

Accounting for differential migration strategies between age groups to monitor raptor population dynamics in the eastern Black Sea flyway

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Migration counts can offer a cost-effective method for monitoring the state of migrant raptor populations. However, differential migration strategies between inexperienced juveniles and experienced non-juveniles are rarely accounted for when inferring population trends from raptor migration counts. Since 2011, the Batumi Raptor Count (BRC) monitors the autumn migration of more than 1 million raptors along the eastern Black Sea coast in the Republic of Georgia. We also systematically sampled age information to assess differential migration timing between age groups and estimate age-specific linear trends in abundance between 2011 and 2018 for eight focal species. In so doing we aimed (1) to reassess the global relevance of BRC counts for each species and the potential for monitoring abundance of juveniles and non-juveniles, and (2) to identify demographic changes underlying recent trends in overall abundance. We found that the mean annual passage of non-juveniles at Batumi represents at least 1% of the estimated global breeding population of five study species. As expected, counts of juveniles were more variable than counts of non-juveniles. Yet despite our short monitoring period our models had sufficient statistical power to detect changes in abundance of 10%/year or less for at least one age group in all species except Pallid Harrier *Circus macrourus*. Our results indicate stable abundance and demography for half of the study species. We also found strong and significant increases in the abundance of Black Kites *Milvus migrans* and Short-toed Eagles *Circus gallicus* that were primarily due to increasing numbers of non-juveniles. By contrast, juvenile Montagu's Harriers *Circus pygargus* and Booted Eagles *Hieraaetus pennatus* significantly decreased in abundance. The first decade of BRC surveys offers an important benchmark for monitoring raptor populations using the eastern African–Palearctic flyway in the 21st century. We discuss possible causes of the observed trends and hope our work will stimulate demographic monitoring at migration count sites.

Keywords: citizen science, migration count, monitoring, phenology, population trends.

Many raptors circumvent large water bodies and other barriers and follow topographical leading lines during long-distance migration. This causes large

seasonal aggregations of migrant raptors at so-called geographical convergence zones or bottlenecks (Kerlinger 1989, Zalles & Bildstein 2000). Such aggregations are especially common among broad-winged soaring migrants with a strong preference to migrate over land, such as buzzards and eagles (Porter & Beaman 1985, Leshem & Yom-Tov 1996,

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Zalles & Bildstein 2000). Trends in the abundance and timing of migrating raptors have been shown to reflect real population change in the past, so that migration counts can be a highly cost-effective method for monitoring large-scale population trends of these species (Bednarz *et al.* 1990, Kjellén & Roos 2000, Farmer *et al.* 2007, 2010, Martín *et al.* 2016).

Whereas it is possible to distinguish juvenile raptors from elder conspecifics based on plumage characteristics during autumn migration (Forsman 2016), few long-term monitoring studies discriminate between age groups for monitoring raptor migration dynamics (Bednarz *et al.* 1990, Kjellén 1998, Mueller *et al.* 2000, Smith *et al.* 2008, Panuccio *et al.* 2017). This is somewhat surprising given that differential migration strategies between age groups have important implications for the interpretation of migration counts. For species that strongly depend on overland flyways for survival, i.e. the largest obligate soaring migrants (Oppel *et al.* 2015, Meyburg *et al.* 2017), juvenile counts may be indicative of breeding productivity and serve as an early-warning system for impending population change (Bednarz *et al.* 1990, Wright 2016). In many other cases, however, juvenile long-distance migrants depart later and migrate slower and over a broader front than elder conspecifics (Kjellén 1992, Maransky & Bildstein 2001, Sergio *et al.* 2014). Consequently, the extent to which juveniles from a given source population aggregate at a geographical bottleneck is likely to vary more between years than for experienced non-juveniles (Kjellén 1992, 1998, Vansteelant *et al.* 2017). In such cases, separating the juvenile counts from the overall species counts should improve our ability to detect changes in breeding populations.

In this study we aimed to assess recent demographic trends for eight raptor species on autumn migration through the Batumi bottleneck, situated between the eastern Black Sea coast and the foothills of the Lesser Caucasus, in the Republic of Georgia (Verhelst *et al.* 2011; Fig. 1). This is one of few places in the world where more than 1 million migrant raptors pass on migration each year. Since 2008 the Batumi Raptor Count has conducted daily migration counts from 17 August until 16 October from two strategic vantage points in the narrowest section of this geographical bottleneck, just to the north of the city of Batumi. Pilot surveys covering all raptor species in 2008 and 2009 indicated that for 13 species at least 1% of

the global population passes through the Batumi bottleneck during autumn (Verhelst *et al.* 2011). We developed a strategy to monitor the abundance and demography for the most relevant species with the help of citizen scientists who are trained and coordinated by expert fieldworkers (Wehrmann *et al.* 2019). Since 2011 we achieved a consistent count effort each year, and here we focus on those species for which we counted an average of at least 1000 individuals per year, and for which we cover the main migration period of both age groups. These included three facultative soaring harriers: Montagu's Harrier *Circus pygargus*, Pallid Harrier *Circus macrourus* and Western Marsh Harrier *Circus aeruginosus*; three medium-sized soaring migrants: Black Kite *Milvus migrans*, European Honey Buzzard *Pernis apivorus* and Booted Eagle *Hieraaetus pennatus*; and two large obligate soaring eagles: Short-toed Eagle *Circus gallicus*, and Lesser Spotted Eagle *Clanga pomarina*.

Most of the raptors passing through the Batumi bottleneck are probably born or breed in western Russia, with smaller numbers coming from as far west as Fennoscandia and as far east as Kazakhstan. There is currently no comprehensive information about the state of raptor populations in the core part of this breeding range. As such it is hard to make informed predictions about the status of our study species at Batumi. However, migration counts at other geographical bottlenecks suggest that raptor populations in the western world have mostly been stable or growing since the mid-20th century, especially due to improved legal protection (Bednarz *et al.* 1990, Kjellén & Roos 2000, Hoffman & Smith 2003, Bensusan *et al.* 2007). More recently, autumn migration counts in the West African–Palaeartic flyway, which also cover some of our study species, have continued to increase markedly in the 21st century. For example, the numbers of Black Kite and Short-toed Eagle passing by watch-sites in the western Pyrenees and at the Strait of Gibraltar nearly doubled between 1999 and 2013 (Martín *et al.* 2016). These increases could be due to continued population recovery in the case of Black Kite, a climate-induced expansion of the western European breeding range for Short-toed Eagle, as well as improved non-breeding survival due to these species increasingly overwintering in Europe (Martín *et al.* 2016). Closer to Batumi, record numbers of migrant raptors have been counted along the western Black Sea coast since 2011 (Michev *et al.* 2018), and

