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Quantifying Migratory Bat Movements in Central Europe Across Seasons and Years Using a Vertical-Looking Radar

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ABSTRACT

Bat migration is an ecologically important yet poorly understood phenomenon. This is in part because monitoring these migrations is challenging, due to bats' nocturnal behaviors and their sometimes high-altitude migratory flights. This study presents the first radar-based examination of multi-annual migratory bat phenology in Europe, utilizing vertical-looking radar data collected on the Swabian Plateau in Germany between September 2019 and December 2022. Bat activity was consistently low in winter and increased gradually from March onwards to a peak between July and September. Across all years, pre-maternity migration began between late February and mid-March, while post-maternity migration ended between late October and mid-November. We estimated peak radar-based migration traffic rates between 1159 and 2473 bats per km, with the highest peak recorded on 4 July 2022. Correlations between radar-derived nightly bat numbers and simultaneously acquired acoustic recordings ranged from 0.47 to 0.70 for the pre-maternity season, and from 0.14 to 0.71 during post-maternity migration. Both monitoring techniques showed peak bat activity during the summer, with smaller surges in September and October. The radar, however, detected significantly more bats overall. These findings showcase how vertical-looking radars can be used to quantify and characterize seasonal variability in high-altitude bat movements. Through strategic future radar deployments and the analysis of available historical datasets, our current understanding of migratory bat seasonality, routes, and intensity could increase drastically, and underpin the development of effective protocols for biodiversity conservation.

ABSTRAKT

Die Migration der Fledermäuse ist ein ökologisch wichtiges, aber noch wenig verstandenes Phänomen. Dies liegt zum Teil daran, dass die Überwachung der Flugbewegungen schwierig ist, da Fledermäuse nachtaktiv und häufig in großer Höhe unterwegs sind. Diese Studie präsentiert die erste radarbasierteUntersuchung von mehrjährig erfassten phänologischen Mustern ziehender Fledermäuse in Europa. Die Daten wurden mit einem vertikal ausgerichteten Radargerät erhoben, das zwischen September 2019 und Dezember 2022 in Deutschland auf der Schwäbischen Alb in Betrieb war. Die Fledermausaktivität war im Winter durchwegs gering und nahm ab März allmählich zu, mit einem Höhepunkt zwischen Juli und September. In allen Jahren begann die prä-maternale Wanderung zwischen Ende Februar und Mitte März, während die post-maternale Wanderung zwischen Ende Oktober und Mitte November endete.

Birgen Haest and Baptiste Schmid shared last authorship.

Wir ermittelten nächtliche Fledermausaktivitätspeaks zwischen 1159 und 2473 Fledermäusen pro Kilometer, wobei der höchste Wert am 4. Juli 2022 registriert wurde. Korrelationen zwischen radarerfassten nächtlichen Fledermauszahlen und gleichzeitig aufgezeichneten akustischen Daten lagen in der prä-maternalen Saison zwischen 0.47 und 0.70, und während der post-maternalen Wanderung zwischen 0.14 und 0.71. Beide Überwachungstechniken registrierten im Sommer die höchste Fledermausaktivität, mit kleineren Anstiegen im September und Oktober. Das Radar detektierte jedoch insgesamt deutlich mehr Fledermäuse. Diese Ergebnisse zeigen, wie vertikal ausgerichtete Radare verwendet werden können, um die saisonale Variabilität von Fledermausbewegungen in großer Höhe zu quantifizieren und zu charakterisieren. Durch eine strategische Platzierung von Radargeräten und die Analyse verfügbarer historischer Datensätze könnte unser derzeitiges Verständnis der Saisonalität, des Verlaufs der Zugwege und der Anzahlen wandernder Fledermäuse erheblich erweitert werden, sowie die Entwicklung wirksamer Artenschutzprotokolle unterstützen.

1 | Introduction

Each year, tons of insects, birds, and bats migrate through the skies in search of seasonally favorable habitats matching the respective phase of their annual cycle. Bats are particularly difficult to study due to their cryptic nocturnal behavior, and as a result, information on the intensity and seasonality of their migratory movements remains limited. Of Europe's 47 bat species, 14 are migratory, with six classified as long-distance migrants, that is, covering over 1000 km during seasonal flights (Fleming et al. 2003; Fleming and Eby 2005; Froidevaux et al. 2023). These include the three *Nyctalus* species present in Europe, being the common noctule *N. noctula*, the Leisler's noctule *N. leisleri*, and the greater noctule *N. lasiopterus*, the parti-colored bat *Vespertilio murinus*, the common pipistrelle *Pipistrellus*, and Nathusius' pipistrelle *Pipistrellus nathusii*. All European bat species are protected under EU Directive 92/43/EEC (Council Directive 92/43/EEC 1992, Annex IV), as they are listed in Annex IV, which ensures strict protection across EU member states. Successfully conserving these species, however, requires a thorough understanding of the time and location of their migratory movements (Wieringa et al. 2021; Lagerveld et al. 2023).

