Full-season spring migration counts reveal seasonal contrasts in raptor migration through the eastern Black Sea Flyway

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The extent to which geographical features like coastlines and mountain ranges funnel migrating birds depends on the seasonal context and direction of migration. Near Batumi, in the Republic of Georgia, the eastern Black Sea coast and Lesser Caucasus funnel over one million raptors through a 10–20 km wide coastal strip every autumn. The funnelling effect of the Lesser Caucasus appears much less evident for northbound migrants. Yet historical data suggest tens of thousands of raptors pass through the region in spring. To elucidate the composition and timing of spring raptor migration we conducted full-season migration surveys near Batumi in 2019, 2020 and 2022. In total, we recorded 33 species and, on average, counted 542,161 raptors (range: 455,799–618,848) annually. The bulk of the spring passage consisted of Black Kite *Milvus migrans* (239,649 ± 22,547 SD) and Steppe Buzzard *Buteo buteo vulpinus* (194,029 ± 102,702). The most diverse and intense spring migration occurred from late March through mid-April when the median passage date of 12 of 15 common species (>100 individuals/year) occurred. Species with longer autumn migration periods tended to have longer spring migration periods, and most species had a longer migration period in spring than in autumn, likely due to larger age differences in timing during spring. Species' abundance was up to an order of magnitude lower in spring than in autumn, consistent with a weaker bottleneck-effect in spring. Nevertheless, our results confirm the eastern Black Sea coast as a principal spring flyway and help redraw the map of East African-Eurasian migration for several Palearctic raptors. Our data provides a baseline for detecting changes in raptor migration through short-term surveys and can help plan migration-based conservation and research at Batumi in spring.

Key words: East African-Eurasian Flyway, monitoring, Caucasus, Batumi Raptor Count, soaring migrants

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Of all animal migrations, the mass migrations of raptors through geographical bottlenecks are among the most accessible and visible migration events. These mass migrations arise from the funnelling effect of coastlines and mountain ranges that act as barriers or leading lines for diurnally migrating raptors seeking the safest, most energy-efficient routes toward their seasonal destinations (Kerlinger 1989, Bildstein 2006). Depending on the seasonal and wider geographical context, tens of thousands up to several million individuals of dozens of species may converge through a bottleneck within just a few weeks. Some of such bottlenecks in North America and Europe have been monitored for over half a century (Porter & Beaman

1985, Kerlinger 1989, Zalles & Bildstein 2000, Bildstein 2006) and new monitoring programs continue to be established at known and newly discovered bottlenecks around the world (Ruelas *et al.* 2000, Batista *et al.* 2004, Porras-Peñaranda *et al.* 2004, McCrary & Young 2008, Verhelst *et al.* 2011, Bayly *et al.* 2014, Fülöp *et al.* 2014, 2018, Heiss *et al.* 2020, Panuccio *et al.* 2021, Noby *et al.* 2022, Shi *et al.* 2023). Yet, there are still gaps in the migration monitoring network and much remains to be learned about raptors' seasonal flyway use. Even within the East African-Eurasian Flyway, used by several million raptors and where much historical research has been conducted (Porter & Beaman 1985, Shirihai *et al.* 2000), knowledge is still fragmentary in many places (Murgatroyd *et al.* 2021, Jobson *et al.* 2021). The seminal review of Shirihai *et al.* (2000) emphasised a particularly urgent need for spring surveys in the southeastern Black Sea region.

In general, more migrants are expected at bottleneck sites after the breeding season, when populations are inflated with large numbers of juvenile birds. Many of these juvenile birds will perish before the following pre-breeding migration (Strandberg *et al.* 2009, Sergio *et al.* 2019, Serratosa *et al.* 2024, Mirski *et al.* 2024). However, the seasonal magnitude of migration at any given site also depends on the configuration of geographic features relative to the seasonal direction of migration. Bottlenecks with an hourglass configuration along a north-south axis such as the Central American Isthmus (Ruelas *et al.* 2000, Bildstein & Zalles 2001, Ruelas *et al.* 2009) or the Strait of Gibraltar (Evans & Lathbury 1973, Finlayson 1992, Bensusan *et al.* 2007, Onrubia 2015) exert a strong funnelling effect in both seasons. In other cases, the magnitude of migration may differ greatly between seasons at a given bottleneck depending on the defining geographic features' orientation relative to the seasonal travel direction of birds, species-specific barrier-crossing abilities (Meyburg *et al.* 2017, Mellone 2020), seasonal time and energy constraints (Agostini *et al.* 2019), and other factors, such as seasonal weather conditions. For example, prevailing winds may exacerbate the barrier effect of a large body of water resulting in narrow-front migration in one season, while allowing a fast and direct water-crossing over a broad front in another season (Panuccio *et al.* 2014, Nourani *et al.* 2016, Agostini *et al.* 2019). As a result, birds engage in seasonal loop migrations, preferring slightly different corridors within a given flyway, or even using entirely different flyways between seasons (Kerlinger 1989, Leshem & Yom-Tov 1996, Shirihai *et al.* 2000, Corso & Cardelli 2004, Katzner *et al.* 2016, Mirski *et al.* 2024). These and other factors like age-specific migration behaviours (Kjellen 1992, Schmid 2000, Sergio *et al.* 2014, Vansteelant *et al.* 2017, Phipps *et al.* 2019, Nourani *et al.* 2020) mean that seasonal migration patterns can vary widely between sites (Kerlinger 1989, Bildstein 2006). Even today we lack basic information about the magnitude, timing and composition of raptor migration in one or both seasons at key bottlenecks (Murgatroyd *et al.* 2021, Jobson *et al.* 2021).

In autumn, the Batumi bottleneck is one of few sites in the world where over one million raptors can be seen in a single season. The eastern Black Sea coast and the northern edge of the Lesser Caucasus make up a very pronounced geographical bottleneck for southbound migrants coming from the Kolkheti lowlands, which becomes progressively narrower from north to south until the mountains reach the sea near the city of Batumi (Andrews *et al.* 1977, Gálvez *et al.* 2005, Verhelst *et al.* 2011, Figure 1A, B). The extent to which raptors concentrate along the coast differs between species, but the use of the coastal routes is intensified by dense cloud cover over the mountains limiting the development of thermal updrafts further inland (especially for obligate-soaring migrants in early autumn) and by easterly winds (especially for facultative-soaring species; Vansteelant *et al.* 2014). The Batumi Raptor Count (BRC, www.batumiraptorcount.org) was established to monitor the autumn migration in 2008 (Verhelst *et al.* 2011), and a consistent survey effort since 2011 has revealed major changes in certain raptor populations using this flyway (Wehrmann *et al.* 2019, Vansteelant *et al.* 2020). Yet, the spring migration has only been roughly quantified in the past (Abuladze 2013).

In this study, we report the first full-season spring migration surveys of northbound raptors in the eastern Black Sea Flyway, in the Republic of Georgia, in the Caucasus region (Figure1). Compared to autumn, the Batumi 'bottleneck' is much less clearly topographically defined in spring. Northbound migrants coming from the Armenian highlands in spring are instead expected to 'filter through' the many mountain passes of the Lesser Caucasus towards the Kolkheti lowlands (Figure 1A, C). Furthermore, climatic factors that may modulate the topographical barrier effect, e.g. through the development of thermal or orographic updrafts, presumably differ between spring and autumn. At a larger scale, certain species or populations that migrate through the eastern Black Sea Flyway in autumn may use other flyways in spring and vice versa (Shirihai *et al.* 2000, Pannucio *et al.* 2014, Vansteelant & Agostini 2021). Scant information about the spring migration of

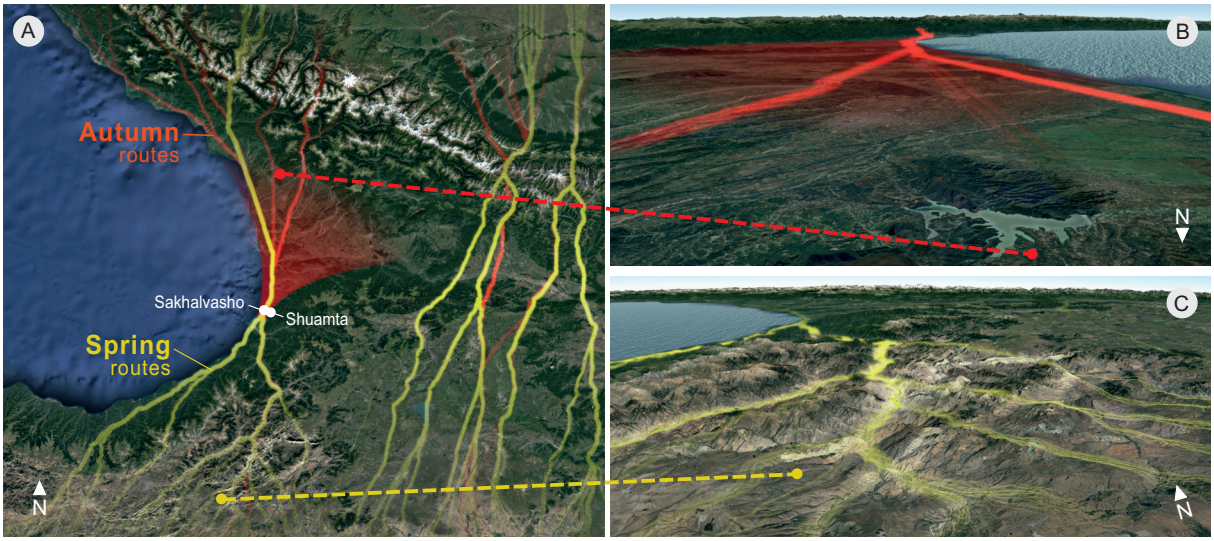

Figure 1. (A) View of the Batumi bottleneck from above, (B) looking south over the Kolkheti lowlands towards the bottleneck and (C) looking north from the Armenian highlands towards the bottleneck. White dots indicate the Batumi Raptor Count watch sites of Sakhalvasho (2 km from the coast at 324 m asl) and Shuamta (6 km from the coast at 414 m asl) located within a 12-km wide bottleneck. Only the Sakhalvasho site was used during the spring surveys. Routes are the shortest paths with the least elevation changes through the Caucasus region (A) and in particular the Batumi bottleneck (B and C). These routes illustrate the likely paths of convergence of birds if they made decisions only based on topography. Note how in autumn (B) the eastern Black Sea coast and the northern edge of the Lesser Caucasus form a wide topographical funnel zone (shaded in red), converging in a narrow 'bottleneck' for birds coming from the north. In spring (C), only the coast acts as an obvious leading line into the bottleneck, though birds might be guided by topography through the valleys of northeast Turkey. Satellite and topography extracted via Google Earth.

raptors across the Caucasus indicates that the spring migration through the eastern Black Sea Flyway is much smaller in magnitude than the autumn migration, but presumably still of global relevance for several species (Shirihai *et al.* 2000, Abuladze & Edisherashvili 2003, Gálvez *et al.* 2005, Abuladze 2013).

After 15 years of autumn surveys by the Batumi Raptor Count and much speculation about what spring migration might look like, we decided to find out by conducting three pilot spring surveys at Batumi, Georgia, in 2019, 2020 and 2022. Our primary aims were to (1) describe the magnitude of migration and species composition, (2) quantify the timing and migration duration of 'relatively common migrants' (i.e. average count >100 individuals/season) and (3) compare the magnitude and duration of migration periods between the spring and autumn seasons within the Batumi bottleneck.