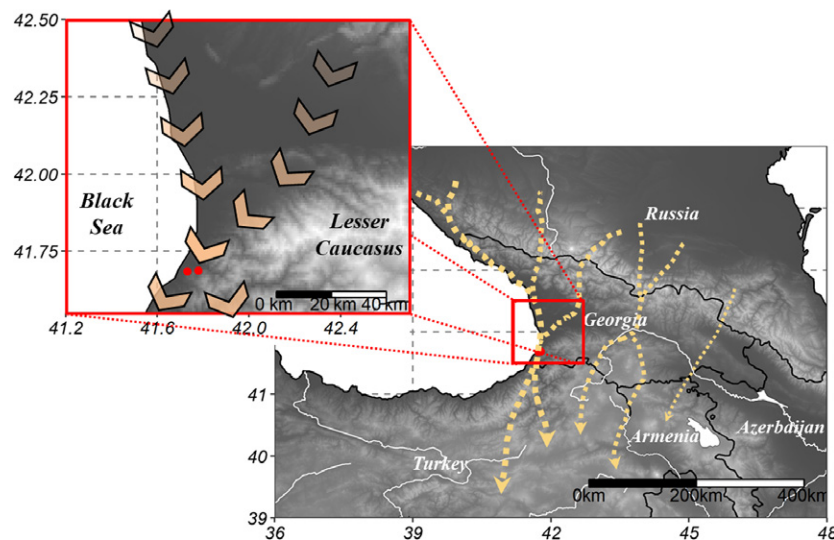


Figure 1. Migrant raptors breeding in Russia are funnelled towards the Caucasus by the Black Sea and Caspian Sea on their autumn migration. Raptors may cross the Greater Caucasus on the Russian–Georgian border along various routes but the most intense passage occurs along the eastern Black Sea coast in western Georgia (main map, based on Abuladze 2013). The eastern Black Sea flyway reaches its narrowest point between the foothills of the Lesser Caucasus in southwestern Georgia (inset). Here, citizen scientists of the Batumi Raptor Count conduct daily autumn raptor migration counts from two hilltop watch-sites (red dots).

counts of Lesser Spotted Eagle, Honey Buzzard and other raptors in Israel during 2000–2012 have been consistently higher than during the 1990s (Krumenacker 2012). An explanation for these increases is currently lacking but based on these reports, and despite the fact that considerable numbers of raptors fall victim to illegal shooting along the East African–Palearctic flyway (Van Maanen *et al.* 2001, Brochet *et al.* 2017, Sandor *et al.* 2017), we suspect that raptor populations using the eastern Black Sea coast are likely to have remained stable or to have grown since 2011.

Before analysing trends in abundance and demography, it is important to consider that not all our study species depend on overland flyways to the same extent. Indeed, facultative soaring species such as harriers typically show higher flexibility in route choice over a broader front compared with obligate soaring migrants such as eagles (Kerlinger 1989, Spaar 1997, Vardanis *et al.* 2011, Vansteelant *et al.* 2015) and thus migration counts of the former species tend to be more variable (Leshem & Yom-Tov 1996, Verhelst *et al.* 2011, Vansteelant *et al.* 2014). Furthermore, as pointed out above, juvenile counts are especially likely to be highly variable in facultative soaring species, which may restrict the potential to detect short-term changes in their abundance. Therefore, in

this study, we carefully assessed how differential migration timing and count variability influence the power of our age-specific linear trend analyses (*cf.* Lewis & Gould 2000). Furthermore, we compared mean annual counts of non-juvenile raptors with the most recent global population estimates (BirdLife International 2018) to reaffirm the global importance of the Batumi bottleneck for our study species. In so doing we acknowledge that non-juveniles may include a substantial proportion of non-breeding sub-adults and adults. However, by excluding juveniles from this comparison we significantly improved upon the original assessment of Batumi's global relevance (Verhelst *et al.* 2011). Having identified meaningful trends, we finally discuss the potential drivers of those trends. To do this we assumed that the annual abundance and proportion of juveniles was a reasonable proxy for annual productivity, whereas changes in non-juvenile abundance primarily reflected survival across the annual range.

METHODS

The Batumi bottleneck

The Batumi bottleneck is shaped geographically by the Black Sea to the west and the Lesser Caucasus

to the east, both considerable barriers for migrant raptors (Fig. 1). In late summer and early autumn, local weather is dominated by a regional sea-breeze circulation, which contributes to the development of dense cloud cover over the mountains and thereby exacerbates the aggregation of raptors towards the coast (Vansteelant *et al.* 2014). As raptors are streaming in from along the coast and across the lowlands of western Georgia, cloud development over the mountains enhances the funnelling effect of the interior mountains. Soaring raptors ultimately converge into a coastal corridor that reaches its narrowest point just to the north of the city of Batumi (Vansteelant *et al.* 2014).

The Batumi Raptor Count stations are situated at strategic vantage points on a line roughly perpendicular to the coast (Fig. 1). Two count stations are needed to be able to cover the weather-dependent flight paths of multiple species within the bottleneck (Vansteelant *et al.* 2014). Station 1 (41°41'04.1"N, 41°43'48.9"E, 324 m asl) is located 2.4 km from the Black Sea coast, and station 2 another 4 km further inland (41°41'13.2"N, 41°46'45.5"E, 414 m asl). Each station was staffed by 6–10 volunteers under the guidance of an experienced count coordinator from 17 August until 16 October. Daily counts took place between 1 h after sunrise until 2 h before sunset and were only interrupted during dangerous thunderstorms or downpours with no visible migration.

Dataset

The complete dataset containing 11 years of migration counts is made publicly available by Batumi Raptor Count through NLBIF (Wehrmann *et al.* 2018). Although counts started in 2008, consistent data quality was achieved only since 2011 after a series of logistical changes, improvements in the count protocol, a switch from analog to digital data recording, and the establishment of a dedicated team of count coordinators (Wehrmann *et al.* 2019). We thus restricted our analyses to the period 2011–2018.

We acknowledge that there is a risk of double-counting birds that pass between the two count stations. Most double counts, however, are avoided by intensive radio communication between count coordinators on both stations. Furthermore, every record is annotated with a distance code relative to the count station that allows for an *ad hoc* removal of remaining double counts, whereby the most

detailed records are retained for analyses. Our automated procedure for removing double counts was calibrated using a reference dataset of known single and double counts, and results in the removal of ~1% of all records per year (Wehrmann *et al.* 2019). For a detailed description of our field protocol, data management strategy and our publicly available dataset, we refer to Wehrmann *et al.* (2019).