Bats migrate at night, including often at high altitudes (McCracken et al. 2008), and without producing sounds audible to the human ear, making them cryptic species that can only be effectively studied using specialized equipment. Commonly used approaches to study bat migration include tracking individual bats using radio telemetry (Dechmann et al. 2014; Bach et al. 2022), GPS (Weller et al. 2016; Vasenkov et al. 2023), and isotope analysis (Sullivan et al. 2012; Cryan et al. 2014), with more recent developments including the use of miniaturized IoT tags (Hurme et al. 2025). These methods have revealed important aspects of bat migration, such as migratory routes, timing, stopover behavior, and individual movement patterns. However, they pose significant challenges for conducting comprehensive, large-scale analyses, as these would require a logistically challenging number of tracking devices, capture events, and/or laboratory analyses (Werber, Sextin, et al. 2023). They also do not allow quantifying migratory intensity, nor provide detailed information on the flight altitude of migratory bats—an important aspect of their migration ecology that remains poorly understood (Hüppop and Hill 2016; Brabant et al. 2020). Bioacoustics, specifically through the use of bat detectors, captures the echolocation calls emitted by bats during flight. While these recordings do not allow for precise estimates of absolute bat numbers, they can be used to assess relative abundance over time or across different locations and, in some cases, altitude layers, when detectors are deployed on aerial platforms (Russo and Jones 2003; Kotila et al. 2023; Werber, Hareli, et al. 2023). In most cases, they also enable the identification of individual species (Russo and Voigt 2016). A main limitation, however, lies in the restricted detection range of the equipment, which typically is only a few tens of meters and almost never exceeds 100 m (Adams et al. 2012). Given the presumed high-altitude migratory bat movements (McCracken et al. 2008; O'Mara et al. 2021), a substantial portion of migrating bats could hence go undetected using acoustics (Hüppop and Hill 2016). Moreover, foraging flights of non-migratory bats further complicate quantifying migratory intensity (O'Mara et al. 2019). Mist netting faces similar limitations, particularly in terms of quantifying migratory intensity and enabling continuous, long-term monitoring; as well as being unsuitable for high-altitude movements. Additionally, it quickly becomes highly resource-intensive (Caprio et al. 2020).

Weather radars have occasionally been used, particularly in the USA, to quantify and study the seasonal abundance of migratory bats (Horn and Kunz 2008; Stepanian et al. 2018; Haest et al. 2021). Weather surveillance radars are continuously operated and collect data on aerial animal movements over several tens of kilometers around their location, creating huge potential for the continuous quantification of migratory bat movements (Shamoun-Baranes et al. 2022; Bauer et al. 2019). The taxonomic detail it can provide, however, remains very limited (Hüppop et al. 2019), with efforts still ongoing to automatically and continuously discern birds, insects, and bats (Gauthreaux and Diehl 2020; Jatau et al. 2021; Hu et al. 2024). Unlike weather radars, vertical-looking radars offer greater potential for distinguishing among broad taxonomic groups, due to their ability to record detailed information on individual animals. These systems can also cover a substantial altitude range—typically up to around 2000 m above ground level (AGL), depending on the target's size (Schmid et al. 2019) —and enable the classification of detected targets into a few general categories (or “classes”) mirroring taxonomic groups (Schmid et al. 2019; Giuntini et al. 2024). Vertical-looking radars have traditionally been used to monitor migratory insect and bird movements. Their application to bats, however, remains limited. Bat passages through vertical-looking radar beams were first described by Bruderer and Popa-Lisseanu (2005), but only recently a dedicated radar study explored quantifying and characterizing the seasonal phenology of high-flying bats in Israel (Werber, Sextin, et al. 2023).

Here, we describe, for the first time in Europe, the migratory phenology of bats as measured by a vertical-looking radar. We quantified the number of bats migrating over our study location in the Swabian Alps plateau (Germany) from September 2019 to December 2022, and defined migratory periods based on the seasonal pattern of bat traffic and on abrupt shifts in smoothed flight directions identified through changepoint analysis. We also compared the nightly migratory phenology estimated through radar with those of acoustic recordings in the same area.

2 | Methods

2.1 | Radar Data

Radar monitoring was carried out using a vertical-looking radar placed at the edge of the plateau of the Swabian Alb (Donzdorf, Germany, 48.666695° N, 9.834278° E; Figure 1). The BirdScan MR1 (manufactured by Swiss Birdradar Solutions AG) is a 25 kW X-band (9.4 GHz, 3.2 cm wavelength) pulse radar equipped with a custom-designed vertical-looking horn antenna, rotating with a 2° nutation on its vertical axis. The nominal beam width at 3 dB is approximately 17.5°. The detection range depends on the pulse duration and the size of the target (Schmid et al. 2019). In this study, the device operated in short pulse mode, with a pulse length of 75 ns and pulse repetition frequency of 1800 Hz, providing an approximate detection range for bats from 50 m up to about 1000 m above the radar. The radar collected data from 12 September 2019 to 31 December 2022 but was inactive due to technical issues from 12 July to 7 August in 2020, from 18 July to 31 July and from 8 to 14 September in 2021, and from 5 October to 2 November in 2022 (Figure 1).

For each animal flying through the radar beam, the temporal reflectivity pattern is analyzed to extract information related to the size, wing-flapping pattern, and shape of the animal (Schmid et al. 2019). Using a reference dataset of identified radar samples (Haest et al. 2021), echoes are automatically classified into broad categories ("classes") corresponding to taxonomic groups such as insects, bats, and different bird categories (passerine-type, wader-type, swift-type, large birds, and unidentified other birds). Using the *birdscanR* R package (Haest, Hertner, et al. 2024), we filtered the radar data to retain only echoes classified as "bat" with a classification probability higher than 0.8. We chose this conservative approach with a rather high classification threshold to strongly reduce the likelihood of including misidentified animals from other taxonomic groups. Only echoes registered between 15:00 UTC and 07:00 UTC were retained: This time window fully encompasses the nocturnal period throughout the study season at the study latitude and was selected to ensure consistency with the temporal coverage of the acoustic recordings. To standardize the spatial unit of the radar counts, we converted them into nightly bat traffic rates (bats*km^{-1}*night^{-1}), a direction-independent version (Haest, Liechti, et al. 2024) of migration traffic rates (Lowery 1951; Liechti et al. 1995).