Overall, we expect the spring migration of raptors to be of substantially lower magnitude than in autumn due to lower numbers of young birds in spring and a weaker funnelling effect of the Lesser Caucasus. However, based on BRC autumn surveys (Verhelst *et al.* 2011) and other spring surveys in the East African-Eurasian Flyway (Shirihai *et al.* 2000), we expect a similar diversity of raptors in spring as in autumn. We anticipate 25–30 species occurring annually, and potentially up to hundreds of thousands of Black Kites *Milvus migrans*, Steppe Buzzards *Buteo buteo vulpinus* and European Honey Buzzards *Pernis apivorus*. Focusing on those species that are common and for which we achieve full coverage in both seasons, we expect most species to have a shorter core migration period in spring when adults are on their way to initiate breeding in a timely fashion, than in autumn when departure times can vary depending on individual breeding success, moult and availability of local food resources (Kokko 1999, Newton 2023). At the same time, we expect a longer total migration period due to a late and protracted migration of immature birds in spring (Leshem & Yom-Tov 1996, Yosef *et al.* 2003, Phipps *et al.* 2019, Mirski *et al.* 2024). We will describe our observations in a larger context of the East African-Eurasian Flyway and of historical data on the timing of spring raptor migration in Georgia and will consider the monitoring and conservation potential at Batumi in spring.

A flock of Black Kites soaring against the rapidly developing skyline of Batumi city (photo Tohar Tal, 30 March 2022).

Short-toed Eagle in front of snow-covered mountains of the Lesser Caucasus, a view unique to our spring surveys (photo Marc Heetkamp, 26 March 2022).

Early spring in Batumi means counting raptors on frozen feet (Tohar Tal, 25 March 2022).

METHODS

Study area, period, and species

The spring counts were conducted from a single count site located NE of Batumi along the west coast of Georgia, in the village of Sakhalvasho (41.6827°N, 41.7291°E). This site is situated on the same hill used during the BRC autumn surveys (Wehrmann *et al.* 2019) but on the south-facing side. The count site is located at roughly 325 m above sea level (asl) and two km east of the Black Sea coast in the foothills of the Lesser Caucasus mountains that rise to elevations of more than 1200 m asl within five to six km from the coast (Figure 1). We conducted daily counts from 21 March until 31 May in 2019 and from 1 March until 26 May in 2020 and 2022. The difference in count period is a result of our observations in 2019, where upon arrival on 20 March there already seemed to be substantial raptor migration. By starting 20 days earlier we aimed to ensure full coverage of early-migrating species in 2020 and 2022. During the surveys, we counted all raptor species and those non-raptor species that are systematically recorded in autumn (Wehrmann *et al.* 2019).

Data recording and processing

The count method used during the pilot spring surveys was a simplified version of our highly standardised autumn protocol (Wehrmann *et al.* 2019). The size of the team was significantly smaller with one to eight active counters on-site surveying from one (instead of two) count site(s). Counters were equipped with tally counters, binoculars, spotting scopes and optionally a camera suitable for bird photography.

Spring counts were more easily interrupted by periods of inclement weather, such as heavy rain or snow, given the absence of any shelter on our pilot count site. This was for instance the case during the first three weeks of March 2022. Due to a constant snowfall resulting in snow cover of more than one meter deep we were often unable to reach the count site, although observations from our nearby guesthouse indicated migration activity was also minimal during that period. In 2019, we counted from a more inland location, but with a similar view as the main count site, on two days (41.6870°N, 41.7793°E). In 2020, due to COVID-19 quarantine measures set by the local government, we were forced to count from the garden of our guesthouse in the lower-lying village of Sakhalvasho (41.6866°N, 41.7335°E) for four consecutive days (26–29 March). The view from the terrace was sufficiently representative of our count site to conduct the daily counts, given that it was only 400 m northeast. During these days, except for the 27th, on which 32,000 birds (approximately 4% of the season total) were counted, the pace of migration was rather slow due to bad weather conditions.

As in autumn, we digitally recorded numbers of birds, with as much additional data as possible on species, age, sex and colour morphs, using a tablet equipped with a modified version of the Trektellen app (www.trektellen.org; Wehrmann *et al.* 2019). Higher-order taxonomic and morphological groups were used for birds that could not be identified to species level, such as the groups 'medium-sized raptors' and 'large eagles'. In our previous autumn analyses in Vansteelant *et al.* (2020) a post-hoc correction was performed to estimate the proportions of species among unidentified birds on each day (Wehrmann *et al.* 2019, Vansteelant *et al.* 2020). However, due to higher numbers of unidentified raptors compared to identified raptors in our spring data, we were unable to develop a similar correction of daily totals for our spring data. Therefore, to make seasonal comparisons, we also used the uncorrected daily species totals for autumn.

Quantifying phenology and migration duration

We calculated seasonal totals and phenological metrics for all relatively common migrant species by aligning different years through converting dates to day of the year. The seasonal timing was assessed based on quantile passage dates (5, 25, 50, 75 and 95%). We then calculated the duration of the main migration period, i.e. central 90%, as the period spanning from the Q5% to the Q95% quantile passage dates and of the core migration period, i.e. central 50%, as the period between the Q25% and the Q75% quantile passage date. As an additional metric, for each species we calculated the proportion of individuals seen on the biggest peak day of each season. We calculated these metrics for spring as well as autumn to allow for seasonal comparisons.

In 2020 and 2022, years in which the spring counts began on the 1 March, we assume to have covered the full migration period of all recorded species as the migration only slowly started to pick up after the start of the count. However, this was not true for 2019, when the counts started on 21 March. This could lead to substantial bias in phenological metrics of the earliest spring migrants, especially the Q5%-passage date and the duration of the main migration period. To determine for which species the late 2019 start could be most problematic, we assessed what percentage of each species passed before 21 March in 2020 and 2022. If this exceeded 3%, we excluded 2019 from the calcu-

lation of phenological metrics of that species. A stricter percentage was found too exclusive for species with relatively low season totals of a few hundred birds. No corrections were needed for calculating the end of the migration periods, as migration of all species ceased before the end of the count in all years.

Visualising paths of convergence

To illustrate likely paths of convergence of migrating raptors as they navigate through the Caucasus and the Batumi bottleneck (Figure 1), we generated artificial tracks of raptors making their way through the mountain passes and valleys based on topographic information. We used a least-cost path analysis, generating paths with the least elevation changes from a starting latitudinal line north of the Greater Caucasus (c. 43.8°N, c. 450 km longitudinally) towards a finishing latitudinal line south of the Lesser Caucasus (c. 40.1°N, 500 km longitudinally) in autumn and vice versa for spring. Tracks were started at 100 evenly spaced locations along the starting line to mimic a potential 'broad front' approach of the Caucasus, and tracks ended when the finish line was reached, regardless of longitude. We used the SRTM 30-m digital elevation model (DEM; NASA JPL 2013), downsampled to 0.005° resolution (c. 400-m pixel size) to make the generation of these tracks computationally feasible while still retaining the dominant topographical landscape features. As the tracks are merely intended to be illustrative of likely general patterns, we used the default Tobler's cost function implemented in the R 'leastcostpath' package (Lewis 2021). To encourage routes to differ seasonally, we 'tilted' the DEM along the seasonal axis of migration. For autumn migration, this involved adding a gradual artificial slope to the DEM linearly ranging from c. 5600 m at the northern boundary to 0 m at the southern boundary and vice versa for spring. While the magnitude of this tilt is substantial in absolute terms, it functions merely as a relative weighting mechanism and is small compared to the complex natural variation in terrain. This procedure gives more weight to landscape features that birds would encounter earlier in their migration, helping to highlight where zones of convergence occur upstream of the Batumi bottleneck (Figure S2). This is intended to weigh the upstream topographical conditions, before birds reach the bottleneck, more strongly than those following crossing the bottleneck. The identified zones of convergence outside the Batumi bottleneck during both seasons broadly overlap with those described in the literature (Van Maanen *et al.* 2001, Gálvez *et al.* 2005, Abuladze *et al.* 2013) and extracted from GPS tracking data of for example Black Kites in autumn (Efrat *et al.* 2025) and spring (Efrat R. pers. comm.).

Comparing spring and autumn abundance and phenology

We used the autumn data of 2018, 2019 and 2021 to compare seasonal abundance and migration periods for those species for which we achieved complete coverage in both seasons. Comparing spring totals to the immediately preceding autumn allows for cleaner comparisons because this accounts for the fact that some species changed significantly in abundance since the start of BRC's autumn surveys (Vansteelant *et al.* 2020). We employed a two-sided unpaired *t*-test to determine whether seasonal differences in the magnitude and duration of main and core migration periods were statistically significant. Furthermore, we used a single-effect linear regression model to assess whether the relative timing (Q50% passage date), the average duration of species' main and core migration periods, and the proportion of birds seen on peak days were correlated between spring and autumn.

All statistical testing and data visualisation was conducted in R v. 4.2.2 (R Core Development Team 2023). The daily spring and autumn data and code to reproduce our analyses are publicly available via the BRC GitHub repository (https://github.com/batumi raptorcount/ spring-migration-paper) and archived at Zenodo (https://doi.org/10.5281/zenodo.16411086).

RESULTS

We observed on average 542,161 raptors (range: 455,799–618,848) per spring across a total of 33 species (Table 1). Spring migration was dominated by Black Kite (239,649 ± 22,547 SD), Steppe Buzzard (194,029 ± 102,702) and European Honey Buzzard (54,994 ± 29,978), with an additional six species with average totals of 1000–10,000 individuals and another six species with average totals of 100–1000 individuals. For four of the 15 most common species (Eastern Imperial Eagle *Aquila heliaca*, Hen Harrier *Circus cyaneus*, Steppe Eagle *Aquila nipalensis* and Western Marsh Harrier *Circus aeruginosus*) we likely missed the first 3% of the spring migration in 2019 by starting 20 days later than in 2020 and 2022. For these species, we excluded 2019 from our calculations (Table 1). Of the 15 common species, 12 species had a median passage date between late March and mid-April and the remaining three common species had median passage dates in late April and early May (Table 1, Figure 2).

Table 1. Overview of raptor species observed during the spring surveys in 2019, 2020 and 2022, including the mean annual total. For the relatively most common species (average total more than 100 individuals) we show the average median passage date, average date with the maximum day count and the average number of individuals on the maximum day count.

Species	Mean spring total	SD	Median date	SD	Peak date	SD	Peak number	SD
Black Kite *Milvus migrans*	239,649	22,547	03/04	2	02/04	3	38,868	9428
Steppe Buzzard *Buteo buteo vulpinus*	194,029	102,702	06/04	2	03/04	4	30,082	19,656
European Honey Buzzard *Pernis apivorus*	54,994	29,978	08/05	3	13/05	11	17,141	14,103
Eurasian Sparrowhawk *Accipiter nisus*	9912	4173	10/04	3	06/04	5	1010	548
Western Marsh Harrier* *Circus aeruginosus*	2170	199	04/04	0	25/03	3	224	50
Booted Eagle *Hieraaetus pennatus*	1375	448	10/04	4	09/04	6	158	29
Levant Sparrowhawk *Accipiter brevipes*	1354	177	02/05	5	01/05	4	691	385
Lesser Spotted Eagle *Clanga pomarina*	1289	462	14/04	5	07/04	13	161	92
Short-toed Eagle *Circaetus gallicus*	1098	277	30/03	2	29/03	5	246	58
Greater Spotted Eagle *Clanga clanga*	190	87	03/04	7	31/03	8	33	14
Hen Harrier* *Circus cyaneus*	176	18	02/04	1	23/03	3	18	2
Eastern Imperial Eagle* *Aquila heliaca*	116	54	31/03	8	31/03	12	18	12
Pallid Harrier *Circus macrourus*	116	24	07/04	7	02/04	1	22	8
Montagu's Harrier *Circus pygargus*	102	57	27/04	6	27/04	8	33	39
Steppe Eagle* *Aquila nipalensis*	102	8	03/04	13	02/04	14	23	8
Long-legged Buzzard* *Buteo rufinus*	86	33						
Eurasian Hobby *Falco subbuteo*	79	51						
Common Kestrel *Falco tinnunculus*	52	13						
Osprey *Pandion haliaetus*	34	10						
Egyptian Vulture *Neophron percnopterus*	12	3						
White-tailed Eagle* *Haliaeetus albicilla*	10	6						
Crested Honey Buzzard *Pernis ptilorhynchus*	8	10						
Eurasian Goshawk *Astur gentilis*	8	3						
Red-footed Falcon *Falco vespertinus*	8	6						
Merlin *Falco columbarius*	6	2						
Common Buzzard* *Buteo buteo buteo*	6	5						
Peregrine Falcon *Falco peregrinus*	6	5						
Lesser Kestrel** *Falco naumanni*	4	4						
Rough-legged Buzzard*** *Buteo lagopus*	4	–						
Golden Eagle *Aquila chrysaetos*	2	1						
Griffon Vulture *Gyps fulvus*	2	1						
Cinereous Vulture *Aegypius monachus*	1	1						
Black-winged Kite*** *Elanus caeruleus*	1	–						
Medium unidentified raptor *Buteo/Pernis/Milvus*	29,681	36,231						
Large eagle *Aquila/Clanga* spp.	2461	1481						
Buzzard unknown *Buteo* spp.	1696	1790						
Unidentified raptor	1128	1613						
Levant/Eurasian Sparrowhawk *Accipiter* spp.	767	984						
Montagu's/Pallid/Hen Harrier	200	158						
Common/Lesser Kestrel	91	78						
Harrier unknown *Circus* spp.	25	25						
Eurasian Hobby/Red-footed Falcon	17	14						
Falcon unknown	12	14						

*Early species: mean totals and quantiles are based on 2020 and 2022 only. **Observed only during two out of three surveys, on which the annual metrics are based. ***Observed only during one out of three surveys, on which the annual metrics are based.