Estimating daily and annual species totals

In this study we focus on eight abundant species for which we cover the main migration period of both age groups (see Introduction). Many birds, however, cannot be identified to species level in the field, due to the sheer intensity of migration that limits the available observation time for individual migrants, the challenging identification of certain species, and the often large distance between observers and birds. In these cases, we used various taxonomic or morphological groups to record such birds as accurately as possible. Within each of these groups we then estimated the daily total of each of the potentially confusing species using the daily proportions of those species among the birds that were identified in the field (*cf.* Verhelst *et al.* 2011, Vansteelant *et al.* 2014). For example, more than half of all *Clanga* and *Aquila* eagles are recorded as 'Large Eagle Spec.' (Table S1) because we encourage counters to only identify birds at sufficiently close range. We then estimated the number of Lesser Spotted Eagle, Greater Spotted Eagle *Clanga clanga* and Steppe Eagle *Aquila nipalensis* among the daily count of 'Large Eagle Spec.' based on the relative abundance of each of those species among the large eagles that were identified to species level. Full details on these calculations are provided in Wehrmann *et al.* (2019). As a proxy for data quality we summarized the proportion of annual species totals that was estimated from morphological groups (Table S1) and refer to Wehrmann *et al.* (2019) for a detailed overview of annual totals per species and morphological group in our raw data.

Estimating daily abundance per age group

Similar to identification, the feasibility of ageing raptors is restricted by the observation time that is

available depending on the intensity of migration. To be able to keep up with intense passage we aged small numbers of birds at regular intervals for the most abundant species: Black Kite and Honey Buzzard. For all other species we identified as many individuals as time permitted, and in the case of harriers we only trust species identification if age information is also recorded. A key task of count coordinators is to ensure observers aged birds regularly on all days. As such, the proportion of aged birds varies among days but the overall abundance and timing of juveniles and adults can be estimated using the daily proportion of each age group among aged birds. The annual proportion of birds that was aged in the field for each species is summarized in Table S2.

Despite the fact that we aged large numbers of birds, there are some gap days in the age data, or days when few individuals were aged due to the substantial numbers that passed. We found that for some species such as Booted Eagle and Black Kite this resulted in unrealistic staggered patterns in cumulative frequency distributions in certain years. To solve this we used the age proportions on the nearest day with five or more aged individuals to represent those days on which fewer than five individuals were aged (taking the earliest day if two values were possible). In so doing we implicitly assumed that age proportions vary gradually from day to day, using a more fine-grained approach than studies where similar estimates are made based on species proportions in larger time blocks (Kjellén 1992). There were some rare cases where large gaps in age data had to be estimated and resulted in odd estimates of juvenile abundance (e.g. Black Kite in 2015) or adult timing (e.g. Honey Buzzard in 2015) (Fig. S1). However, this did not result in major deviations of our estimates for age-specific timing and abundance in 2015 compared with other years.

Differential migration timing

We computed cumulative frequency distributions and calculated the Julian quantile passage dates of each age group (Q5%, Q25%, Q50%, Q75%, Q95%), as well as the duration of their respective main migration period (Q95–Q5%) and peak migration period (Q75–Q25%). We used a basic two-sided *t*-test to check for differences in the mean quantile passage dates of juveniles and non-juveniles in each species.

Modelling trends in abundance

Following data processing we summed daily abundance estimates to add up totals for each species and age group. As we achieved full-season coverage in all years we did not use effort-adjusted indices of migration intensity but directly used our estimates of annual abundance per species and age group as response variables in our trend analyses. Count data usually deviate significantly from normality, but we found linear models assuming a normal error distribution were best suited for our analyses, as alternative error distribution types resulted in higher skewedness in residual plots. The numerical variable 'year' was the only predictor in each of our models. Following linear regression analyses we computed the relative change in populations by dividing the effect size in abundance models (birds/year) by the mean annual count for each species and age group. We also tested for linear trends in quantile passage dates to ensure trends in abundance were not biased by a change in migration timing across our study period.

To help interpret model results we computed the coefficient of variation (CV; cf. Lewis & Gould 2000) for each species and age group:

$$CV = [RMSE / \text{mean annual count}] \times 100$$

whereby RMSE is the root-mean square error estimated from linear regression models, which may be described as the standard deviation of model residuals. RMSE is the measure of the disagreement between our linear models and the data. By standardizing this measure of model fit relative to mean annual counts we can use it as a proxy for the power of our models. When $CV < 30\%$ for a given species or age group, we should be able to detect changes in its abundance as small as 10%/year or less across our study period (Lewis & Gould 2000).

All analyses were performed in R Language for Statistical Programming (R v.3.3.0, R Core Development Team 2013). Graphs and maps were produced using the ggplot2 package. See the 'Data availability' section for more details regarding reproducibility of our analyses.

RESULTS

Table 1 summarizes our estimates of juvenile, non-juvenile and total species abundance, in

comparison with global breeding population estimates for each species. Daily abundance curves (Figs 2 and 3, left panels) and relative cumulative frequency distributions (Figs 2 and 3, middle panels) revealed noticeable differences in migration timing between age groups, which we tested based on quantile passage dates (Table 2). Using this information, we also calculated the mean duration of peak and main migration periods per species and age group (Table S2). We cover the bulk of the migration for both age groups in all species (Figs 2 and 3, left panels), which increases confidence in our analyses of demographic trends (Figs 2 and 3 right panels, Table 3).

Montagu's Harrier – *Circus pygargus*

Montagu's Harrier was the earliest migrant among our study species. Non-juveniles passing through Batumi represented a considerable fraction of the global breeding population (Table 1). Non-juveniles thereby outnumbered and preceded their juvenile conspecifics (Fig. 2, top left and middle; Table 1). Migration started around the same time for both age groups but non-juveniles peaked earlier (Table 2, Q50) and completed migration over a shorter period compared with juveniles (Table S2). However, relatively high daily counts of non-juvenile Montagu's Harriers at the start of our count season indicate that small numbers of this age group passed before our count season started (Fig. 2, top left). Variability in annual counts restricted our ability to detect moderate

trends, especially for juveniles (Fig. 2, top right; Table 3, CV > 30%). Nevertheless, annual counts showed a considerable negative trend ($P = 0.06$, Table 3) and we found a highly significant and strong decrease of 17%/year in the annual abundance of juveniles (Fig. 2 top right, Table 3), which was not associated with a change in timing (Fig. S2, Tables S3 and S4).

Pallid Harrier – *Circus macrourus*

Non-juvenile Pallid Harrier counts at Batumi represented a substantial portion of the global population of this near threatened species (Table 1). However, the extremely high variability of annual counts in both age groups of this species (CV > 40–50%, Table 3) prohibited detection of age-specific and overall trends in abundance (Fig. 2, 2nd right; Table 3). This was also the only species in which juveniles outnumbered non-juveniles in several years (Fig. 2, 2nd right; Table 1). The timing of passage of the 25th percentile (Q25) differed significantly between age groups (Table 2). However, this may well be a spurious signal driven by exceptionally early juvenile passage or exceptionally late adult passage in certain years (Fig. 2, 2nd middle).