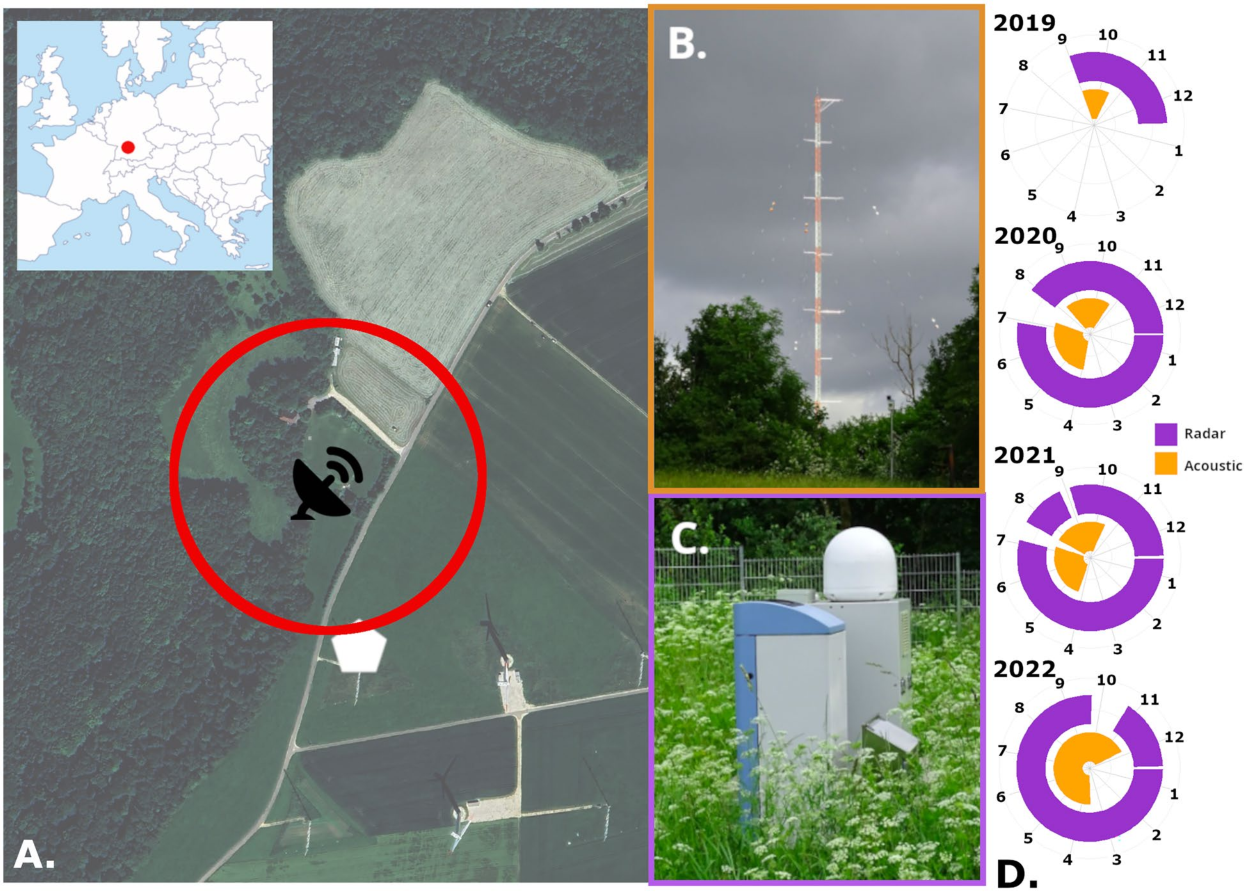

FIGURE 1 | (A) Location of the BirdScan MR1 radar device (black symbol) and of the meteorological mast equipped with bat detectors (white symbol) on the Swabian Alps plateau (Germany). The red circle highlights the radar's approximate detection range, with a maximum diameter of ca. 300 m at 800 m agl. (B) The meteorological mast housing bat detectors at 65 and 95 m agl. (C) The BirdScan MR1 radar. (D) Radar data acquisition periods (purple) and acoustic data acquisition periods (orange) across the four years analyzed. Month labels, represented by numbers, are positioned at the midpoint of each month.

2.2 | Acoustic Data

Acoustic detectors were deployed on a 100 m high meteorological mast, located at a distance of about 170 m south–southeast (48.665194° N, 9.834767° E) from the Birdscan MR1 radar (Figure 1). Acoustic data were collected using the bat detector system BATmode S+ (bat bioacoustictechnology GmbH). The Batmode S+ system records bat call sequences and saves them in high quality (300 kHz, 16 bit). A recording control system largely eliminates background noise. The recording parameters of the BATmode S+ system, which is based on the Avisoft system (Avisoft Bioacoustics), were set according to the specifications of the research project by Behr et al. (2016). The trigger threshold was set to 37 dB. With the BATmode S+ system, the post-trigger is controlled via a hold time of 1 s, which means that the entire series of calls of one individual, for example, of the common noctule, are recorded in one recording. In order to get the bat species composition and to filter out non-bat-calls, all acoustic signals were manually labeled by a bat specialist from the Freiburger Institut für angewandte Tierökologie GmbH (FrInaT) using the BATscreen PRO program (version 2.0.1, January 15, 2019) from bioacoustictechnology GmbH.

Data were collected throughout each night, from 15:00 UTC to 07:00 UTC the following day, from 12 September to 28 October in 2019, from 11 April to 4 November in 2020, from 21 April to 27 October in 2021, and from 31 March to 5 December in 2022. Technical issues prevented the bat detectors from recording data between 22 July and 19 August 2020 (Figure 1). Bat detectors were installed at various heights (5, 10, 35, 65, and 95 m above ground level), but only the data recorded at 65 and 95 m were kept to exclude local foraging bats and focus on migrating individuals. We summed the number of bat call sequences per night for comparison with the radar-derived nightly bat traffic rates (Figure 2). To ensure that the same calls were not recorded twice by both devices, we examined a subset of the raw data and calculated the proportion of recordings detected at exactly the same time on both recorders. The mean proportion of potential duplicate recordings was 2.45% (SD = 0.81%). As this likely represents an overestimate, we considered it negligible.