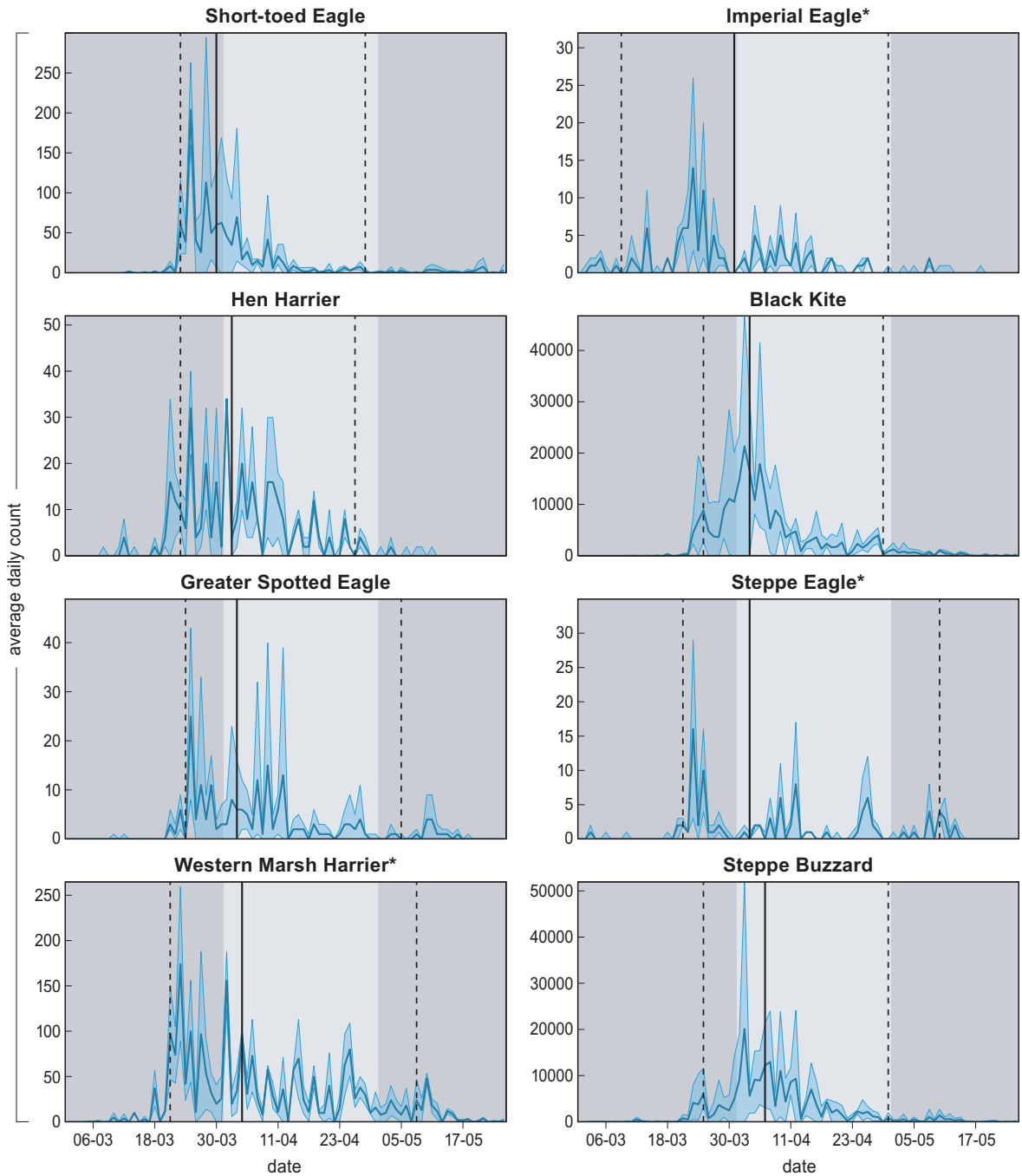

Figure 2A. Spring phenology of the first 8 of 15 most common raptors in spring (average total > 100 ind/yr). Dark blue lines show the mean daily count with the minimum and maximum count in light blue. Vertical lines indicate the median passage date (Q50%, solid) and the Q5% and Q95% quantile passage dates (dashed). Background shading indicates consecutive months: March (dark), April (light) and May (dark). *Early species: data based on 2020 and 2022 only.

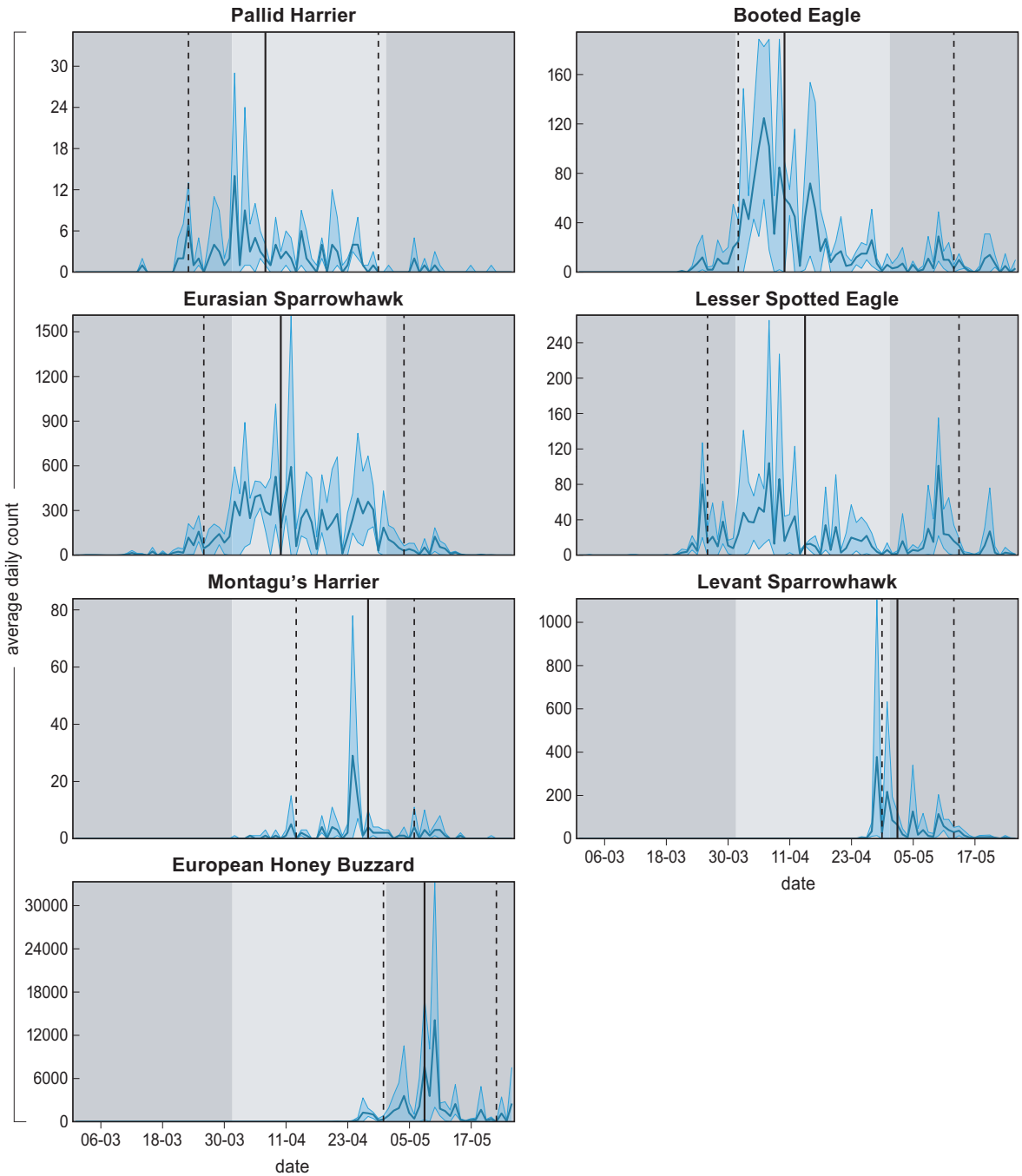

Figure 2B. Spring phenology of the last 7 of 15 most common raptors in spring (average total > 100 ind/yr). Dark blue lines show the mean daily count with the minimum and maximum count in light blue. Vertical lines indicate the median passage date (Q50%, solid) and the Q5%– and Q95% quantile passage dates (dashed). Background shading indicates consecutive months: March (dark), April (light) and May (dark).

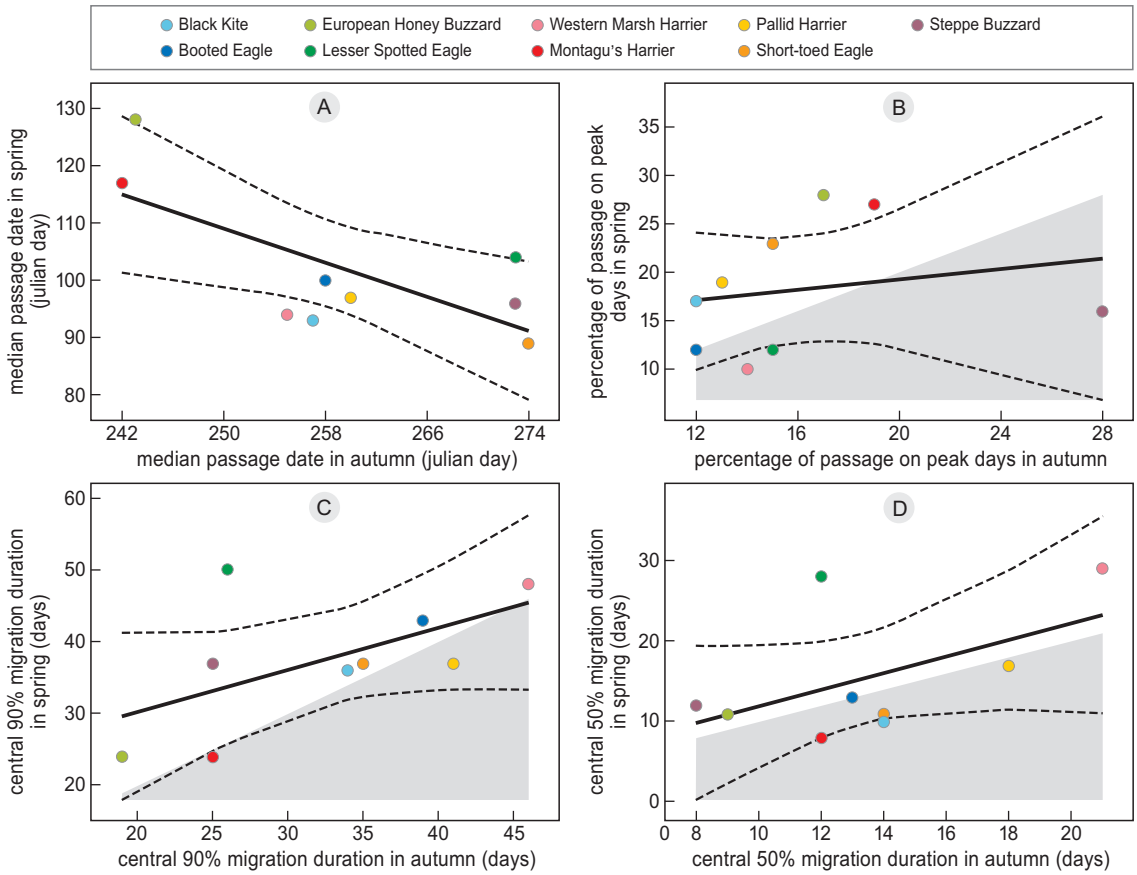

Figure 3. Seasonal comparison of (A) the median passage date, (B) percentage of birds passing on peak days, (C) duration of the main 90% migration period and (D) duration of the core 50% migration period for the nine species with an average of more than 100 individuals per season and complete coverage during both spring and autumn. In all figures, a linear model is fitted (solid black line) including the lower and upper 95% confidence intervals (dashed black lines). In Figures B, C and D we included the intercept of the *x*- and *y*-axis to help distinguish between autumn values higher than spring values (shaded) or autumn values lower than spring values (unshaded). Only the median passage date of species was significantly correlated between the spring and autumn seasons. For all other phenological metrics, we found no significant correlations.