Western Marsh Harrier – *Circus aeruginosus*

Non-juvenile counts of Marsh Harrier represented a smaller fraction of the global breeding

Table 1. Mean (sd) of annual estimates for juveniles, non-juveniles and total passage of eight focal species

Species	Juveniles		Non-juveniles		Total		Global pop. size ^a (breeding ind.)	Proportion global pop. at Batumi (%)	
	Mean	sd	Mean	sd	Mean	sd		Min.	Max.
Montagu's Harrier	2491	1345	4436	1204	6927	1959	100 000–499 999	0.9	4.4
Pallid Harrier	747	505	744	407	1491	612	18 000–30 000	2.5	4.1
Marsh Harrier	2359	341	4130	871	6489	982	500 000–999 999	0.4	0.8
Black Kite	41 236	12 389	95 718	28 652	136 953	36 461	1 000 000–2 499 999	3.8	9.6
Honey Buzzard	30 502	12 154	500 066	94 539	530 568	96 563	280 000–420 000	119.1	178.6
Booted Eagle	1435	442	5040	700	6475	665	149 000–188 000	2.7	3.4
Short-toed Eagle	236	82	1192	110	1427	155	100 000–200 000	0.6	1.2
Lesser Spotted Eagle	1534	745	6181	882	7715	1462	40 000–60 000	10.3	15.5

We calculated the minimum and maximum proportion of the global breeding population, which uses the Batumi bottleneck using the mean annual count of non-juveniles and the most recent population estimates of each species. Species for which counts at Batumi represent minimally 1% of the global population are highlighted in bold. ^aSource: online datzone BirdLife International.

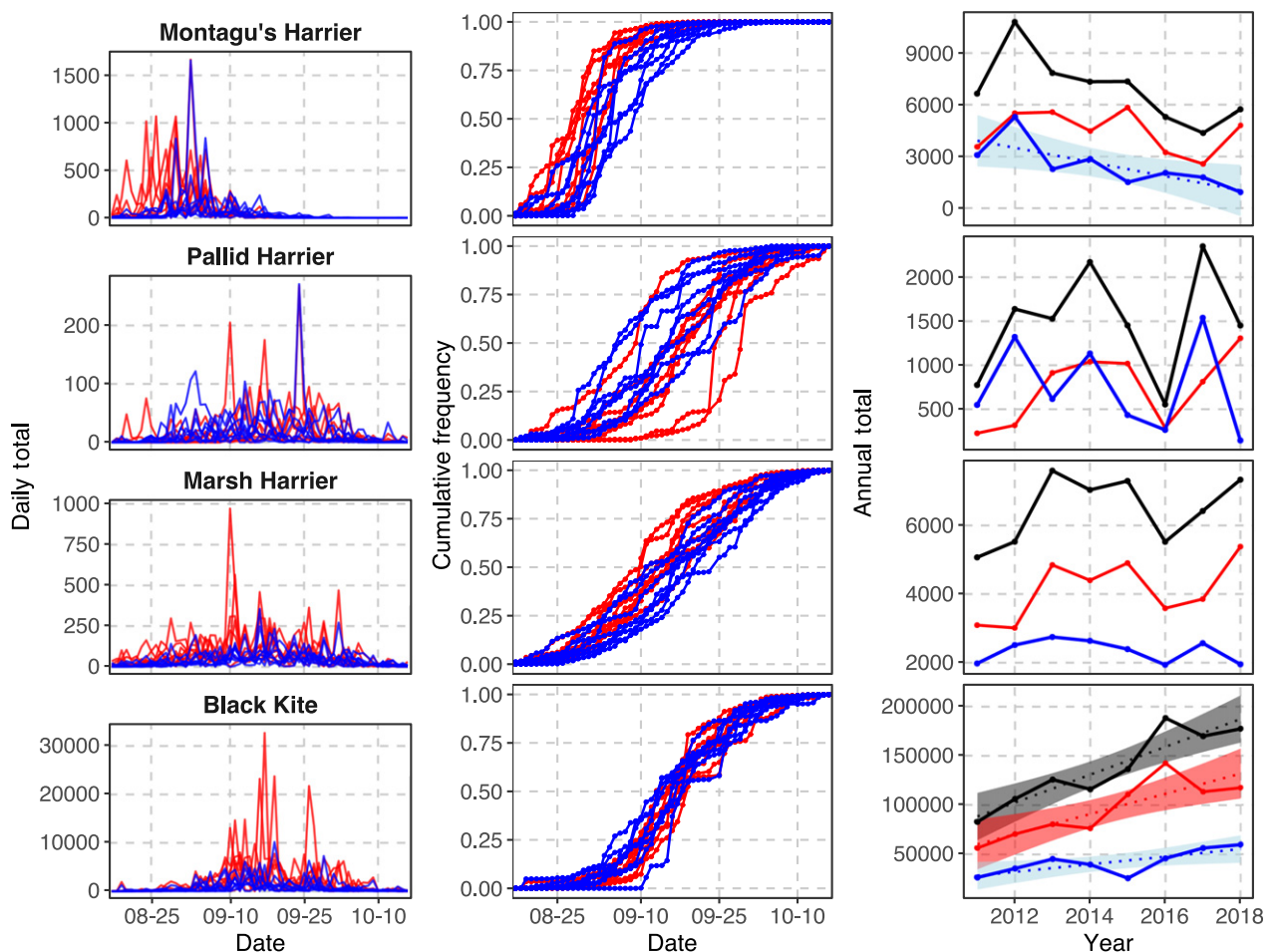


Figure 2. Daily abundance (left), relative migration timing (middle) and annual abundance (right) of juvenile (blue) and non-juvenile (red) Montagu's Harrier (*Circus pygargus*, top), Pallid Harrier (*C. macrourus*, 2nd row), Marsh Harrier (*C. aeruginosus*, 3rd row) and Black Kite (*Milvus. migrans*, bottom) at Batumi Raptor Count 2011–2018. Annual abundance graphs (right) also feature total species counts (black). Significant linear trends in annual abundance are shown as dotted lines with shaded areas indicating 95% confidence intervals.

population than previously estimated (Table 1, cf. Verhelst *et al.* 2011). Juveniles accounted for at least one-third of the annual Marsh Harrier counts (Table 1) and variability in annual counts was remarkably low for both age groups ($CV < 20\%$), which strengthened our finding that there were no significant trends in abundance of either age group (Fig. 2, 3rd right; Table 3). The migration period of Marsh Harriers is the longest of all our study species (Table S2) and we found no significant differences in quantile passage dates between age groups (Fig. 2, 3rd middle; Table 2). We found no significant trends in timing of either age group (Fig. S2, Tables S3 and S4).