2.3 | Estimating Migratory Bat Seasons

We determined pre- and post-maternity migration timing of each year using a combination of the nightly bat traffic rates and flight directions. We defined the onset of pre-maternity migration as the first night of each year on which the cumulative radar bat traffic, calculated forward in time, reached 10% of the total spring traffic. Conversely, the end of post-maternity migration was defined as the first night on which the cumulative traffic, calculated backward in time from the end of the autumn season, reached 10% of the total autumn traffic. Due to consistently high flight activity in summer, changes in abundance did not clearly indicate the end of pre-maternity or the start of post-maternity migration. Instead, we estimated the nightly mean flight direction using the R package *circular* (Agostinelli and Lund 2017), and then applied a 60-day moving circular average to these nightly means to obtain smooth temporal trends. The 60-day period for the moving average analysis was decided on using visual inspection of the smoothed temporal trend as being the minimal period resulting in an overall smooth seasonal trend line, that is, removing the short-term, within-night variation. Short-term, night-to-night variability was not excluded but was reduced through the moving circular averaging procedure. For each night, we also calculated the Rayleigh r statistic to quantify the strength of directional consistency among bats (vector length), again using the circular package. This smoothed temporal time series of mean nightly flight directions was then converted to a time series of the successive nightly rates of directional change, that is, the difference between the smoothed direction of that night and the night before. To identify the timing of seasonal shifts in flight direction, we then applied the *cpt.meanvar()* function from the *changepoint* R package (Killick and Eckley 2014) to this time series of directional change. In 2019, radar measurements only started when the post-maternity migratory season was well on its way, so only the end date of the post-maternity migration could be identified. All analyses were conducted using R (R Core Team 2023).

2.4 | Comparison of Phenologies Derived From Radar and Acoustics

We assessed the correspondence between nightly abundances estimated from radar and acoustic data using Pearson correlations. Correlations were calculated separately for each migratory season and also for the summer (non-migratory) maternity season. These comparisons were only performed for periods during which data from both sources were available (Figures 4 and S1).

3 | Results

3.1 | Radar-Based Quantification of Migratory Bats Across the Year

The radar-derived bat flight activity showed a similar seasonal pattern across all years: bat activity was minimal in winter (December–February), remained relatively low but gradually increased in spring and early summer (March–June), and then rose sharply from early July to a peak between July and late August. After the summer peak, bat traffic gradually declined during October and November, reaching its lowest levels again by December (Figure 2).

Notwithstanding this general seasonal pattern, the precise timing and strength of peak activity differed substantially between years. In early 2020, bat traffic rates remained low until mid-February, then gradually increased in March and reached average levels of 31 bats·km^{-1}·night^{-1} in April and 70 bats·km^{-1}·night^{-1} in May, remaining relatively stable until June. Flight activity was highest in July (during maternity season) and late August (post-maternity season), with maxima of 1159 bats·km^{-1}·night^{-1} on 7 July 2020, 1455 bats·km^{-1}·night^{-1} on 31 August 2021, and 2473 bats·km^{-1}·night^{-1} on 4 July 2022. In 2021, the overall flight activity pattern was shifted towards later in the year compared to 2020 and 2022. In 2019, radar

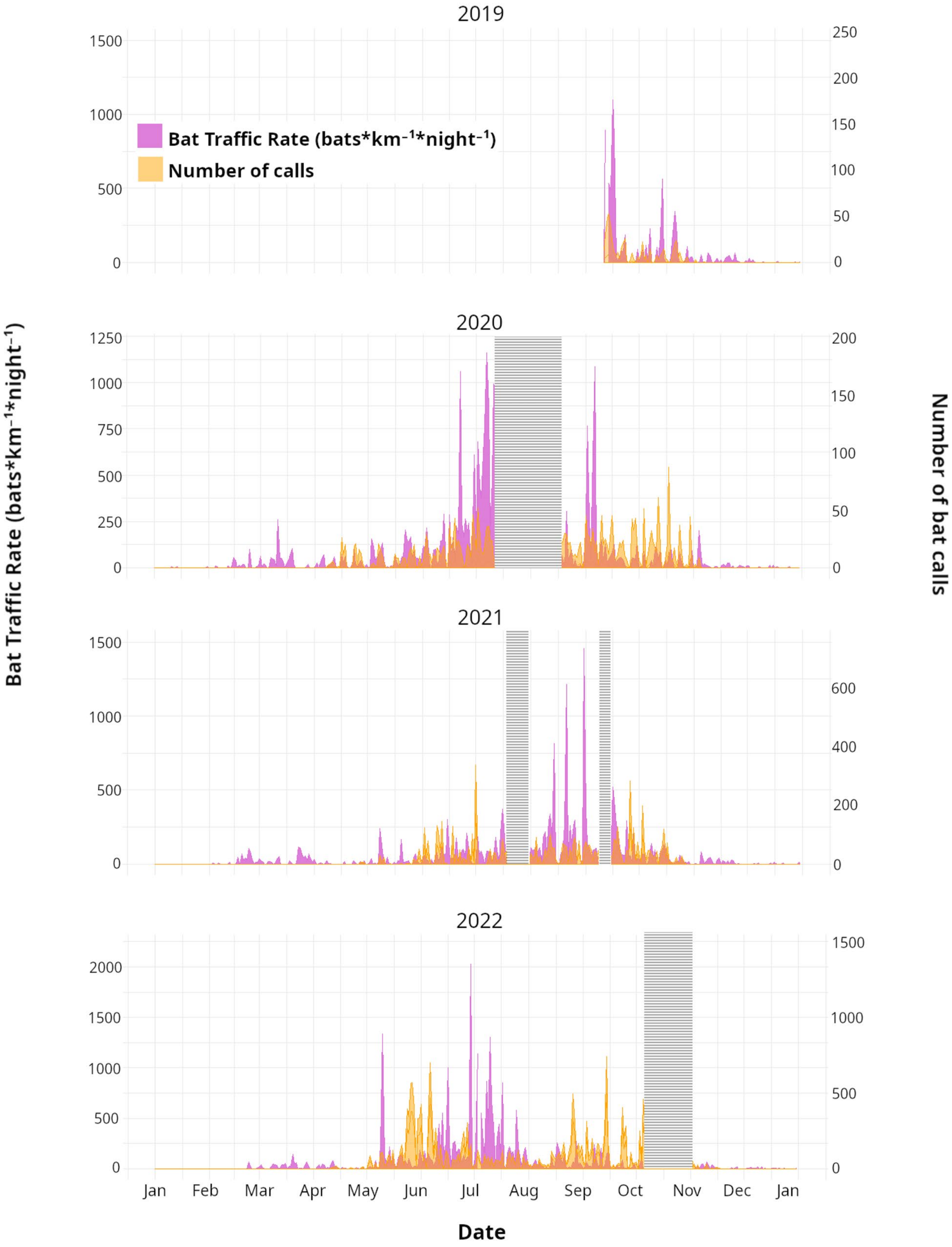

FIGURE 2 | Nightly bat traffic rates (purple) and number of bat calls (orange) recorded in the study area from autumn 2019 until 31 December 2022. Grey bands indicate times of missing radar data.