Spring vs. autumn abundance

Of the three species that make up the bulk of migration in both seasons, the two early spring migrants, Steppe Buzzard and Black Kite, show no significant difference between spring and autumn in the magnitude of migration (Table 2). Black Kite counts were slightly, but consistently higher in each spring than in the preceding autumn (Table 2). All other common species (groups), except 'medium-sized raptors' and 'large eagles', occurred in significantly lower numbers in spring than in autumn (Table 2). In the most extreme cases, spring abundance was an order of magnitude lower than autumn abundance. Among common species, this was true for two of the three late spring migrants: Honey Buzzard (tens of thousands in spring vs. hundreds of thousands in autumn) and Montagu's Harrier *Circus pygargus* (100+ in spring vs. thousands in autumn). Such a strong underrepresentation in spring was also observed for Pallid Harrier *Circus macrourus* and unidentified Montagu's/Pallid/Hen Harriers in general (at most a few hundred in spring versus thousands in autumn; Table 2).

We did not formally test seasonal differences in abundance for species (groups) that were uncommon (< 100 ind/yr) in one or both seasons or not systematically counted in recent autumn surveys. However, a qualitative comparison reveals that all annual species for which we achieved full coverage during the comprehensive pilot autumn surveys in 2008–2010, or during more recent autumn surveys, were less abundant in spring than autumn. This was particularly the case for small falcons *Falco* spp. and Osprey *Pandion haliaetus*,

of which we recorded tens in spring vs. hundreds in autumn (Verhelst *et al.* 2011, Hoekstra *et al.* 2020). The few annual species that showed higher spring than autumn totals were all species for which we achieved much better spring than autumn coverage, such as Eurasian Sparrowhawk *Accipiter nisus*, Hen Harrier, Eastern Imperial Eagle and Long-legged Buzzard *Buteo rufinus* (Hoekstra *et al.* 2020). Comparable spring and autumn maxima only occurred in non-annual species, e.g. Black-winged Kite *Elanus caeruleus* and Rough-legged Buzzard *Buteo lagopus*.

Spring vs. autumn phenology

In general, the median passage data in spring was significantly and negatively correlated to the median passage data in autumn ($\beta = -0.740 \pm 0.277$ SE, $P = 0.032$, $r^2 = 0.434$). In other words: the latest spring migrants tended to be the earliest autumn migrants and vice versa (Figure 3A). The percentage of birds passing on peak days (Figure 3B) shows no clear correlation between spring and autumn ($\beta = 0.273 \pm 0.486$, $P = 0.593$, $r^2 = -0.094$). Despite Figure 3C–D suggesting clear positive correlations of main and core migration periods between spring and autumn, these were not significant (main migration period: $\beta = 0.585 \pm 0.315$, $P = 0.105$, $r^2 = 0.235$, core migration period: $\beta = 1.030 \pm 0.611$, $P = 0.136$, $r^2 = 0.187$).

The main migration period generally tended to last (slightly) longer in spring than in autumn (Figure 3C, note seven of nine species in white area). While this difference was significant for only two species, i.e. Steppe Buzzard and Lesser Spotted Eagle *Clanga pomarina* (Table 3), the relatively long main migration periods in spring seemed to be associated with very long tails of slow-paced migration in nearly all species. Hence, the second half of the migration period from Q50%–Q95% is generally much longer than the first half from Q5%–Q50% (Figure 2). These long tails are much more pronounced in spring than in autumn. Note the less skewed daily abundance curves of the same species during autumn in Vansteelant *et al.* (2020). Furthermore, the only two species for which the main migration period was (not significantly) shorter in spring than autumn, Montagu's Harrier and Pallid Harrier, would likely show longer spring main migration periods if we could account for the unidentified ringtail harriers that showed a much longer spring than autumn migration period (Table 3). Contrary to the main migration period, we found no general seasonal difference in the duration of species' core migration periods or the percentage of birds passing on peak days (Figure 3B, D, Table 4, 5).

Other noteworthy observations

Every spring, we were struck by the strong tendency of Black Kites to aggregate along the coastline much more than in autumn, even making short-distance sea crossings (estimated 20–25 km) from, roughly, Batumi to Kobuleti and frequently soaring several kilometres offshore. Additionally, each spring, a substantial portion

Table 2. Comparison of the spring and autumn rounded mean annual total including results of the unpaired two-sided *t*-tests ($P < 0.05$ in italics and $P < 0.01$ in bold) for species of which we presume to have covered the entire migration period in both seasons.

Species	Mean annual count				*P*-values
	Spring	SD	Autumn	SD	
Black Kite *Milvus migrans*	239,649	22,547	217,980	66727	0.639
Steppe Buzzard *Buteo buteo vulpinus*	194,029	102,702	331,317	96,672	0.167
European Honey Buzzard *Pernis apivorus*	54,994	29,978	499,263	14,169	**<0.001**
Western Marsh Harrier *Circus aeruginosus*	2170	199	8326	1687	*0.022*
Booted Eagle *Hieraaetus pennatus*	1375	448	6683	1348	*0.014*
Lesser Spotted Eagle *Clanga pomarina*	1289	462	4085	421	**0.002**
Short-toed Eagle *Circaetus gallicus*	1098	277	1977	462	0.060
Pallid Harrier *Circus macrourus*	116	24	445	73	*0.010*
Montagu's Harrier *Circus pygargus*	102	57	1892	373	*0.013*
Medium raptor *Buteo/Pernis/Milvus*	29681	36,231	61,490	29,563	0.306
Large eagle *Aquila/Clanga*	2461	1481	6582	2377	0.075
Harrier unknown *Circus* spp.	200	158	4392	755	**0.008**
Total – all species	542,162	81,954	1,153,558	154,570	**0.008**

of Black Kites passing the count site in mid-April would engage in aerial foraging (a behaviour that we never observed in autumn before), opportunistically hunting small insects that swarmed between 11 and 18 April (Tal *et al.* 2021).

Throughout the spring seasons we recorded eight non-raptor species, summarised in Table S1. More anecdotal observations can be found in the spring migration reports published on the BRC website (Tal & Jansen 2019, Tal 2020, Hoekstra & Jansen 2022).

DISCUSSION

After establishing the significance of the Batumi bottleneck as one of the world's major autumn raptor migration bottlenecks, and over a decade of standardised volunteer-based autumn surveys, we are now able to provide a detailed description of spring raptor migration through the eastern Black Sea Flyway. In line with our expectations, we recorded a similar diversity of raptors using the eastern Black Sea Flyway in spring

Table 3. Comparison of the spring and autumn rounded mean main migration duration (central 90%) in days including results of the unpaired two-sided *t*-tests ($P < 0.05$ in italics and $P < 0.01$ in bold) for species of which we presume to have covered the entire migration period in both seasons.

Species	**Length of central 90%** (days)				***P*-values**
	Spring mean	SD	Autumn mean	SD	
Black Kite *Milvus migrans*	36	3	34	6	0.617
Steppe Buzzard *Buteo buteo vulpinus*	37	5	25	4	*0.041*
European Honey Buzzard *Pernis apivorus*	24	8	19	3	0.427
Western Marsh Harrier *Circus aeruginosus*	48	4	46	4	0.484
Booted Eagle *Hieraaetus pennatus*	43	4	39	4	0.193
Lesser Spotted Eagle *Clanga pomarina*	50	3	26	4	**<0.001**
Short-toed Eagle *Circaetus gallicus*	37	3	35	7	0.689
Pallid Harrier *Circus macrourus*	37	5	41	4	0.336
Montagu's Harrier *Circus pygargus*	24	6	25	2	0.658
Medium raptor *Buteo/Pernis/Milvus*	41	2	28	9	0.115
Large eagle *Aquila/Clanga*	48	1	22	2	**<0.001**
Harrier unknown *Circus* spp.	42	3	28	2	**0.002**

Table 4. Comparison of the spring and autumn rounded mean core migration duration (central 50%) in days including results of the unpaired two-sided *t*-tests ($P < 0.05$ in italics and $P < 0.01$ in bold) for species of which we presume to have covered the entire migration period in both seasons.

Species	**Length of central 50%** (days)				***P*-values**
	Spring mean	SD	Autumn mean	SD	
Black Kite *Milvus migrans*	10	3	14	5	0.293
Steppe Buzzard *Buteo buteo vulpinus*	12	4	8	5	0.352
European Honey Buzzard *Pernis apivorus*	11	10	9	2	0.684
Western Marsh Harrier *Circus aeruginosus*	29	5	21	6	0.179
Booted Eagle *Hieraaetus pennatus*	13	5	13	2	0.923
Lesser Spotted Eagle *Clanga pomarine*	28	14	12	2	0.186
Short-toed Eagle *Circaetus gallicus*	11	6	14	1	0.364
Pallid Harrier *Circus macrourus*	17	3	18	9	0.910
Montagu's Harrier *Circus pygargus*	8	6	12	1	0.369
Medium raptor *Buteo/Pernis/Milvus*	25	4	12	6	*0.036*
Large eagle *Aquila/Clanga*	15	6	10	3	0.271
Harrier unknown *Circus* spp.	23	5	13	1	0.068

(33 species total) as in autumn (34 in 2008–2009 pilot surveys of Verhelst *et al.* 2011, and 38 species to date). As expected, 13 of the 15 common species for which we covered the full migration period in both seasons were much less abundant in spring than in autumn. Similar to our autumn surveys, the three most abundant species were Black Kite, Steppe Buzzard and Honey Buzzard, with the former two species showing a similar abundance with hundreds of thousands of individuals in both seasons. Contrastingly, the numbers of Honey Buzzards were an order of magnitude lower in spring (54,994 ± 29,978) than in autumn (499,263 ± 14,169). While we could not detect significant seasonal differences in phenological metrics based on three years of spring and autumn data, a great majority of species showed consistently longer main migration periods in spring, characterised by a relatively long tail of slow-paced migration.

Because we ran spring surveys with a relatively small team from only one count site, and spring counts were more often interrupted by bad weather than autumn counts, we likely underestimated true abundance more in spring than in autumn. However, the seasonal differences we found in species' abundances (and migration periods) are too large to be explained solely by seasonal differences in coverage and are unlikely to be due to differences in detectability (e.g. there are no major apparent seasonal difference in flight altitudes; Berthiaume *et al.* 2009, Panuccio *et al.* 2013). So we are confident our results reflect true seasonal differences in species' population sizes and regional or large-scale flyway use that are discussed in more detail below. Another downside of working with small teams is that we had less time to spare for ageing and sexing, especially at times of intense migration. Recording demographic data also proved to be challenging because age-related features were less pronounced after the non-breeding period. Feathers of second calendar-year birds, for example, can be faded, worn or already replaced, making it harder to distinguish them from older immatures and adults in spring (Forsman 2016). As a result, contrary to previous autumn analyses (Wehrmann *et al.* 2019, Vansteelant *et al.* 2020), we were unable to account for demographic factors like age in our spring analysis.