Black Kite – *Milvus migrans*

Black Kite was the third most abundant migrant at our study site (Verhelst *et al.* 2011) and the second most abundant of our study species. Non-juvenile counts at Batumi on average represented at least 3.8% of the global breeding population. Juveniles on average made up approximately one-third of the annual passage (Fig. 2, bottom right; Table 1) and migrated at the same time as non-juveniles (Fig. 2, bottom middle; Table 2). The variability in annual counts was moderate to low in both age groups and we detected highly significant increases of $\sim 11\%$ and $\sim 10\%$ /year in non-juvenile and total counts of this species, respectively (Fig. 2, bottom right;

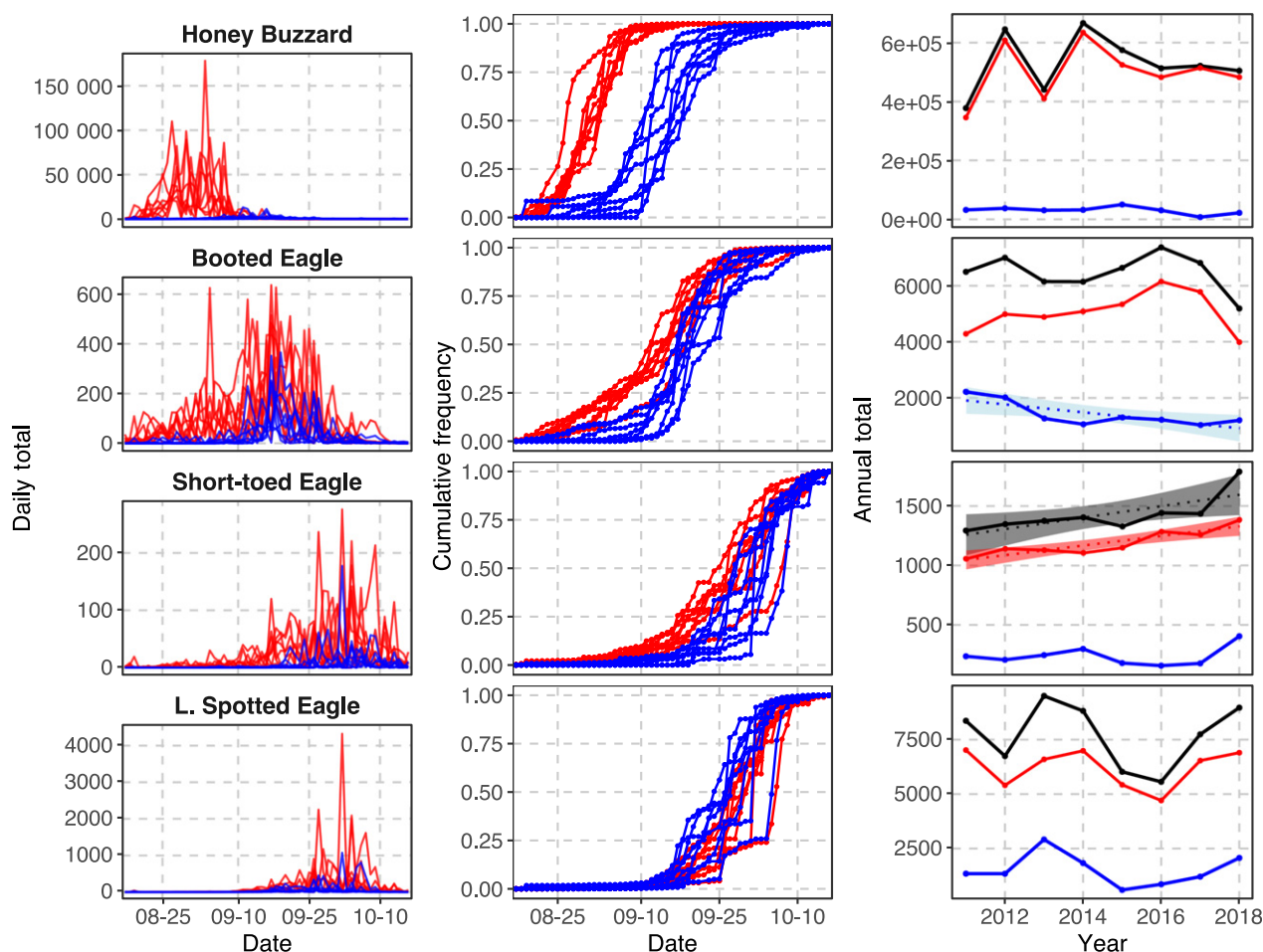


Figure 3. Daily abundance (left), relative migration timing (middle) and annual abundance (right) of juvenile (blue) and non-juvenile (red) Honey Buzzard (*Pernis apivorus*, top), Booted Eagle (*Hieraaetus pennatus*, 2nd row), Short-toed Eagle (*Circaetus gallicus*, 3rd row) and Lesser Spotted Eagle (*Clanga pomarina*, bottom) at Batumi Raptor Count 2011–2018. Annual abundance graphs (right) also feature total species counts (black). Significant linear trends in annual abundance are shown as dotted lines, with shaded areas indicating 95% confidence intervals.

Table 3). The non-juvenile passage thereby more than doubled during our study period and is clearly the main factor driving the increase in total counts for this species (Fig. 1). Juveniles have also increased by ~9% but this trend became weakly significant only recently ($P = 0.05$, and $P > 0.05$ if 2018 is excluded). We found no significant changes in quantile passage dates of either age group (Fig. S2, Tables S3 and S4).

European Honey Buzzard – *Pernis apivorus*

The average annual count of non-juvenile Honey Buzzards at Batumi represented at least 119.1% of the most recent global population estimates

(Table 1). It is by far the most numerous raptor migrant at Batumi and variation in its annual total is determined mostly by variation in the number of non-juveniles (Fig. 3). That is because Honey Buzzard passage was characterized by an extremely small number of juveniles (Fig. 3, top left; Table 1) that migrated much later than their non-juvenile conspecifics compared with any other species (Fig. 3, top middle; Table 2). We found no significant linear change in abundance of this species, or either age group, but note that high variability in juvenile counts prohibited detection of moderate changes in abundance (Fig. 3, top right; Table 3). The migration period of non-juvenile Honey Buzzards was shorter (Table S2) and quantile passage dates were the least variable of all

Table 2. Mean and sd of quantile passage dates for each age group and two-sided *t*-test for differences between age groups