data were only available during the post-maternity season (August–late November), with a total of 8887 bats·km^{-1}. The other seasonal migration totals for each year are reported in Table 1 and Figure S2. The mean flight altitude measured across the different years consistently remained around 500 m AGL (SD ≈ 200 m; Table S1).

TABLE 1 | Seasonal bat traffic (expressed in bats·km^{-1}) for each year and migratory season.

	Pre-maternity	Summer	Post-maternity
2019	—	—	8887
2020	2500	11,977	6850
2021	2236	5917	10,969
2022	1376	12,457	12,142

Note: Seasons were defined following the criteria described in the Methods Section 2.3. A dash (—) indicates periods not covered by radar monitoring.

3.2 | Pre- and Post-Maternity Migratory Bat Seasons

Across all three years, a consistent northeastern flight direction was observed from early in the year until mid-May. In contrast, a pronounced southwest direction was evident in the latter part of the year, beginning around mid-August in 2020 and 2021, and approximately one month earlier in 2022. Movement directions during the identified maternity season showed no consistent pattern, while nightly Rayleigh r-values indicated that pre- and post-maternity flights were highly directed, in contrast to largely random movements during the summer maternity season (Figure 3B). Across all years, bats exhibited a stable northeasterly flight orientation during spring, followed by a predominantly southwesterly orientation later in the year (Figure 3A).

To objectively delineate the transition between these seasonal movement phases, we applied a changepoint analysis to the time series of nightly mean flight directions (see Methods 2.3). This analysis detected an abrupt positive shift marking the end of pre-maternity migration and the onset of a stable northeast orientation, and a later negative shift indicating the beginning of post-maternity migration, followed by stabilization towards a southwestern direction. The pre-maternity migration period consistently started between late February and mid-March, while post-maternity migration ended between late October and mid-November in all three years (Figure 4 and Table S2). In 2020, pre-maternity migration started on 24 February, in 2021 on 21 February, and in 2022 on 14 March. Post-maternity migration ended on 25 October in 2020, 17 November in 2021, and 8 November in 2022. In 2020, summer maternity season extended between 15 May and 10 August; in 2021, between 27 May and 12 August; and in 2022, between 9 May and 5 July (Figures 3B and 4; Table S2).

3.3 | Acoustically Derived Bat Migration Phenology

Bat call activity generally rose in spring (April–May), peaked in summer (June–September) and, after a second peak between late September and early October, subsequently declined in autumn (October–November). In 2019, the number of calls recorded was relatively high in September, with an average of 17.8 calls per night, before dropping to 8 calls per night in October and stabilizing around 2 calls per night in November. The highest number of bat calls (53 calls) was recorded on the night of 14 September. In 2020, the first calls were recorded on the night of 11 April (6 calls), with a monthly average of 10.4 calls per night. This average increased to 16.7 in June and 25.2 in July, remaining relatively stable until October. The night with the highest number of calls recorded in 2020 (87 calls) was 18 October. In 2021, the average number of bat calls per month remained below 10 until June, with a rapid increase to 37 bat calls per night. Monthly average values remain high (38–39 calls per night) in July and August, peaking in September (69 calls per night), before dropping back to around 30 bat calls per night in October. The night with the highest number of calls recorded was 1 July (336 calls). Finally, in 2022, the number of calling bats recorded was significantly higher than in previous years. Bat activity was already relatively high by late May (with an average of 138 calls per night), and peaks of around 600 bats per night were observed in both June and September. The highest count, 740 bats, was recorded on the night of 14 September (Figure 2).

Overall, 45% of the recorded activity was attributed to species belonging to the Nyctaloid group (including possible species such as *Nyctalus leisleri*, *Nyctalus noctula*, *Eptesicus serotinus*, *Eptesicus nilssoni*, and *Vespertilio murinus*). A further 27% of records were assigned specifically to *Nyctalus noctula*, followed by 25% to *Pipistrellus pipistrellus*. Smaller proportions included 2% *Pipistrellus nathusius* and 1% unidentified pipistrelloids.

3.4 | Comparison of Radar- and Acoustics-Derived Migratory Bat Numbers

The radar and acoustic bat numbers were significantly correlated for the post-maternity period in 2019 (Pearson's $r = 0.71$), pre-maternity in 2020 (Pearson's $r = 0.47$), 2021 ($r = 0.60$), and 2022 ($r = 0.70$), and non-migratory period in 2020 ($r = 0.45$, Figures 4 and S1). Corresponding linear regression slopes (β_1) were positive in these periods, ranging from 2.6 to 19, indicating that while nightly acoustic call counts increased with radar-derived bat numbers, radar-estimated abundances were up to 20 times higher, primarily due to the substantially larger detection range of radar compared to acoustic sensors (Figure S1).