Seasonal contrasts in raptor abundance

That most raptors would migrate past Batumi in lower numbers in spring than in autumn was expected due to the smaller numbers of young birds in the spring populations and a weaker funnelling effect of the Lesser Caucasus on northbound migrants. Moreover, except for Honey Buzzard, all species underrepresented by an order of magnitude in spring compared to autumn are relatively slender-winged species such as ringtail harriers, Osprey and small falcons. These species are well adapted to sustained powered flight and much less prone than broad-winged raptors to concentrate at bottleneck sites (Spaar 1997, Bildstein 2006), including Batumi in autumn (Verhelst *et al.* 2011). Focusing on more typical bottleneck species, the only two species that were equally abundant in spring and autumn –

Table 5. Comparison of the spring and autumn rounded mean percentage of passage on peak days including results of the unpaired two-sided *t*-tests ($P < 0.05$ in italics and $P < 0.01$ in bold) for species of which we presume to have covered the entire migration period in both seasons.

Species	Percentage of passage on peak days				*P*-values
	Spring mean	SD	Autumn mean	SD	
Black Kite *Milvus migrans*	17	5	12	4	0.333
Steppe Buzzard *Buteo buteo vulpinus*	16	6	28	6	0.071
European Honey Buzzard *Pernis apivorus*	28	8	17	6	0.122
Western Marsh Harrier *Circus aeruginosus*	10	3	14	6	0.496
Booted Eagle *Hieraaetus pennatus*	12	3	12	4	0.965
Lesser Spotted Eagle *Clanga pomarina*	12	4	15	4	0.346
Short-toed Eagle *Circaetus gallicus*	23	3	15	3	*0.039*
Pallid Harrier *Circus macrourus*	19	6	13	5	0.246
Montagu's Harrier *Circus pygargus*	27	18	19	6	0.523
Medium raptor *Buteo/Pernis/Milvus*	32	21	26	6	0.641
Large eagle *Aquila/Clanga*	14	3	29	3	**0.005**
Harrier unknown *Circus* spp.	14	4	23	3	*0.040*

despite presumably smaller spring flyway populations – were both early-spring migrants: Steppe Buzzard and Black Kite (Figure 2A). And while the remaining early-spring species did show significantly lower spring than autumn abundance, they still occurred in a similar order of magnitude in both seasons. Contrastingly, the only specialist soaring migrant for which spring abundance was an order of magnitude lower than autumn abundance was Honey Buzzard, the latest spring migrant of all. Interestingly, this species stands out by the very low number of juveniles seen at Batumi in autumn (< 10%; Vansteelant *et al.* 2020). As such, the seasonal contrast in the abundance of Honey Buzzards cannot be explained by the smaller (immature) population in spring. Instead, the exceptionally strong under-representation of this late-spring species could arise if the funnelling-effect of the Armenian Highlands and Lesser Caucasus towards the Black Sea coast is weakened over the course of the spring season.

Species passing in early spring face much harsher conditions by crossing the Armenian Highlands and Lesser Caucasus far inland (Gyllin 1974) than they do along the milder, coastal climate of the Black Sea-route past Batumi. Low temperatures and extensive snow cover can increase the energetic cost of crossing the Lesser Caucasus in early spring, for example through thermoregulation and weaker thermals necessitating active flight (Bildstein 2006, Bohrer *et al.* 2012) and limiting opportunities for refuelling (Niles *et al.* 1996, Bildstein 2006, Limiñana *et al.* 2007, Trierweiler 2010). The fact that we observed hardly any visible migration during the late and severe winter spell in the southeastern Black Sea region in March 2022 certainly suggests snow and frost can block or divert migration (own obs.). Through mid and late spring, the interior of the Lesser Caucasus might become less hostile due to the greening up of the region. The contribution of geographic and seasonal climatic factors to the concentration of northbound raptors into the eastern Black Sea Flyway could be disentangled by tracking early- and late-spring migrants.

Batumi spring migration in a flyway context

Spring migrants coming from Africa enter the Middle East via Egypt into Israel, or via Djibouti into Yemen by crossing the Bab-el-Mandab strait. From the Middle East they are presumed to follow one of three principal routes back to their respective breeding ranges (Shirihai *et al.* 2000): (1) northwestward over Turkey and into eastern Europe via the Bosphorus Strait, (2) northward across the Armenian Highlands and the Caucasus in which the eastern Black Sea Flyway is located or (3) northeastward via the Caspian Sea into Central Asia. Our findings reveal that the magnitude of migration along the eastern Black Sea Flyway matches the expectations of Shirihai *et al.* (2000) for some raptor species but exceeds previous estimations for others.

Species like the Lesser Spotted Eagle, that predominantly breed west of the Black Sea in Central and Eastern Europe, migrate en masse via the Bosphorus in both seasons (Meyburg *et al.* 2000, 2004, Meyburg & Meyburg 2009, Üner *et al.* 2010, Meyburg 2021). A relatively small minority of 5000–10,000 birds take the eastern Black Sea route in autumn (Verhelst *et al.* 2011, Vansteelant *et al.* 2020), which likely originate from the easternmost populations in Ukraine, Belarus, westernmost Russia and the Caucasus region itself (at least several dozen breeding pairs; Keller *et al.* 2020). We now confirm a few thousand Lesser Spotted Eagles also take this route in spring (Shirihai *et al.* 2000); a seasonal contrast that can likely be accounted for by considerable juvenile mortality during the non-breeding season and a weaker topographic barrier effect in spring.

For species with substantial breeding populations north of the Caucasus, our data give new insights into seasonal flyway use. For example, we can confirm the expectation of Shirihai *et al.* (2000) that similar numbers of Steppe Buzzards use the eastern Black Sea Flyway in spring as in autumn (Table 2; Verhelst *et al.* 2011), albeit much higher numbers than were assumed to use this flyway. The seasonal passage at Batumi is also much greater than what has been recorded in other flyways around the Black and Caspian Sea in either season (Ullman & Ullman 2010, Heiss 2013, Stanciu *et al.* 2017, Panuccio *et al.* 2018, E. Talebi pers. comm.), and accounts for the vast majority of Steppe Buzzards entering the Middle East via Israel in spring (c. 300,000 individuals; Shirihai *et al.* 2000, Yosef *et al.* 2002). The Black Kite is a species for which different authors have formulated contradicting expectations about spring flyway use (Shirihai *et al.* 2000, Abuladze 2013, Panuccio *et al.* 2014). While Shirihai *et al.* (2000) suggested the majority of the flyway population uses the eastern Black Sea Flyway in both seasons, our results reveal that the concentration of Black Kites in the eastern Black Sea Flyway is even greater in spring than in autumn (Table 2), with spring counts being slightly higher than autumn counts despite the flyway population being smaller in spring. Tracking data of Black Kites, satellite-tagged at non-breeding grounds in Israel, support the hypothesis that kites engage in a more narrow-front coastal migration over Batumi in spring than in autumn (R. Efrat pers. comm.). The

number of Black Kite in BRC autumn surveys doubled from less than 100,000 to nearly 200,000 in the period 2011–2018 (Vansteelant *et al.* 2020) and reached close to 300,000 in recent years (www.batumiraptorcount.org/data). Hindcasting this trend to the early 21st century suggests that the importance of the eastern Black Sea Flyway for Black Kites in spring has been underestimated in the past (Panuccio *et al.* 2014).

The major seasonal difference in Honey Buzzard abundance at Batumi (Table 2) at first glance supports the suggestion of Shirihai *et al.* (2000) that relatively more individuals migrate west over the Bosphorus in spring. However, spring migration surveys along the western routes through Turkey yielded strikingly low Honey Buzzard counts, even considering incomplete coverage (< 10,000 individuals; Üner *et al.* 2010, Arslangündogdu *et al.* 2018, Altundağ & Karatas 2020). As it seems unlikely that Honey Buzzards breeding in northeastern Europe and western Russia migrate east along the Caspian Sea, we suggest that most of the hundreds of thousands of Honey Buzzards entering the East African-Eurasian Flyway in spring (e.g. 360,184 ± 231,062 at Eilat, Israel; Shirihai *et al.* 2000) do cross the Caucasus, albeit over a much broader front than in autumn (e.g. fewer than 1000 individuals at Besh Barmag, Azerbaijan in 2012; Heiss 2013). As stated above, being one of the latest spring migrants, Honey Buzzards likely encounter relatively hospitable conditions over the Lesser Caucasus (see also Gyllin 1974). Similarly, for other (earlier) species with substantial breeding populations north of the Caucasus, the lower spring than autumn abundance at Batumi can be explained without the use of alternative flyways. Instead, a greater proclivity for broad-front migration in spring can account for the particularly severe seasonal contrasts in the abundance of slender-winged species like Montagu's Harrier. The comparatively moderate underrepresentation of soaring migrants in both early and late spring, such as Short-toed Eagle *Circaetus gallicus*, Booted Eagle *Hieraaetus pennatus* and Levant Sparrowhawk *Accipiter brevipes*, falls within expectations assuming a smaller spring flyway population in combination with a weaker funnelling effect of the Lesser Caucasus. Indeed, to our knowledge, there is little to no evidence that any of these species show a stronger spring than autumn concentration along the western Black Sea or Caspian Flyways (Üner *et al.* 2010, Michev *et al.* 2011).

Besides trans-Caucasian migration occurring over a broader front, raptors breeding in central Asia, such as Steppe Eagles and Pallid Harriers, might generally be less inclined to detour through the (western) Caucasus in spring than in autumn. Steppe Eagle counts at Batumi were significantly lower in spring (Table 1) compared to autumn (average 610; Zaytseva *et al.* 2022). However, counts on the eastern side of the Caucasus, at Besh Barmag (estimated 798 ± 0; Heiss 2016), are higher than our spring and autumn counts, and also higher than autumn counts at the same site (estimated 250; Heiss 2016). This likely reflects a tendency of Steppe Eagles to take a more easterly course over the Caucasus to return to their relatively eastern breeding areas in spring. Nevertheless, the passage across both ends of the Caucasus represents a small minority of the total Steppe Eagle population passing through the East African-Eurasian Flyway (15,192 ± 1553 entering through Israel; Weiss *et al.* 2019, several thousand wintering on the Arabian Peninsula; e.g. Keijmel *et al.* 2020). Tracking data of Steppe Eagles wintering in the Middle East and breeding in Central Russia (Meyburg *et al.* 2012, Javed *et al.* 2014, Karyakin *et al.* 2019, 2023), corroborates that the vast majority of Steppe Eagles breeding in Central Asia enter and leave the Middle East southeast of the Caspian Sea (Shirihai *et al.* 2000), where systematic autumn surveys have recently been established (Panuccio *et al.* 2018, E. Talebi pers. comm.). The few Central Asian birds that do cross the Caucasus in autumn are even fewer in spring. Tracking data of Pallid Harriers from Kazakhstan similarly showed that birds migrating across the Caucasus in autumn returned to Central Asia via more easterly routes south of the Caspian Sea in spring (Terraube *et al.* 2012).

While we correctly anticipated the lower numbers of birds using the Eastern Black Sea in spring than autumn for many species, seasonal flyway use remains highly context-dependent, even within species. This is illustrated by Black Kites that use a broader front in spring than autumn in the Central Mediterranean Flyway (Panuccio *et al.* 2014, Onrubia *et al.* 2021), while we unexpectedly found the opposite scenario for Black Kites crossing the Caucasus. It remains challenging to generalize or predict such patterns, and so there remains much scope for dedicated observers to help complete the puzzle of seasonal raptor flyways through structured surveys across one or a few seasons.