Species	Timing	Juveniles		Non-juveniles		<i>t</i> -test	
		Date	sd (days)	Date	sd (days)	<i>t</i> (days)	<i>P</i>
Montagu's Harrier	Q5	08-26	4.5	08-24	4.1	−0.63	0.536
	Q25	08-31	3.5	08-28	3.8	−1.58	0.136
	Q50	09-05	3.2	08-31	2.6	−3.10	0.008
	Q75	09-09	3.9	09-03	2.0	−3.96	0.002
	Q95	09-19	5.2	09-12	4.2	−2.98	0.010
Pallid Harrier	Q5	08-29	3.9	09-04	9.5	1.51	0.163
	Q25	09-07	5.1	09-15	8.1	2.22	0.047
	Q50	09-15	7.0	09-19	6.2	1.32	0.209
	Q75	09-22	6.2	09-26	6.4	1.23	0.240
	Q95	10-04	5.7	10-05	5.8	0.57	0.580
Marsh Harrier	Q5	08-28	4.2	08-26	3.2	−1.13	0.277
	Q25	09-09	4.3	09-05	3.4	−2.06	0.060
	Q50	09-18	4.5	09-14	3.1	−1.94	0.075
	Q75	09-27	3.9	09-22	4.9	−2.25	0.042
	Q95	10-07	2.9	10-04	2.6	−2.73	0.016
Black Kite	Q5	09-02	5.3	09-04	3.8	0.98	0.347
	Q25	09-11	3.1	09-12	1.9	0.77	0.455
	Q50	09-16	2.0	09-17	2.0	0.88	0.392
	Q75	09-25	2.5	09-24	3.4	−0.59	0.568
	Q95	10-06	3.6	10-03	2.1	−1.43	0.180
Honey Buzzard	Q5	09-03	8.2	08-23	1.8	−3.60	0.008
	Q25	09-11	3.0	08-28	1.5	−11.69	3.44E-07
	Q50	09-15	3.0	09-01	2.1	−11.12	7.29E-08
	Q75	09-18	3.7	09-04	2.6	−9.03	7.03E-07
	Q95	09-27	5.5	09-08	2.2	−8.75	9.31E-06
Booted Eagle	Q5	09-08	8.1	08-26	3.5	−4.03	0.003
	Q25	09-17	1.8	09-07	3.5	−6.74	4.12E-05
	Q50	09-20	2.4	09-15	2.2	−3.84	0.002
	Q75	09-24	2.9	09-21	2.7	−2.12	0.052
	Q95	10-02	4.2	09-29	4.0	−1.34	0.202
Short-toed Eagle	Q5	09-18	6.1	09-08	3.4	−3.95	2.32E-03
	Q25	09-29	3.9	09-22	4.1	−3.66	0.003
	Q50	10-03	3.4	09-30	3.7	−1.62	0.128
	Q75	10-06	1.8	10-05	2.5	−1.62	0.131
	Q95	10-13	1.8	10-11	2.0	−1.86	0.084
Lesser Spotted Eagle	Q5	09-18	3.6	09-18	3.7	0.21	0.839
	Q25	09-23	4.3	09-27	4.2	1.87	0.082
	Q50	09-29	3.6	10-01	2.9	0.92	0.376
	Q75	10-02	2.8	10-04	1.5	1.99	0.073
	Q95	10-06	1.6	10-09	2.3	2.60	0.022

Highly significant ($P < 0.01$) differences in quantile passage are highlighted in bold and other significant differences ($P < 0.05$) in italics.

study species (Table 2). We found no significant linear change in quantile passage dates of either age group (Fig. S2, Tables S3 and S4).

Booted Eagle – *Hieraaetus pennatus*

The average annual count of non-juvenile Booted Eagles at Batumi was equivalent to ~3% of the global breeding population (Table 1). Juveniles represented about one-fifth of this passage (Fig. 3, 2nd

left; Table 1). A larger proportion of the juvenile passage took place late in the season compared with non-juveniles but throughout the entire season non-juveniles outnumber juveniles (Fig. 3, 2nd left and middle; Table 2, Q5–Q50). Moderate to low variability in annual counts indicates good monitoring potential for this species at Batumi (Table 3, CV < 10–20%). A stable overall population trend masked a marked and significant decrease of ~10%/year for juvenile Booted Eagles

Table 3. Output of linear regression models for age-specific and overall changes in abundance of our study species between 2011 and 2018, showing the magnitude (i.e. effect) and significance (P) of each trend, the relative effect size (i.e. effect divided by mean annual count) and Adjusted R^2 as a proxy for the proportion of variability explained by linear trends. Groups in which significant trends ($P < 0.05$) occurred are highlighted in bold

Species	Group	Effect (ind./year)	P_{effect}	Relative effect (%/year)	Adjusted R^2	CV (%)
Montagu's Harrier	Juvenile	-413	0.032	-17	0.49	33.32
	Non-juvenile	-138	0.501	-3	-0.08	24.38
	Total	-550	0.059	-8	0.39	19.19
Pallid Harrier	Juvenile	-42	0.632	-6	-0.12	61.97
	Non-juvenile	97	0.128	13	0.23	41.47
	Total	56	0.597	4	-0.11	37.44
Marsh Harrier	Juvenile	-24	0.687	-1	-0.13	13.33
	Non-juvenile	196	0.158	5	0.19	16.49
	Total	172	0.289	3	0.05	12.78
Black Kite	Juvenile	3629	0.045	9	0.43	19.58
	Non-juvenile	10 233	0.004	11	0.73	13.56
	Total	13 862	0.001	10	0.85	9.07
Honey Buzzard	Juvenile	-2373	0.231	-8	0.10	32.74
	Non-juvenile	6973	0.669	1	-0.13	17.39
	Total	4600	0.783	1	-0.15	16.91
Booted Eagle	Juvenile	-138	0.027	-10	0.51	18.59
	Non-juvenile	67	0.576	1	-0.10	12.63
	Total	-71	0.533	-1	-0.09	9.27
Short-toed Eagle	Juvenile	7	0.622	3	-0.12	31.79
	Non-juvenile	41	0.001	3	0.81	3.44
	Total	48	0.029	3	0.51	6.59
Lesser Spotted Eagle	Juvenile	-37	0.774	-2	-0.15	45.09
	Non-juvenile	-28	0.855	0	-0.16	13.31
	Total	-65	0.797	-1	-0.15	17.62

Models highlighted in grey are cases where the coefficient of variation (CV) of annual counts exceeded 30%, the maximum threshold for detecting annual changes of ~3%/year over a 25-year period and changes of ~10%/year over a 10-year period, with 80% power (cf. Lewis & Gould 2000).

(Fig. 3, 2nd right; Table 3). We detected this decline when we first ran our analyses without 2018 data, at which time we also found that non-juvenile abundance increased significantly between 2011 and 2017 ($P < 0.05$). This trend was broken by unusually weak passage of non-juveniles in 2018. Booted Eagles usually fly close to the coast near Station 1 (Vansteelant *et al.* 2014) but in 2018 there was remarkably weak coastal passage during exceptionally fair weather in early September (see distance codes in GBIF dataset). We found no significant trends in quantile passage dates (Fig. S2, Tables S3 and S4).

Short-toed Eagle – *Circaetus gallicus*

Short-toed Eagle was the least abundant of our study species and non-juvenile counts represented ~1% of the global breeding population. Less than one-fifth of the annual passage at Batumi consisted of juveniles (Fig. 3, Table 1), and juveniles

initiated their migration over a week later than elders (Table 2, Q5–Q25). However, their migration period overlapped with the late migration period of non-juveniles, so that juveniles were always outnumbered by non-juveniles (Fig. 3, 3rd left and middle). They were the latest migrant among our study species, and the Q95 passage date of juveniles occurred only 3 days before the end of our annual surveys (13 October), suggesting that small numbers of juvenile Short-toed Eagles passed the bottleneck after our seasonal counts finished (Fig. 3, 3rd left; Table 2). This may contribute to high count variability that restricts monitoring potential for juveniles. However, count variability was extremely low for non-juveniles, allowing us to detect an increase of just 3%/year in non-juvenile and total abundance (Fig. 3, 3rd right; Table 3). Linear trends in abundance were not associated with trends in the timing of either age group (Fig. S2, Tables S3 and S4).