4 | Discussion

Using a vertical-looking radar, we estimated the number of migratory bats and characterized the migration phenology across more than 3 years at a location in the Swabian Alps in Germany. Pre-maternity migration started between mid-February and March and ended between mid and late May. Post-maternity migration started around July–early August and ended in November. Consistent with prior studies, bat abundance during spring migration was lower than in summer-autumn (Furmankiewicz 2003; Rydell et al. 2014; Hüppop and Hill 2016; Bartonička et al. 2019). Pre-maternity migration ranged from about 1400 to 2500 bats·km^{-1}·season^{-1}, while post-maternity migration totals were higher, between 6800 and 12,000 bats·km^{-1}·season^{-1}. Summer totals were even higher (up to about 15,000 bats·km^{-1}·season^{-1}), which is to be

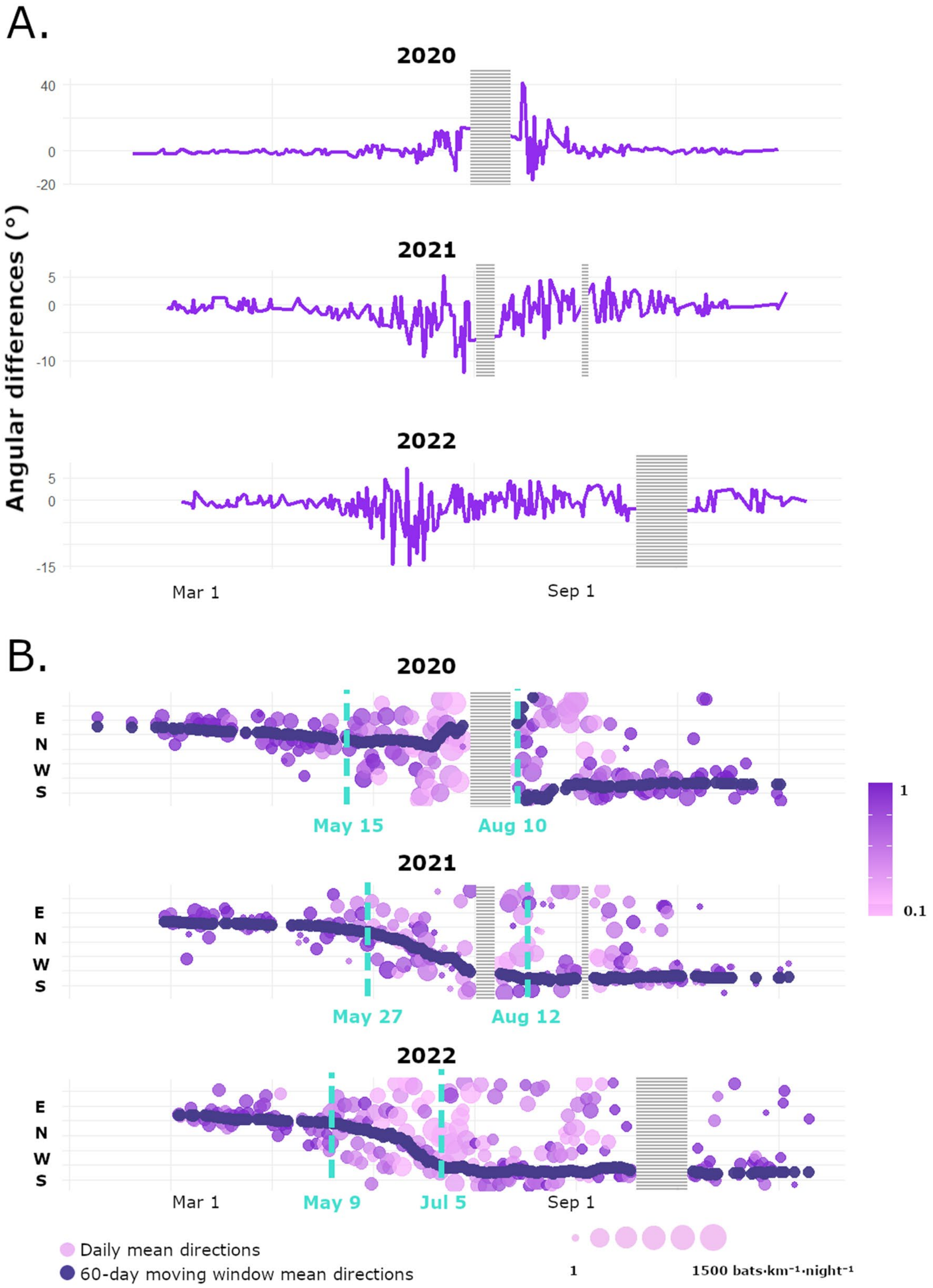

FIGURE 3 | (A) Circular angular differences in mean flight direction (Δ°) across the study years (2020–2022), based on daily data smoothed with a 60-day moving average. Each line represents the magnitude of directional change between consecutive days, computed with respect to circularity. Peaks in the violet lines correspond to periods of abrupt directional shifts, whereas flatter segments indicate directional stability. Grey bands cover periods of missing data. (B) Average nightly flight directions of bat radar echoes recorded in 2020, 2021, and 2022. Pink/purple dots represent nightly mean directions, with dot size proportional to bat traffic rate and dot color intensity indicating the Rayleigh r value (strength of directionality) for that night. Dark purple lines show the 60-day moving average of the mean direction. Vertical turquoise dotted lines indicate changepoint days used to mark the end of pre-maternity migration and the beginning of post-maternity migration. Grey bands represent periods with missing radar data.

