low oxygen pressure and temperatures (review in Berthold 1996). Obvious decline of migratory intensity with altitude, and very low numbers of migrants between 5000 and 9000 m asl raise, however, questions about limiting conditions and physiological capacities of the birds. Combining our results with Pennycuick's (2008) overview of the aerodynamic and physiological background, we conclude the following:

The upper limit of migration is probably defined by the maximum height at which the birds can just get sufficient oxygen to fly at $V_{mr}$. This limit may be pushed upwards if wind support is so strong that birds would tend to fly close to their minimum power speed ($V_{mp}$), enabling them to reduce oxygen consumption.

Increasing flight altitude improves convective cooling, because a climb of 1000 m will on average provide a reduction in ambient temperature of about 6°. While convective cooling is free of cost, evaporative cooling requires water from the birds' body. The water-carrying capacity of the air decreases exponentially with decreasing temperature; therefore, evaporative cooling is more effective at high flight levels, but would need increasing amounts of water as long as birds are not able to control the water content of exhaled air: Besides variation of the frequency and depth of breathing, it seems that birds are able to control the air flux from the posterior air sacs through the lungs by contracting or dilating the diameter of the parabronchi (Pennycuick 2008 ). This would offer the possibility to divert a varying proportion of the inhaled air either through the lungs or directly through the primary bronchus to the anterior air sacs, thus favouring either gas exchange in the lungs or cooling only, according to actual needs. Engel et al. (2006) emphasized the crucial effect of exhaled air temperature for water economy. They found a high correlation between ambient and exhaled air temperature, and suggested that this might result from a temporal counter-current heat exchange in the nasal passages, as proposed by Jackson and Schmidt-Nielsen (1964).

# Conclusions and prospects

In the normal case (i.e. without orographic or meteorological distortions), height distribution of bird migration decreases at a high rate with altitude, with usually less than 10% of the birds found between 2000 and 4500 m asl, and only few birds climbing towards 6500 m. Altitudes of up to 9000 m are only reached under particular conditions. When crossing mountain ridges, the low-flying birds are forced upwards and often continue at the altitude reached while crossing. At least for nocturnal migrants in the trade-wind zone, wind support seems to be the most important factor for the altitude choice of nocturnal migrants even if they have to put up with stress factors like extremely high temperatures and low humidity. Concentrations of migrants at higher than normal flight levels are, however, also reported for spring migration in temperate regions under anticyclonic conditions with favourable winds high up.

Two types of radar data provided the basis for the present paper: (1) densities (of mainly) and frequencies (of exclusively) bird echoes integrated from various elevations of a pencil-beam radar provided information on the average number of targets per height interval of 200 m from 30 m up to about 4000 m above the radar. In spite of the fact that these data could also be used to show height distributions per night (Bruderer 1971), they were in the present case averaged over full seasons in order to balance the influence of short-term weather effects, thus providing site-specific information from different geographic regions. (2) In order to obtain exact information on the temporal and spatial appearance of targets (also at altitudes above 4000 m), we used the tracking method. Both methods had been automatized in recent years to eliminate bias by human operators (as long as no visual identification is aimed at).

Method (1) could in the near future be improved by combining the vertically aiming BirdScan MT1 (Bruderer et al. 2012, https://swiss-birdradar.com/birdscan-mt.html) with the new short-range/wide-angle radar BirdScan MR1 (https://swiss-birdradar.com/birdscan-mr.html) covering heights of about 40–1000 m, while the MT1 radar would cover heights between 200 m and 4000–6000 m (for birds of different size). Thanks to a slight rotation of the beam, the MR1 can also measure flight directions, a feature that could also be added to the MT1.

Operational weather radars provide less detailed information on the height distribution of migration, but due to their large range, continent-wide distribution and continuous recording, they can provide a general view of seasonal and day-to-day changes in the altitudinal distribution of migrants (Kemp et al. 2013; La Sorte et al. 2015). In the near future, we may expect to see vertical cross-sections through broad front movements along considerable parts of migratory routes, this in comparison with regional environmental condition.

Most promising novel information on en route variation of flight altitudes can be expected from individual tagging (of usually low numbers of individuals). Limiting factors are the weight and cost of transmitters, both considerably reduced in the case of loggers (but with the necessity to recover the loggers for downloading the data). Satellite telemetry using GPS transmitters are increasingly able to provide altitude information (of still relatively large birds). For smaller birds (even small passerines), the best research tools presently available are miniaturized multi-sensor loggers. Such equipment can record, e.g. time, light, temperature, magnetic field, acceleration, and air pressure, and can thus be used to measure the number and duration of flight bouts, the time and rate of climbing and descending, as well as the individual flight times spent at specific altitudes. It will now become possible to check or validate radar data on the altitude choice of night migrants in the trade-wind zone of Israel, on their time of climb-out, on climbing and descending rates at dawn and dusk, as well as throughout the night (Bruderer et al. 1995b). The first logger results received from small passerines and medium-sized non-passerines over a series of flight bouts from Europe to the wintering ranges in Africa seem prone to confirm not only this climbing and descending behaviour and preferred flight levels in Israel, but also the distribution of highest flights as reported in the present study (F. Liechti, pers. communication). The big advantage of loggers is that they provide species-specific information that can be associated with en route conditions.

suggestions for improvement. Franz Bairlein encouraged us to present our long-term studies in a review article. The studies comply with the laws of the countries in which they were performed. The authors declare that they have no conflicts of interest.

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