Lesser Spotted Eagle – *Clanga pomarina*

Lesser Spotted Eagle was the most abundant eagle at Batumi and non-juvenile counts on average represented at least 10% of the global breeding population (Table 1). Approximately one-fifth of the annual passage was made up of juveniles (Fig. 3, bottom left; Table 1). The latter migrated at the same time as non-juveniles (Fig. 3, bottom middle; Table 2). The annual counts of non-juveniles were substantially less variable than those of juveniles but we did not find significant linear trends in the abundance of either age group, or in total counts of this species (Fig. 3, bottom right; Table 3). We found no significant changes in the timing of juvenile and non-juvenile Lesser Spotted Eagles across our study period (Fig. S2, Tables S3 and S4).

DISCUSSION

With more than 1 million raptors passing the Batumi bottleneck every autumn, the eastern Black Sea flyway is one of the main flyways for migrant raptors in the world (Verhelst *et al.* 2011). To compare non-juvenile counts with recent global population estimates (BirdLife International 2018) it is important to recognize that non-juvenile migrants include an unknown portion of non-breeding immatures and adults. However, even if we assume that half of these birds are floaters, the Batumi Raptor Count monitors at least 1% of the global breeding populations of five of our study species. The passage of non-juveniles of the remaining species (Montagu's Harrier, Marsh Harrier, Short-toed Eagle) undoubtedly represents an important proportion of their regional populations (Verhelst *et al.* 2011). The fact that non-juvenile Honey Buzzards counted at Batumi represent 119–179% of the estimated global number of breeding adults suggests a severe underestimation of this species' breeding population, especially in the poorly surveyed forests of western Russia (BirdLife International 2018). We cannot exclude the possibility that this problem also exists for other species.

Differential migration, count variability and implications for monitoring

As expected, counts of experienced non-juvenile migrants varied less between years than for

inexperienced juveniles. Juvenile counts of Montagu's Harrier, Pallid Harrier, Honey Buzzard and Lesser Spotted Eagle are too variable to detect moderate changes in juvenile abundance over our time period, but are within an acceptable range for long-term monitoring in most cases (*cf.* Lewis & Gould 2000). By contrast, our high and consistent count effort already yielded sufficiently low variability in non-juvenile counts to detect changes in non-juvenile abundance of 10%/year or less for all species except Pallid Harrier.

Like Kjellén (1992) at Falsterbo (Sweden), we found that adult long-distance migrants preceded juveniles. This was true among Montagu's Harriers (*cf.* Kjellén 1992), Booted Eagles, Short-toed Eagles (*cf.* Agostini *et al.* 2017) and especially Honey Buzzards. The extreme differences in abundance and timing between juvenile and non-juvenile Honey Buzzards match patterns revealed by other observation and tracking studies of this species (Hake *et al.* 2003, Agostini 2004, Trabalon & García 2015, Vansteelant *et al.* 2015, 2017). However, like Kjellén (1992), we also found exceptions to the 'rule' that adults migrate before juveniles. Neither Marsh Harrier nor Black Kite showed a discernible difference in migration timing between age groups, and a particularly long migration period for both age groups (Kjellén 1992, 1998). We suspect this is due to partial migration in these species, whereby short-distance migrant individuals of both age groups migrate later than long-distance migrants (Panuccio *et al.* 2013, 2014).

Another exception was Lesser Spotted Eagle, where both age groups had a very short but nevertheless strongly overlapping peak migration period. We consider that there is a strong selective advantage for juveniles in all large obligate soaring migrants to synchronize their first autumn migration with adult conspecifics, as this ought to facilitate social learning of safe traditional flyways via geographical bottlenecks (Mellone *et al.* 2011, 2016, Oppel *et al.* 2015, Meyburg *et al.* 2017). Indeed, even though passage of juvenile Booted Eagle and Short-toed Eagles started relatively late, most still passed during the peak and late migration period of non-juveniles. Given that these species are known to depend on social information to learn migration routes, we found it surprising to find considerable variability in counts of juvenile eagles, but also non-juvenile eagles. However, we know annual differences in regional weather conditions may generate considerable fluctuations in

migration counts of soaring birds, even for experienced non-juveniles (Allen *et al.* 1996, Vansteelant *et al.* 2014, Miller *et al.* 2016). In certain years the passage of large eagles at Batumi can be severely delayed by bad weather events blocking the flyway further north. Such events are usually followed by mass migration events, which result in the characteristic 'jaggedness' of cumulative frequency distributions for both age groups of these species (Fig. 3). Such events often also result in record counts that account for much of the variability in annual totals (Wehrmann 2012). We are optimistic that it will be possible to correct for weather-induced variation in migratory passage in future trend analyses (Shamoun-Baranes *et al.* 2006, Miller *et al.* 2016).

The extremely high coefficient of variation (*cf.* Lewis & Gould 2000) in annual counts of Pallid Harrier indicates that there is no consistent proportion of the potential source population aggregating at Batumi. Indeed, substantial numbers of Pallid Harrier cross the Caucasus as far east as Azerbaijan (Heiss & Gauger 2011, Terraube *et al.* 2012, Abuladze 2013). As such it seems unlikely we can infer population trends from migration counts of this species now or in the future. However, the aggregation of closely related Montagu's Harriers at Batumi seems to be reasonably repeatable, and we are keen to monitor this species because it is a relatively frequent casualty of illegal shooting along the eastern Black Sea coast (Sandor *et al.* 2017). To estimate Montagu's Harriers among harriers that could not be identified to species level in the field, we must continue counts of Pallid Harrier as well.

Interpreting age-specific trends in abundance

We are confident that the lack of significant trends in non-juvenile counts of Honey Buzzards, Marsh Harrier and Lesser Spotted Eagle indicate stable breeding populations for those species. In the case of Montagu's Harrier, Black Kite, Booted Eagle and Short-toed Eagle we believe that the significant trends we found were representative of demographic changes in those populations using the eastern Black Sea flyway. That is because these trends occurred rather consistently across years, rather than being driven by 'unusual' years at either end of our short study period. Moreover, species for which we failed to detect trends did not necessarily exhibit

higher variability in counts. For our interpretation we assume that juvenile counts reflect changes in breeding conditions, whereas changes in non-juvenile counts reflect changes in annual survival, primarily outside the breeding season.

We found highly significant increases in the non-juvenile counts of Black Kite between 2011 and 2018, to a lesser extent for Short-toed Eagle, and until 2017 also for Booted Eagle. These species stand out from other study species as their non-breeding ranges seem to be shifting northward, from sub-Saharan Africa into Europe and the Middle East (Baghino *et al.* 2007, Panuccio *et al.* 2014, Martín *et al.* 2016, Literák *et al.* 2017). Migrants that forego the perilous Sahara crossing probably have a higher likelihood of survival than conspecifics that do not, especially during spring migration (Strandberg *et al.* 2010, Klaassen *et al.* 2014). We would expect such a mechanism to result in increasing numbers of non-juveniles on autumn migration at Batumi, and we find compelling evidence that this is happening in the eastern African–Palearctic flyway in the case of Black Kite.