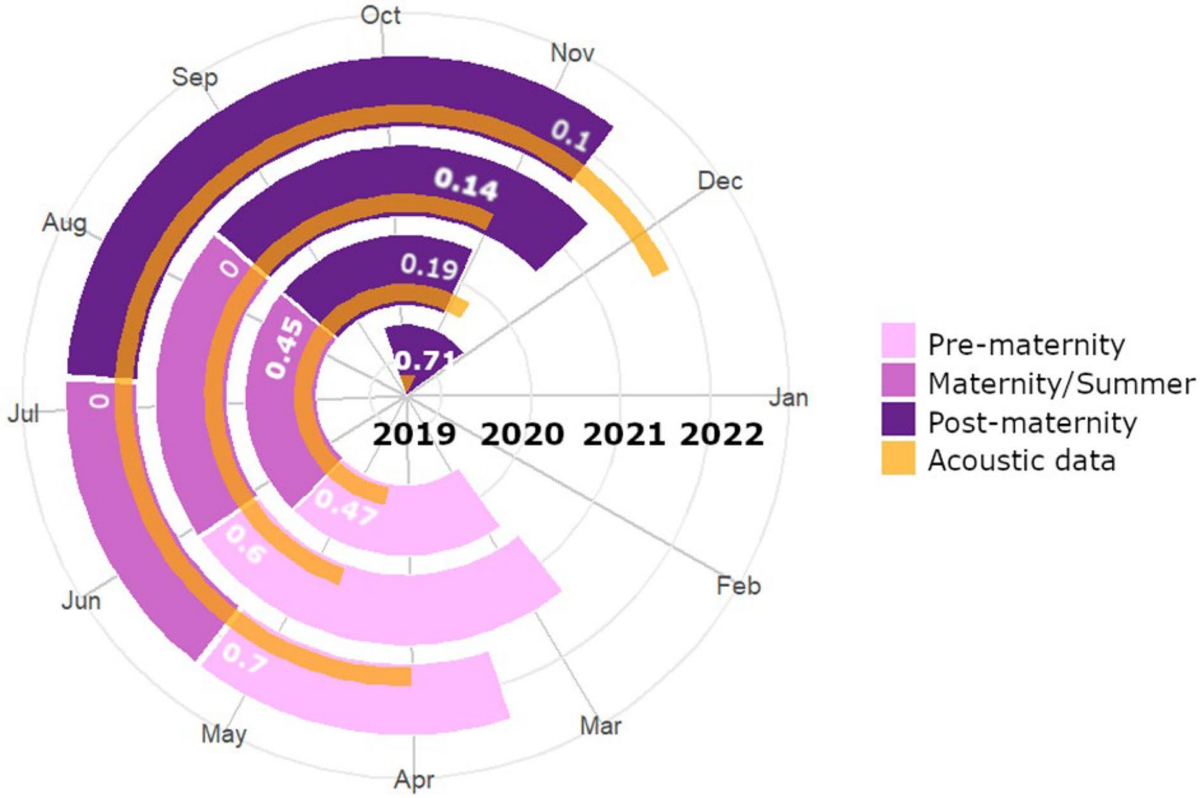

FIGURE 4 | Phenology of the pre- and post-maternity migration seasons and the non-migratory season derived from radar data (shades of purple), shown alongside the periods of acoustic monitoring (in orange). Overlaid numbers indicate Pearson correlation coefficients calculated between radar and acoustic data for the different seasons. In 2019, data availability limited the estimation to the end of the post-maternity migration season.

expected given these are more likely to be foraging flights that will lead to a single individual being detected repeatedly during and across nights. The summer of 2021, however, showed rather low numbers, for unknown reasons (Table 1). Nightly peak traffic varied between 1150 and 2470 bats·km^{-1}·night^{-1}, depending on the year: for context, these values are substantially lower than migration traffic rates typically reported for nocturnal bird migration at similar latitudes, which often reach average values of several hundred to over a thousand individuals km^{-1} h^{-1} (Nilsson et al. 2019; Giuntini et al. 2022; Hirschhofer et al. 2024). The occasional presence of bats in the radar data during the winter period is most likely attributable to classification errors by the radar algorithm. However, winter activity of bats at this latitude, while rare, has been previously documented (Zahn and Kriner 2016; Spitzenberger et al. 2023), and the rarity of these detections overall attests to the generally high accuracy of the classifier. Also, nightly Rayleigh *r*-values confirmed that flights during pre- and post-maternity migration were highly directed, whereas movement during the summer maternity season was largely random. This not only further supports the robustness of our radar-based monitoring, but also validates the approach used to define pre- and post-maternity migration periods.

The migratory directions we observed aligned with typical migration routes in Central Europe (Alcalde et al. 2020; Vasenkov et al. 2023). Most current information on European bat migration timing is based on acoustic monitoring or mist netting (Furmankiewicz 2003; Gukasova and Vlaschenko 2011; Rydell et al. 2014; Heim et al. 2016; Hüppop and Hill 2016; Bartonička et al. 2019; Caprio et al. 2020; Lagerveld et al. 2023). Pre-maternity migration in Central Europe generally extends from mid-April to early June (Rydell et al. 2014; Heim et al. 2016; Hüppop and Hill 2016; Hurme et al. 2025). While our observations align with this range, we detected earlier movements beginning in mid-February, suggesting again potential regional variations or the ability of radar to detect bat movements that other monitoring methods might miss. In any case, previous research indicates that migration timing varies annually by about 10 days (Rydell et al. 2014), and peak vocal activity can differ by up to three weeks across sites (Bartonička et al. 2019). In our study, the onset of pre-maternity migration happened at similar times of the year in 2020 and 2021 but about three weeks later in 2022. In 2021, pre-maternity migration ended about 20 days later than in 2020 and 2022 (Figure 4 and Table S2). Post-maternity migration began roughly a month earlier in 2022 than in previous years and lasted 20 days longer in 2021 (Figure 4 and Table S2). Assuming that a 10-day interannual variation is expected (Rydell et al. 2014), the 20+ day discrepancies—if not an artefact due to gaps in data collection (Figures 2 and 3)—could reflect actual shifts in migration timing influenced by factors such as air pressure, wind patterns, and temperature fluctuations (Dechmann et al. 2017; Haest et al. 2021; Lagerveld et al. 2021; Hurme et al. 2025). Beyond migration timing, although mean flight altitudes observed by radar were consistently around 500 m AGL (Table S1), we did not explore seasonal differences in greater detail, as radar detection probability is size-dependent and changes in species composition may bias average observed altitudes independently of true behavioral shifts.