Seasonal contrasts in migration phenology

Based on nine species for which we have data of comparable quality in both seasons, the main spring migration period lasted 24–50 days (Table 3) and the core migration period was 8–29 days (Table 4). The duration of species' migration periods was not significantly correlated between seasons. Species with longer

core and main migration periods in autumn tended to have longer migration periods in spring (Figure 3C, D). The order in which species migrated was significantly and negatively correlated between seasons (Figure 3A), meaning that the earliest spring migrants tended to be the latest autumn migrants (e.g. Short-toed Eagle) and latest spring migrants tended to be the earliest autumn migrants (e.g. Honey Buzzard). Such between-species differences in the phenology and duration of migration tend to be associated with life-history and functional traits such as migration distance, length of breeding season, breeding area size, longevity, wing morphology (and associated flight mode) and the extent to which demographic groups differ in timing within species (Leshem & Yom-Tov 1996, Bildstein 2006, Newton 2023).

Generally, adult birds are expected to exhibit a higher pace of migration, and potentially a more synchronised passage in spring compared to autumn in an attempt to reach the breeding grounds earlier and occupy high-quality territories (Kokko 1999, Nilsson *et al.* 2013). That the majority of common species showed (significantly) longer main migration periods in spring than autumn at Batumi seemingly suggests otherwise. However, as no distinction was made between age classes in this study, this effect is likely due to a larger spread in the timing of different age groups during spring migration (Phipps *et al.* 2019, Weiss *et al.* 2019). Long tails typically accounted for a much larger portion of the main migration period than the early or core migration periods. Contrary to the main migration period (i.e. central 90% period), the duration of the core migration period (i.e. central 50% period) did not differ significantly between seasons in any species. This points more towards these core periods mostly involving adult breeders. There are likely also sex differences in timing of adults that we could not uncover in this study. But while previous studies have revealed that males and females may pass in reverse order in spring than in autumn, we do not expect that the longer spring migration periods in Batumi are due to greater sex differences in timing (Cento *et al.* 2021, Chiatante *et al.* 2024).

The seasonal difference in duration of the main migration period is by far most pronounced for the Lesser Spotted Eagle. A long-lived species with a protracted immature phase, in which juveniles and adults show strong overlap in autumn migration timing (Meyburg *et al.* 2017, Vansteelant *et al.* 2020), whereas immatures migrate much later than adults in spring (Meyburg *et al.* 2001). A similar seasonal pattern would be expected and also seems to emerge from our seasonal data, for other large and long-lived *Aquila* and *Clanga* eagles at Batumi. Unfortunately, we achieved insufficient coverage of these species in autumn to make a formal seasonal comparison. The seasonal difference in migration duration seems to be only small for species like Short-toed Eagle, Booted Eagle and especially Honey Buzzard (Mirski *et al.* 2024). These species show long tails in spring migration and tend to show delayed immature migration in spring as do *Aquila* and *Clanga* eagles, but also the autumn migration of juveniles is delayed by several days or weeks compared to adults (Vansteelant *et al.* 2017, 2020). In other species with relatively small seasonal differences in migration duration, like Black Kite, there is hardly any difference in the autumn timing of juveniles and adults – as has been previously found in large eagles (Vansteelant *et al.* 2020); however, Black Kite was found to differ from large eagles in that limited age differences in timing were also found during spring (Sergio *et al.* 2014).

Current spring phenology in the context of historical data

Comparing the timing of various species in our spring surveys to historical spring migration data from the 1970s and 80s summarised by Abuladze (2013), it appears that the spring migration period of Black Kites has remained identical, with the main period occurring from late March to mid-April, with the peak in the first week of April. By contrast, Short-toed Eagles showed a substantially earlier spring migration in our surveys (peak at the end of March) compared to historical data (peak 10–20 April). As such, Short-toed Eagle is the only species for which our data suggest a substantial advance in timing may have taken place compared to several decades ago, which would be consistent with general expectations about how migrants ought to respond to climate change (Newton 2023). Furthermore, short-distance migrants are expected to respond more quickly to climate change than long-distance, trans-Saharan migrants (Newton 2023), and (a seemingly growing) part of the Short-toed Eagle population spends the non-breeding season around the Mediterranean (Vansteelant *et al.* 2020). However, for almost all other species for which historical data are provided by Abuladze (2013), our data suggest that spring migration now occurs later in the season than it did several decades ago, regardless of the species' non-breeding distributions. For example, Abuladze (2013) suggests that the Steppe Buzzard already showed relatively strong movement during early March whereas we only saw substantial passage after 20 March with peak

days in early April. Other examples, where our data indicate a substantially later peak and longer tails in spring migration periods, are Marsh, Montagu's and Pallid Harrier, Levant and Eurasian Sparrowhawk, Lesser Spotted Eagle and Booted Eagle. While these comparisons are fraught with numerous issues, the implied phenological changes would be quite large in some cases (up to 2–3 weeks) and cannot easily be dismissed, even if they run counter to general expectations.

Implications for monitoring, conservation and avitourism

The possibility of monitoring juvenile numbers, and thus reproductive success, is often what makes post-breeding autumn migration the primary focus of long-term raptor migration surveys (Jobson *et al.* 2021). Even though our pilot surveys proved the eastern Black Sea coast to be a principal spring migration flyway for many Palearctic raptors, the potential for systematic monitoring of spring raptor abundance and demography seems more limited than in autumn. Nevertheless, the data presented here offer a useful baseline to detect long-term changes in raptor migration by repeating small-scale spring surveys every 6–10 years. Even though this would limit the power to detect only moderate to large changes (Lewis & Gould 2000), intermittent migration counts may still be used for population and conservation assessments of selected species (Weiss *et al.* 2019).

Furthermore, our pilot surveys provide great potential to expand conservation and environmental education efforts in the Batumi region during spring migration. In particular, the knowledge we gained about the intensity and timing of spring migration can help designing and planning migration-based education projects. This is relevant because schools in the region are mostly operating field excursions in spring, whereas schools are closed until far into the autumn migration.

Similar to autumn, the Batumi region has the potential to attract significant migration-based avitourism activity in spring. Aside from the spectacular migration of large eagles and Black Kites early in the season, our field experience suggests that the presence of non-raptor migrants throughout the season, both on the count site and in surrounding natural areas, is much more pronounced in spring than in autumn. Additionally, illegal bird hunting – which is a persistent issue that affects migrating raptors (Sándor *et al.* 2017, Sándor & Anthony 2018) and keeps many potential ecotourists from visiting Batumi in autumn – rarely takes place in spring (van Maanen *et al.* 2001, Sándor *et al.* 2017, own obs.). And while the absence of a dedicated monitoring team may make the site somewhat less attractive in spring, some potential visitors may prefer to visit outside the main avitourism season. The general housing availability remains similar to autumn and the current lack of infrastructure tailored to spring conditions (i.e. an appropriately placed, sheltered observatory) could be remediated relatively easily by targeted investments.

Conclusions

In conclusion, our full-season spring surveys yielded novel insights into the seasonal importance of the eastern Black Sea Flyway for Palearctic raptor species. In fact, our publicly visible data have already been used to this end by several authors (e.g. Altundağ & Karatas 2020, McGrady *et al.* 2021, Meyburg 2021, Onrubia & Martin 2021, Stark & Liechti 2021, Väli & Mirski 2021). BRC does not deem it favourable to invest in structured annual spring monitoring. However, intermittent spring migration surveys may allow the detection of demographic and phenological changes in Palearctic raptor species. As migration survey and monitoring efforts continue to grow at known bottlenecks (Murgatroyd *et al.* 2021, Noby *et al.* 2022) and newly discovered sites (Panuccio *et al.* 2018, Jobson *et al.* 2021), and with new tracking studies underway (Efrat *et al.* 2025), we can look forward to exciting discoveries about East African-Eurasian raptor migration in the near future.

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REFERENCES

Abuladze A. 2013. Birds of prey of Georgia. Institute of Zoology, Ilia State University.

Abuladze A.V. & Edisherashvili G.V. 2003. Raptor migration in Georgia in spring and autumn 1998. In: Prof. Galushin (ed.) Proceedings of the 4th Conference on Raptors of Northern Eurasia. Rostov-on-Don State Pedagogical University, pp. 106–109.

Agostini N., Prommer M., Váczi M. & Panuccio M. 2019. Repeated large scale loop migrations of an adult European honey buzzard. Avocetta 43: 13–21.

Altundağ U.A. & Karataş A. 2013. Soaring bird migration in 2015 spring at Belen Pass, Hatay, Turkey. Biharean Biol. 14: 109–115.

Andrews J., Beaman M., Fisher P., Hereward T., Heubeck M., Morton M., Porter R. & Round P. 1977. A new raptor migration route through N.E. Turkey. Bull. Ornithol. Soc. Turkey 14: 2–5.

Arslangündoğdu Z., Smith L., Yardim, Vanmarcke P. J. & Payne M. 2018. Soaring bird migration research at the Bosphorus Strait, Turkey. App. Ecol. Environ. Res. 16: 7953–7968.

Batista C., Miro R., Angehr G. & Bildstein K. 2004. More than three million migrating raptors counted ocean-to-ocean in Panama, autumn 2004. Hawk Migr. Stud. Fall 2004: 5–6.

Bayly N.J., Cárdenas Ortiz L., Rubio M. & Gómez C. 2014. Migration of raptors, swallows and other diurnal migratory birds through the Darien of Colombia. Ornitol. Neotrop. 25: 63–71.

Bensusan K.J., Garcia E.F.J. & Cortes J.E. 2007. Trends in abundance of migrating raptors at Gibraltar in spring. Ardea 95: 83–90.

Berthiaume É., Bélisle M. & Savard J.P. 2009. Incorporating detectability into analyses of population trends based on hawk counts: a double-observer approach. Condor 111: 43–58.

Bildstein K.L. (ed.) 2006. Migrating raptors of the world: their ecology and conservation. Cornell University Press, Ithaca.

Bildstein K.L. & Zalles J. 2001. Raptor migration along the Mesoamerican land corridor. In: Bildstein K. & Klem D. (eds) Hawkwatching in the Americas. Cornell University Press, Ithaca, pp. 119–141.

Bohrer G., Brandes D., Mandel J.T., Bildstein K.L., Miller T.A., Lanzone M., Katzner T., Maisonneuve C. & Tremblay J.A. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. Ecol. Lett. 15: 96–103.

Cento M., Malpassuti V., Dell'Omo G. & Agostini N. 2021. Differential timing of autumn migration between sex groups in adult European honey buzzards *Pernis apivorus*. Avian Biol. Res. 14: 55–58.

Chiatante G., Gustin M., Cento M., Dell'Omo G. & Agostini N. 2024. Sex differences in the timing of spring migration of adult European honey buzzards (*Pernis apivorus*) in the Central Mediterranean. J. Ornithol. 165: 841–845.

Corso A. & Cardelli C. 2004. The migration of Pallid Harrier across the central Mediterranean: with particular reference to the Strait of Messina. Br. Birds 97: 238–246.

Efrat R., Lehnardt Y., Berkowic D., Leshem Y., Dor R., Bragin A., Bragin E., Katzner T. & Sapir N. 2025. Using GPS tracking data to validate the conservation value of bird migration counts. Biol. Cons. 302: 110959.

Evans P.R. & Lathbury G.W. 1973. Raptor migration across the Straits of Gibraltar. Ibis 115: 572–585.

Finlayson C. 1992. Birds of the Strait of Gibraltar. T. & A.D. Poyser, London.

Forsman D. (ed.) 2016. Flight identification of raptors of Europe, North Africa and the Middle East. Bloomsbury Publishing, London.

Fülöp A., Kovács I., Baltag E., Daróczi S.J., Dehelean A.S., Dehelean L.A., Kis R.B., Komáromi I.S., Latková H., Miholcsa T., Nagy A., Ölvedi S.Z., Papp T., Sándor A.K., Zeitz R. & Kelemen M.A. 2014. Autumn migration of soaring birds at Bosporus: validating a new survey station design. Bird Study 61: 264–269.

Gálvez R.A., Gavashelishvili L. & Javakhishvili Z. (eds) 2005. Raptors and owls of Georgia. GCCW and Buneba Print Publishing, Tbilisi.

Gyllin R. 1974. Spring migration of raptors over East Turkey and Northwest Iran. Die Vogelwarte 27: 243–247.