Black Kite has long been a common wintering raptor in the Caucasus and parts of the Middle East, most notably Israel (Shirihai *et al.* 2000, Abuladze 2013, Literák *et al.* 2017). Since the turn of the century, however, flocks of up to 60 or more Kites have colonized non-breeding sites across south-eastern Europe and the Balkans (Literák *et al.* 2017) and 1000s have started wintering on landfills in southern Anatolia (Biricik & Karakaş 2011). Moreover, the wintering population in Israel increased from at most a few 1000 Kites in the late 1980s to *c.* 10 000 Kites in the late 1990s (Shirihai *et al.* 2000), and up to several 10 000s now. The bulk of these birds, approximately 30 000 individuals, use the country's largest landfill (Dudaim) in the Negev desert (R. Dor personal website). That is equivalent to roughly 30% of the mean annual passage at Batumi, and of the 100 000 Black Kites that have been estimated to breed in European Russia (Mischenko 2004 in Mebs & Schmidt 2006). Moreover, a strong connection between the Batumi bottleneck and the Israel non-breeding population of Black Kites has been confirmed by satellite-tracking (D. Berkowicz unpubl. data).

By wintering on landfills in the Middle East, Black Kites not only forego perilous trans-Saharan migrations, they also reduce foraging costs

compared with conspecifics that track natural resources in the Sahel during the non-breeding season (Gilbert *et al.* 2016, Flack *et al.* 2016, Rotics *et al.* 2017). It has been suggested that Black Kites recently started using landfills north of the Sahara more frequently as a result of improving winter conditions (Literák *et al.* 2017). However, in that case it remains unclear why only small numbers of Black Kites are doing the same in the western African–Palearctic flyways, in contrast to other facultative scavengers such as White Storks *Ciconia ciconia*, which are increasingly wintering north of the Sahara in the western as well as the eastern African–Palearctic flyway (Gilbert *et al.* 2016, Martín *et al.* 2016). In fact, the Israeli winter population of Black Kites started to grow rapidly only after the creation of the Dudaim landfill in the Negev desert at the turn of the century. As such we hypothesize that increased food availability at landfills, rather than climate warming, is the primary factor driving the growth of the non-breeding Black Kite population in the Middle East, and consequently the autumn passage of Black Kites at Batumi.

The significant increase in the number of non-juvenile Short-toed Eagles occurred much more slowly than for Black Kites. These Eagles migrate in much smaller flocks and do not winter gregariously. Colonization of northern wintering areas is thus probably mostly driven by a minority of juveniles that fail to cross the Mediterranean and that are increasingly better able to survive due to milder winter conditions (Mellone *et al.* 2016). Unfortunately, we lack comprehensive information on the non-breeding status of this species in the Middle East. Anecdotal observations, including two young Short-toed Eagles wintering as far north as Crimea in 2013, do corroborate the notion that milder winters are opening up new wintering areas for this species in the eastern flyway. However, we emphasize that this is a very tentative interpretation, and other factors such as improved availability of cold-blooded prey in the breeding range may also positively influence this species (Martín *et al.* 2016).

The contrasting trends we found for juvenile and non-juvenile Booted Eagles are intriguing. However, we found no evidence supporting the notion that this species is increasingly wintering north of the Sahara in the eastern African–Palearctic flyway. Moreover, it remains to be determined whether the significant increase in

non-juvenile counts of Booted Eagle that took place between 2011 and 2017 will persist in 2019, and whether the low non-juvenile count of this species in 2018 was truly due to an exceptional migration event (cf. Baghino *et al.* 2007, Premuda *et al.* 2007).

We currently do not have any concrete indications as to what factors are driving the significant declines of 17% and 10%/year in the annual counts of juvenile Montagu's Harriers and Booted Eagles at Batumi. Such sharp declines in the abundance of juveniles suggest that breeding conditions and reproductive success are deteriorating for these species. This could well be due to expansion of agricultural land in western Russia (Lesiv *et al.* 2018) or agricultural intensification, but then it is not clear why this would not have affected other species in similar ways. Other factors such as illegal shooting might play a role as well (Brochet *et al.* 2017, Sandor *et al.* 2017). But even while we cannot confidently identify the causes of these declines, the fact such concerning trends were masked by stable bulk counts of these species emphasizes the importance of separating trends in migration counts between age groups.

CONCLUSIONS

Globally important numbers of migrant raptors pass through the Batumi bottleneck every year and our study provides an important benchmark for monitoring raptor populations in the eastern African–Palearctic flyway during the 21st century. Indeed, there are few other long-term migration surveys operating in the region, and no comprehensive raptor surveys are available from the vast breeding range of our target species in Russia (M. Kalyakin pers. comm.). The changes we observed in raptor passage at Batumi over the past 8 years indicate that populations of our study species north of the Caucasus are currently mostly stable (e.g. Honey Buzzard, Marsh Harrier, Booted Eagle, Lesser Spotted Eagle) or increasing (Black Kite, Short-toed Eagle). Positive trends in overall species counts were associated to increasing counts of non-juveniles, which indicates these trends were driven by survival rather than high breeding success. In the case of Black Kite there is good evidence that this is due to an ongoing shift towards novel wintering sites north of the Sahara and Mediterranean. For other species we lack information across the entire annual range to reliably

identify causes of trends. Nevertheless, the fact that concerning declines of juvenile Montagu's Harrier and Booted Eagle were masked by total species counts emphasizes the importance of incorporating standardized ageing procedures at migration watch-sites.

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CONFLICT OF INTEREST

None.

DATA AVAILABILITY

The full BRC dataset is provided through GBIF (Wehrmann *et al.* 2018) with extensive documentation of our count and data processing protocol in Wehrmann *et al.* (2019). All scripts needed to reproduce the analyses in this paper are provided through GitHub (<https://github.com/batumiraptorcount>).

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SUPPORTING INFORMATION

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

Table S1 The mean and standard deviation (SD) of the annual proportion of individuals that was aged in the field, and the proportion of the annual species total that was estimated from unidentified individuals (UID, i.e. individuals that were originally not identified to species level in the field).

Table S2 Duration of the peak migration period (central 50%) and main migration period (central 90%) for both age classes of each study species.

Table S3 Linear trends in quantile passage date of non-juveniles of each study species. None of the trends were significant.

Table S4 Linear trends in quantile passage dates of juveniles of each study species. None of the trends were significant.

Figure S1. Gaps in seasonal coverage of migration periods with ageing data, as indicated by the

number of days on which fewer than five birds were aged but more than five were recorded for a given species.

Figure S2. Annual quantile passage dates (Q5, Q25, Q50, Q75, Q95) of non-juveniles (left) and juveniles (right) for each of our study species (labels).