In Central Europe, post-maternity migration typically begins around mid-August. For instance, Nathusius' pipistrelle along the southern North Sea coast peaks in early September and continues until mid-October (Lagerveld et al. 2023). Similar timings have been observed in Germany, where post-maternity migration of *Pipistrellus nathusii* begins in mid-August, peaks in early to mid-September, and continues until mid-October, while Nyctalus species migrate from late August to early September, with peak abundance in September and ongoing movement throughout autumn (Meschede et al. 2017). Comparable patterns have also been documented in other regions (Furmankiewicz 2003; Heim et al. 2016), including offshore platforms (Hüppop and Hill 2016). Our data suggest a slightly later timing of post-maternity migration, possibly due to our site's lower latitude or may result from pooling all species together: later-migrating species in our dataset could shift the overall seasonal peak.

Despite consistent overall trends, bat traffic was generally higher in 2022. Since this is the first European radar-based study of migratory bat traffic, direct comparisons with broader trends are not possible. However, fluctuations in bat abundance—with differences of up to 50% between years in some species (Bernard et al. 2019)—may result from population changes, as bats' long lifespan and low reproductive rates make them particularly vulnerable to variations in adult mortality (Ijäs et al. 2017). Additionally, because we only monitored a single site, changes in migratory routes could also strongly contribute to these divergences in single location counts (Lehnert et al. 2018; Russo and Jones 2003).

Our study also revealed differences in migration phenology depending on the method used. While radar and acoustic monitoring showed similar trends during certain periods, their correlation was inconsistent across all seasons. Similarly low correlations were reported in the only other study attempting to match X-band radar data with acoustic bat detections, although the radar type and setting differed slightly (Krapivnitckaia et al. 2024). This discrepancy likely stems from the fundamental differences between the two techniques. Radar detects echoes from flying bats over a somewhat broader spatial and especially altitudinal range but cannot register individuals flying below 50 m. In contrast, acoustic detectors, though species-specific, have a more limited detection range and are influenced by environmental conditions such as temperature and humidity, which can affect sound propagation, potentially leading to under- or overestimation of bat numbers (Goerlitz 2018). Changes in flight altitude due to weather (Cryan and Barclay 2009) or behavioral factors, such as increased autumn mating activity (Staton and Poulton 2012; Browning et al. 2021), could further explain the observed differences.

The two methods also might capture different types of bat movements. While radar likely detects higher-altitude migration, acoustic monitoring might register local foraging activity, especially if migrating bats emit fewer calls than non-migrating individuals (Cryan and Barclay 2009). Citizen science data (Observation International 2024) support this interpretation, as bat records from online platforms align more closely with radar observations. These records, spanning 15 years for *P. pipistrellus, P. nathusii, N. noctula*, and *N. leisleri*, follow an approximate normal distribution with a peak in July. Notably, the first individuals were recorded as early as February, consistent with our radar-based findings (Figure S3).

Both methods have their strengths and limitations to capture migratory bat information. Radar provides flight direction, aiding in defining migration periods, and has the potential to measure flight speed and altitude, but so far still lacks taxonomic detail. Acoustic monitoring does allow for species-specific detections, but the range of detection is rather limited and is strongly sensitive to environmental conditions (Russo and Voigt 2016), complicating accurate quantification (Béasse et al. 2025). When possible, integrating both techniques, hence, would enable extracting more accurate and complete migratory bat estimates (Werber, Hareli, et al. 2023; Giuntini et al. 2024).

All migratory bat species found in Europe, except for the greater noctule, have been reported in or near the study area (Biosphärengebiet Schwäbische Alb 2019; Musiol et al. 2023; Printz and Jung 2023). Obtaining an accurate understanding of bat migration is essential, particularly considering that all these species are protected under EU legislation. These bats face significant threats, including low reproductive rates, habitat loss, and the impacts of climate change (Frick et al. 2020). This need becomes even more pressing in light of the ongoing rapid expansion of wind farms. While wind energy is an efficient and sustainable solution for the energy transition, it may also pose significant risks to bat conservation (Lehnert et al. 2014; Gaultier et al. 2020). By integrating radar-based monitoring with acoustic methods, future studies could leverage the strengths of both techniques to achieve a more comprehensive understanding of bat migration dynamics. This combined approach could not only enhance species-specific monitoring but also provide critical insights into flight altitudes and behaviors, offering valuable tools for target-tailored conservation strategies.

Author Contributions

Silvia Giuntini: conceptualization, formal analysis, investigation, methodology, project administration, software, validation, visualization, writing – original draft, writing – review and editing. **Janine Aschwanden:** data curation, funding acquisition, project administration, resources, validation, visualization, writing – review and editing. **Damiano G. Preatoni:** writing – review and editing, funding acquisition. **Fabian Hertner:** software, writing – review and editing. **Birgen Haest:** conceptualization, data curation, funding acquisition, formal analysis, investigation, methodology, resources, supervision, software, validation, project administration, writing – review and editing, visualization. **Baptiste Schmid:** conceptualization, methodology, software, investigation, validation, formal analysis, supervision, funding acquisition, visualization, project administration, writing – review and editing.

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Data Availability Statement

The acoustic and radar bat migration traffic rate datasets are available on Zenodo: https://zenodo.org/communities/vora/records.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Scatter plots of the relationships between nightly bat call counts and bat MTR by season. The turquoise line represents the linear regression fitted to the data used to calculate the Pearson correlation, with its regression coefficient (β_1) top right in each panel. **Figure S2:** Cumulative nightly migration traffic rates (MTR) of bats across the study years (2019–2022) and three seasonal periods (pre-maternity, maternity, post-maternity). Each line represents the cumulative sum of nightly MTR for a given year within the defined season. Horizontal dashed grey lines indicate the total cumulative MTR at the end of each season. **Figure S3:** Seasonal distribution of bat records from the citizen science platform Observation International (observation-international.org) for *P. pipistrellus*, *P. nathusii*, *N. noctula*, and *N. leisleri* over a 15-year period. The x-axis represents months of the year, and the y-axis shows the number of records. **Table S1:** Mean flight altitude, in meters above ground level (AGL), of bat echoes detected by radar, with corresponding standard deviation. **Table S2:** Phenology of the pre- and post-maternity migration season and non-migratory season derived from radar data. In 2019, data availability limited the estimation to the end of the post-maternity migration season.