Heiss M. 2013. The importance of Besh Barmag bottleneck (Azerbaijan) for Eurasian migrant birds. Acta Ornithol. 48: 151–164.

Heiss M. 2016. Records of globally red-listed bird species migrating through the Besh Barmag bottleneck, Azerbaijan Republic. Podoces 11: 43–52.

Heiss M., Gauger K., Himmel C., Fetting P., Haraldsson T.A., Caucal G., Fərəcli Z. & Sultanov E. 2020. The development of the Besh Barmag Bird Migration Count in Azerbaijan and its importance for the monitoring of Eurasian migrant birds. Sandgrouse 42: 29–45.

Hoekstra E. & Jansen E. 2022. Spring report 2022 – Batumi Raptor Count. www.batumiraptorcount.org/spring-report-2022

Javed S., Khan S., Nazeer J., Ahmed S., Al Hammadi A. & Al Hammadi E. 2014. Satellite tracking of a young Steppe Eagle from the United Arab Emirates during two spring and autumn migrations. Ostrich 85: 131–138.

Jobson B., Allinson T., Sheldon R., Vansteelant W., Buechley E., Oppel S. & Jones V.R. 2021. Monitoring of migratory soaring birds in the East African–Eurasian flyway: a review and recommendations for future steps. Sandgrouse 43: 2–23.

Karyakin I.V., Nikolenko E.G. & Shnayder E.P. 2023. Steppe Eagle in the Altai-Sayan Region – Research results 2019–2023. Raptors Conservation – Proceedings of Conferences, Suppl. 2: 233–241.

Karyakin I.V., Nikolenko E.G., Shnayder E.P., Zinevich L.S., Pulikova G.I., Bartoszuk K., Horváth M., Juhász T., Aghababyan K. & Andreyenkova N.G. 2019. Results of the GPS/GSM-tracking of juvenile Steppe Eagles from Russia and Kazakhstan. Raptors Conserv. 39: 71–227.

Katzner T.E., Bragin E.A., Bragin A.E., McGrady M., Miller T.A. & Bildstein K.L. 2016. Unusual clockwise loop migration lengthens travel distances and increases potential risks for a central Asian, long-distance, trans-equatorial migrant, the Red-footed Falcon *Falco vespertinus*. Bird Study 63: 406– 412.

Keijmel M., Babbington J., Roberts P. & Meyburg B.-U. 2020. The world's largest gathering of Steppe Eagles *Aquila nipalensis* discovered in central Saudi Arabia. Sandgrouse 42: 59–68.

Keller V., Herrando S. & Vorisek P. (eds) 2020. European Breeding Bird Atlas 2: distribution, abundance and change. European Bird Census Council & Lynx Editions, Barcelona.

Kerlinger P. (ed.) 1989. Flight strategies of migrating hawks. University of Chicago Press, Chicago.
Kjellen N. 1992. Differential timing of autumn migration between sex and age groups in raptors at Falsterbo, Sweden. Ornis Scand. 23: 420–434.
Kokko H. 1999. Competition for early arrival in migratory birds. J. Anim. Ecol. 68: 940–950.
Leshem Y. & Yom-Tov Y. 1996. Routes of migrating soaring birds. Ibis 140: 41–52.
Lewis S.A. & Gould W.R. 2000. Survey effort effects on power to detect trends in raptor migration counts. Wildl. Soc. Bull. 28: 317–329.
Limiñana R., Soutullo A. & Urios V. 2007. Autumn migration of Montagu's harriers *Circus pygargus* tracked by satellite telemetry. J. Ornithol. 148: 517–523.
McCrary J.K. & Young D.P. 2008. New and noteworthy observations of raptors in southward migration in Nicaragua. Ornitol. Neotrop. 19: 573–580.
McGrady M., Bragin E., Karyakin I., Batbayar N. & Katzner T. 2021. Steppe Eagle *Aquila nipalensis*. In: Panuccio M., Mellone U. & Agostini A. (eds) Migration strategies of birds of prey in Western Palearctic. CRC Press, Boca Raton, pp. 108–116.
Mellone U. 2020. Sea crossing as a major determinant for the evolution of migratory strategies in soaring birds. J. Anim. Ecol. 89: 1298–1301.
Meyburg B.-U., Bergmanis U., Langgemach T., Graszynski K., Hinz A., Börner I., Meyburg C. & Vansteelant W.M.G. 2017. Orientation of native versus translocated juvenile lesser spotted eagles (*Clanga pomarina*) on the first autumn migration. J. Exp. Biol. 220: 2765–2776.
Meyburg B.-U., Ellis D.H., Meyburg C., Mendelsohn J.M. & Scheller W. 2001. Satellite tracking of two lesser spotted eagles, *Aquila pomarina*, migrating from Namibia. Ostrich 72: 35–40.
Meyburg B.-U., Meyburg C., Bělka T., Šreibr O. & Vrana J. 2004. Migration, wintering and breeding of a lesser spotted eagle (*Aquila pomarina*) from Slovakia tracked by satellite. J. Ornithol. 145: 1–7.
Meyburg B.-U. 2021. Lesser spotted eagle *Clanga pomarina*. In: Panuccio M., Mellone U. & Agostini A. (eds) Migration strategies of birds of prey in Western Palearctic. CRC Press, Boca Raton, pp. 76–87.
Meyburg B.-U. & Meyburg C. 2009. Annual cycle, timing and speed of migration of a pair of lesser spotted eagles (*Aquila pomarina*) – a study by means of satellite telemetry. Populationsökologie Greifvogel- und Eulenarten 6: 63–85.
Meyburg B.-U., Meyburg C. & Paillat P. 2012. Steppe eagle migration strategies revealed by satellite telemetry. Br. Birds 105: 506–519.
Meyburg B.-U., Scheller W. & Meyburg C. 2000. Migration and wintering of the lesser spotted eagle *Aquila pomarina*: a study by means of satellite telemetry. Glob. Environ. Res. 4: 183–193.
Michev T.M., Profirov L., Nyagolov K. & Dimitrov M. 2011. The autumn migration of soaring birds at Bourgas Bay, Bulgaria. Br. Birds 104: 16–37.
Mirski P., Vansteelant W. & Byholm P. 2024. Natal dispersal and process of recruitment in a long-lived, trans-continentally migrating bird. BioRxiv. doi:10.1101/2024.05.17.594760
Murgatroyd M., Buechley E.R., De La A., Muñoz C., Ramirez Roman J., Caucal G., Ruffo A. & Rayaleh H. 2021. Observations of large-scale diurnal raptor migration in the Horn of Africa. Sandgrouse 43: 24–33.
NASA JPL 2013. NASA Shuttle Radar Topography Mission Global 1 arc second [Data set]. NASA EOSDIS Land Processes Distributed Active Archive Center. (accessed 1/5/2025) doi:10.5067/measures/srtm/srtmgl1.003
Newton I. (ed.) 2023. The migration ecology of birds, 2nd ed. Elsevier Ltd, Amsterdam.
Niles L.J., Burger J. & Clark K.E. 1996. The influence of weather, geography, and habitat on migrating raptors on Cape May Peninsula. Condor 98: 382–394.
Nilsson C., Klaassen R.H.G. & Alerstam T. 2013. Differences in speed and duration of bird migration between spring and autumn. Am. Nat. 181: 837–845.
Noby K. *et al.* & Oppel S. 2022. Globally important proportions of six raptor populations migrate past Galala Bird Observatory, Egypt, in spring. Sandgrouse 44: 410–420.
Nourani E., Vansteelant W.M.G., Byholm P. & Safi K. 2020. Dynamics of the energy seascape can explain intra-specific variations in sea-crossing behaviour of soaring birds. Biol. Lett. 16: 1–5.
Nourani E., Yamaguchi N.M., Manda A. & Higuchi H. 2016. Wind conditions facilitate the seasonal water-crossing behaviour of Oriental honey-buzzards *Pernis ptilorhynchus* over the East China Sea. Ibis 158: 506–518.
Onrubia A. 2015. Spatial and temporal patterns of soaring bird migration through the Straits of Gibraltar. PhD dissertation, University of Leon.
Onrubia A. & Martín B. 2021. Black kite *Milvus migrans*. In: Panuccio M., Mellone U. & Agostini A. (eds), Migration strategies of birds of prey in Western Palearctic. CRC Press, Boca Raton, pp. 165–179.
Panuccio M., Agostini N., Baghino L. & Bogliani G. 2013. Visible migration of Short-toed Snake Eagles: interplay of weather and topographical features. J. Raptor Res. 47: 60–68.
Panuccio M., Agostini N. & Mellone U. 2021. Raptors as models to study animal migrations. In: Panuccio M., Mellone U. & Agostini A. (eds) Migration strategies of birds of prey in Western Palearctic. CRC Press, Boca Raton, pp. 1–10.
Panuccio M., Agostini N., Mellone U. & Bogliani G. 2014. Circannual variation in movement patterns of the Black Kite (*Milvus migrans migrans*): a review. Ethol. Ecol. Evol. 26: 1–18.
Panuccio M., Ghafouri B. & Nourani E. 2018. Is the slope between the Alborz Mountains and Caspian Sea in northern Iran a bottleneck for migrating raptors? J. Raptor Res. 52: 530–533.
Phipps W.L. *et al.* & Vallverdú N. 2019. Spatial and temporal variability in migration of a soaring raptor across three continents. Front. Ecol. Evol. 7: 1–14.
Porras-Peñaranda P., Robichaud L. & Branch F. 2004. New full-season count sites for raptor migration in Talamanca, Costa Rica. Ornitol. Neotrop. 15: 267–278.
Porter R.F. & Beaman M.A.S. 1985. A resume of raptor migration in Europe and the Middle East. ICBP Technical Publication 5: 237–242.
Ruelas E.I., Hoffman S.W., Goodrich L.J. & Tingay R. (eds) 2000. Conservation strategies for the world's largest known raptor migration flyway: Veracruz the River of Raptors. In: Chancellor R.D. & Meyburg B.U. (eds) Raptors at risk. WWGBP/Hancock House, Cambridge, pp. 591–596.

Ruelas E.I. *et al.* & Barrios J.G. 2009. Long-term conservation of migratory birds in México: the Veracruz River of Raptors project. Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics, pp. 577–589.

Sandor A. & Anthony B.P. 2018. Mapping the conflict of raptor conservation and recreational shooting in the Batumi Bottleneck, Republic of Georgia. J. Threat. Taxa 10: 11850–11862.

Sandor A., Jansen J. & Vansteelant W.M. 2017. Understanding hunters' habits and motivations for shooting raptors in the Batumi raptor-migration bottleneck, southwest Georgia. Sandgrouse 39: 4–17.

Schmid H. 2000. Getrennte Wege der Herbstzug von juvenilen und adulten Wespenbussarden *Pernis apivorus* – eine Synthese. Ornithol. Beob. 97: 191–222.

Sergio F., Tanferna A., De Stephanis R., Jiménez L. L., Blas J., Tavecchia G., Preatoni D. & Hiraldo F. 2014. Individual improvements and selective mortality shape lifelong migratory performance. Nat. 515: 410–413.

Sergio F., Tavecchia G., Tanferna A., Blas J., Blanco G. & Hiraldo F. 2019. When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: individual vs population implications. Sci. Rep. 9: 1–8.

Serratosa J. *et al.* & Jones V.R. 2024. Tracking data highlight the importance of human-induced mortality for large migratory birds at a flyway scale. Biol. Conserv. 293: 1–16.

Shi X. U., Xiao X., Zhao X., Sun R., Zhao X., Choi C.Y. & Lin W. 2023. Raptor migration at Guantouling, south-west China: phenology, weather influence and persecution pressure. Bird Conserv. Int. 33: 1–14.

Shirihai H., Yosef R., Alon D., Kirwan G. & Spaar R. 2000. Raptor migration in Israel and the Middle East. Technical Publication International Birding & Research Centre, Eilat.

Spaar R. 1997. Flight strategies of migrating raptors; a comparative study of interspecific variation in flight characteristics. Ibis 139: 523–535.

Stanciu C.R., Zaharia R., Chişamera G.B., Cobzaru I., Gavril V.D. & Murariu D. 2017. Migration strategies of common buzzard (*Buteo buteo* Linnaeus, 1758) in Dobruja. Trav. Mus. Natl. Hist. Nat. Grigore Antipa 60: 537–545.

Stark H. & Liechti F. 2021. Levant sparrowhawk *Accipiter brevipes*. In: Panuccio M., Mellone U. & Agostini A. (eds) Migration strategies of birds of prey in Western Palearctic, CRC Press, Boca Raton, pp. 125–128.

Strandberg R., Klaassen R.H.G. & Thorup K. 2009. Spatio-temporal distribution of migrating raptors: a comparison of ringing and satellite tracking. J. Avian Biol. 40: 500–510.

Tal T. 2020. Spring Report 2020 – Batumi Raptor Count. www.batumiraptorcount.org/spring-report-2020

Tal T., Jansen D. & Vansteelant W.M.G. 2021. Opportunistic in-flight foraging behaviour of black kites *Milvus migrans* during spring migration through the Batumi bottleneck, Georgia. Sandgrouse 43: 247–252.

Tal T. & Jansen D. 2019. Spring Report 2019 – Batumi Raptor Count. www.batumiraptorcount.org/spring-report-2019

Terraube J., Mougeot F., Cornulier T., Verma A., Gavrilov A. & Arroyo B. 2012. Broad wintering range and intercontinental migratory divide within a core population of the near-threatened pallid harrier. Divers. Distrib. 18: 401–409.

Trierweiler C. 2010. Travels to feed and food to breed: the annual cycle of a migratory raptor, Montagu's harrier, in a modern world. PhD dissertation, University of Groningen.

Ullman M. & Ullman M. 2010. Migration of harriers and other raptors at Ashura deh, Iran, April 2008. Sandgrouse 32: 4–12.

Üner O., Ali Boyla K., Bacak E., Birel E., Celikoba I., Dalyan C., Tabur E. & Yardim Ü. 2010. Spring migration of soaring birds over the Bosphorus, Turkey, in 2006. Sandgrouse 32: 20–33.

Väli Ü. & Mirski P. 2021. Eurasian buzzard *Buteo buteo*. In: Panuccio M., Mellone U. & Agostini A. (eds) Migration strategies of birds of prey in Western Palearctic, CRC Press, Boca Raton, pp. 188–199.

Van Maanen E., Goradze I., Gavashelishvili A. & Goradze R. 2001. Opinion; trapping and hunting of migratory raptors in western Georgia. Bird Conserv. Int. 11: 77–92.

Vansteelant W.M.G. & Agostini N. 2021. European honey buzzard *Pernis apivorus*. In: Panuccio M., Mellone U. & Agostini A. (eds) Migration strategies of birds of prey in Western Palearctic. CRC Press, Boca Raton, pp. 125–128.

Vansteelant W.M.G., Kekkonen J. & Byholm P. 2017. Wind conditions and geography shape the first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan Africa. Proc. R. Soc. B. 284: 1–9.

Vansteelant W.M.G., Verhelst B., Shamoun-Baranes J., Bouten W., van Loon E.E. & Bildstein K.L. 2014. Effect of wind, thermal convection, and variation in flight strategies on the daily rhythm and flight paths of migrating raptors at Georgia's Black Sea coast. J. Field Ornithol. 85: 40–55.

Vansteelant W.M.G., Wehrmann J., Engelen D., Jansen J., Verhelst B., Benjumea R., Cavaillès S., Kaasiku T., Hoekstra B. & de Boer F. 2020. Accounting for differential migration strategies between age groups to monitor raptor population dynamics in the eastern Black Sea flyway. Ibis 162: 356–372.

Verhelst B., Jansen J. & Vansteelant W. 2011. South West Georgia: an important bottleneck for raptor migration during autumn. Ardea 99: 137–146.

Wehrmann J., de Boer F., Benjumea R., Cavaillès S., Jansen J., Verhelst B. & Vansteelant W.M.G. 2019. Batumi Raptor Count: autumn raptor migration count data from the Batumi bottleneck, Republic of Georgia. ZooKeys 836: 135–157.

Weiss N., Haviv E., Alon D., Perlman Y. & Schäckermann J. 2019. How fast does the steppe eagle population decline? Survey results from Eilat, Israel. Raptors Conservation 38: 59–67.

Yosef R., Fornasari L., Tryjanowski P., Bechard M.J., Kaltenecker G.S. & Bildstein K. 2003. Differential spring migration of adult and juvenile Levant sparrowhawks (*Accipiter brevipes*) through Eilat, Israel. J. Raptor Res. 37: 31–36.

Yosef R., Tryjanowski P. & Bildstein K.L. 2002. Spring migration of adult and immature buzzards *Buteo buteo* through Eilat, Israel: timing and body size. J. Raptor Res. 36: 115–120.

Zalles J.I. & Bildstein K.L. (eds) 2000. Raptor watch: a global directory of raptor migration sites. BirdLife International & Hawk Mountain Sanctuary.

Zaytseva O., Hoekstra B., Jansen J., Engelen D., de Boer F., Benjumea R., Wehrmann J., Cavaillès S., Kaasiku T., Jansen D., Fetting P., Aintila A. & Vansteelant W. 2022. Thirteen years of counting raptor migration in Batumi: observations and their importance for raptor conservation in Russia. Raptors Conserv. 44: 10–42.

SAMENVATTING

De mate waarin trekvogels gebruikmaken van specifieke trekroutes, hangt voor een belangrijk deel af van geografische obstakels die ze tegenkomen, zoals grote wateren en gebergtes. Ook het jaargetijde en de trekrichting spelen daarbij een rol. Nabij Batumi, Georgië, vormen de oostelijke Zwarte Zeekust en de Kleine Kaukasus, een 10–20 km brede trechter waar ieder najaar ruim één miljoen roofvogels doorheen trekken. Hoewel deze obstakels in het voorjaar minder prominent lijken, wijzen historische waarnemingen erop dat ook dan vele duizenden roofvogels het gebied passeren. Om inzicht te krijgen in de samenstelling en aantallen van die voorjaarstrek voerden wij in 2019, 2020 en 2022 systematische, seizoensdekkende tellingen uit. In totaal werden 33 roofvogelsoorten geregistreerd, met gemiddeld 542.161 individuen per voorjaar (spreiding: 455.799–618.848). De meest talrijke soorten waren Zwarte Wouw *Milvus migrans* (239.649 ± 22.547) en Steppebuizerd *Buteo buteo vulpinus* (194.029 ± 102.702). De hoogste intensiteit van trek vond voor de meeste soorten plaats van eind maart tot half april, gebaseerd op de doortrekmediaan van 12 van de 15 meest algemene soorten (>100 individuen/jaar). Soorten met een langere trekperiode in het najaar vertoonden ook een relatief langere trekperiode in het voorjaar. Voor de meeste soorten was de totale trekperiode in het voorjaar echter langer, vermoedelijk door leeftijdsafhankelijke migratiestrategieën binnen de soorten. Voor de meeste soorten waren de totale aantallen in het voorjaar kleiner dan in het najaar, vermoedelijk door een zwakker effect van geografische obstakels. Vooral laat doortrekkende soorten waren in het voorjaar minder talrijk, mogelijk door veranderende weerspatronen later in het voorjaar, waardoor vogels minder naar de kust worden gedrukt. Desalniettemin tonen onze resultaten aan dat de oostelijke Zwarte Zeekust een belangrijke schakel vormt tijdens de voorjaarstrek langs de oostelijke Afrikaans–Euraziatische trekroute van meerdere Palearctische roofvogelsoorten. Daarnaast biedt ons onderzoek een belangrijke basis voor het monitoren van veranderingen in trekpatronen en voor het ontwikkelen van beschermings- en onderzoeksactiviteiten in de Batumi regio gedurende het voorjaar.

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SUPPLEMENTARY MATERIAL

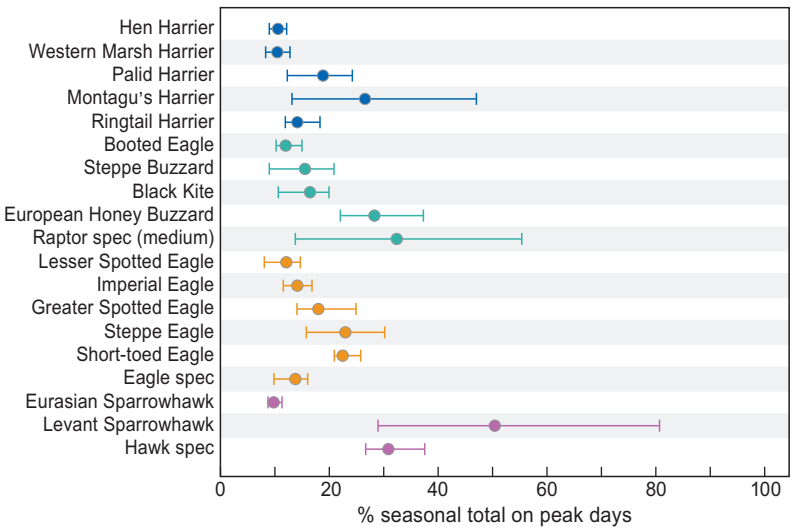

Figure S1. The mean percentage of birds seen on the biggest peak day of each season (dot). The whiskers indicate the minimum and maximum percentage recorded for each species in any of the years. Colours denote morphological groups (blue: harriers, green: medium raptors, orange: large eagles and purple: sparrowhawks).

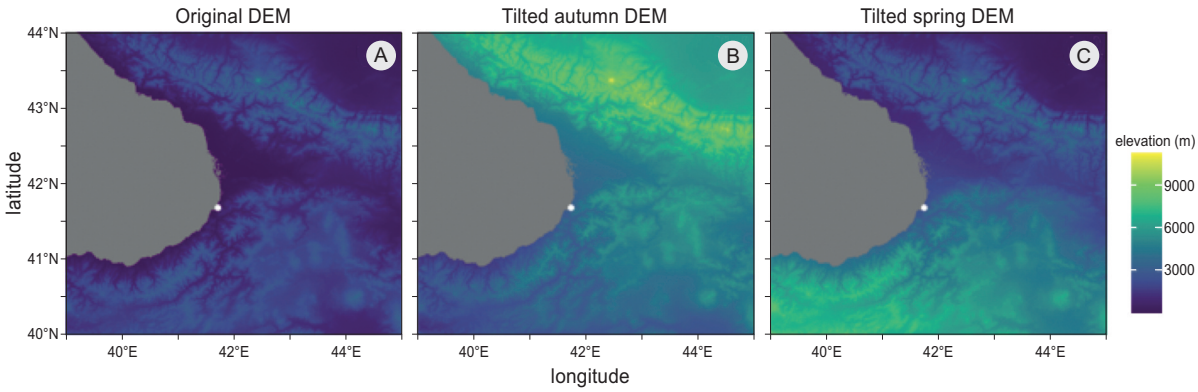

Figure S2. (A) The DEM without tilt, (B) the tilted DEM for autumn and (C) the tilted DEM for spring. The colour indicates the geographical elevations used in the least-cost path analysis shown in Figure 1.

Table S1. Comparison of the spring and autumn rounded mean annual counts for non-raptor species. Including the standard deviation and the number of years (i.e. seasonal surveys) in which the species has been observed and on which the annual metrics are based.

Species	Spring			Autumn		
	Mean	SD	Years	Mean	SD	Years
Black Stork *Ciconia nigra*	435	153	3	1732	181	3
Eurasian Crane *Grus grus*	282	186	3	248	73	3
European Roller *Coracias garrulus*	12	6	3	1534	530	3
Stock Dove *Columba oenas*	100	120	3	1188	607	3
European Turtle Dove *Streptopelia turtur*	6	4	2	1354	1192	3
Great White Pelican *Pelecanus onocrotalus*	3	–	1	90	–	1
White Stork *Ciconia ciconia*	85	47	3	470	151	3
Common Wood Pigeon *Columba palumbus*	433	197	3	752	756	3