IDENTIFICATION OF IMPORTANT MIGRATION CONCENTRATION AREAS OF EGYPTIAN VULTURES *NEOPHRON PERCNOPTERUS* FROM THE BALKAN POPULATION TRACKED BY SATELLITE TELEMETRY

TRAINING REPORT

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ABSTRACT

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Avian scavengers are among the most threatened groups of birds around the world but they are very poorly protected. In Europe, the most endangered vulture species is the Egyptian vulture *Neophron percnopterus*, the only one migrating long distances to winter in Africa. The Iberian population has been intensively studied in the last years and their migration routes and wintering areas have been understood. Conversely, little is known about the Balkan population which has to fly a detour to avoid crossing the Mediterranean that may lead to areas where migrating birds concentrate. To identify the most important migration hotspots, i.e. where birds concentrate at roosting areas, and bottlenecks, i.e. where flight paths converge in space, we tracked 14 Egyptian vultures from the Balkan population using satellite transmitters. Between 2010 and 2016 we obtained 11251 locations from adults and immatures that described different migration routes between autumn and spring. Because of the Mediterranean, the birds have to fly a detour creating bottlenecks at the northern (autumn) and the southern (spring) margin of the sea, where birds congregate that encounter the barrier of the Mediterranean Sea. Thus, the Egyptian vultures from the Balkans are flying longer and more tortuous migration routes than the birds from the Iberian population. The most important bottleneck was positioned in the Gulf of Iskenderun (South Turkey) and included more than 70 % of all the migrations. The second one was located around Suez in Egypt with exactly 70 % of the migrations passing through the area. The main concentration area was located in central Anatolia around Beypazari, a well-known breeding area for Egyptian vultures in Turkey where genetic exchange could occur. Threats (wind-farms) were located in important concentration areas but we need more research on the ground to assess and mitigate other threats along the flyway of the Egyptian vultures.

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INFORMATION ABOUT THE CONTRIBUTION

The data were collected automatically from the transmitters via GPS satellites. We attempted to capture two adult Egyptian vultures during two weeks to equip them with satellite transmitters. The total amount of time spent on the field was 17 % of the duration of the internship. The other 83 % were spent to import, sort and analyze the data.

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INTRODUCTION

Long distance migrant birds in Europe are declining very rapidly compared with residents or short distance migrants (Sanderson et al., 2006). Migration is risky and birds are exposed to many threats in different places and can die along their way (Hewson et al., 2016). The mortality rate during migration can reach very high value for small songbirds (85% of the annual mortality of *Dendroica caerulescens* occurred during migration, Sillett & Holmes, 2002), but may be equal to other life events in larger raptors (Klaassen et al., 2014). The costs of migration might increase with the distance travelled, e.g. because of increasingly heavy fuel loads (Alerstam and Hedenstrom, 1998; Alerstam et al., 2003) therefore we need to understand how far the individuals of declining populations migrate.

Some long-distance migrants can be protected for at least one part of their annual cycle, for example on breeding grounds (Nest protection of Osprey, Dennis, 2007, and Egyptian vulture, Liberatori & Penteriani, 2001) or in wintering areas (Martin et al., 2007; Rendón et al., 2008; Thiollay, 2006). However, most long-distance migrants are very poorly protected along their migratory routes (Runge et al., 2015) and most conservation strategies failed to take into account the migratory connectivity of the birds (Martin et al., 2007). If threats occur in any one of the part of the annual cycle of a migratory species, where a large proportion of the birds are concentrated, the whole population could be affected. Thus, there is a clear need to identify important migration concentration areas, as well as roaming areas of long-distance migrants to target sensitive regions.

Avian scavengers are decreasing and are one of the most threatened groups of birds around the world (Buechley & Şekercioğlu, 2016; Ogada, Keesing, & Virani, 2012; Ogada et al., 2016; Virani, Kendall, Njoroge, & Thomsett, 2011). Among the European vultures, the Egyptian vulture *Neophron percnopterus* is the most threatened and the only one which is a long-distance migrant. While the migration routes and wintering areas of the Iberian population are well-known, the routes, distances and duration for the Balkan population are very poorly understood. The eastern European population of Egyptian vultures is declining very rapidly (Velevski et al., 2015) and these birds are migrating to East Africa (Gradev et al., 2012; Meyburg et al., 2004; Oppel et al., 2015), but there is very little information about the location of migratory routes. The Iberian population migrates to West Africa through Gibraltar (García-Ripollés et al., 2010; López-López et al., 2014), which may be an easier migration than for the Balkan population, because this route does not require a detour. Soaring birds as Egyptian vulture avoid crossing large bodies of water, and the Mediterranean is a big natural barrier for soaring migrants in general (Agostini, Panuccio, & Pasquaretta, 2015). Egyptian vultures from the Balkan population suffer large mortality when trying to cross the Mediterranean (Oppel et al., 2015), therefore most birds will head for the shortest water crossing or detour around large water bodies, thus creating migration bottlenecks (Hilgerloh et al., 2011; Oppel et al., 2014). Because the Balkan birds avoid crossing the Mediterranean they follow large flyways around the Eastern Mediterranean Sea through Turkey and the Middle East (Porter and Beaman, 1985; Sutherland and Brooks, 1981). Because illegal killing of birds is pervasive in the East Mediterranean region (Brochet et al., 2016), we need to identify migration bottlenecks for Egyptian vultures along the East Mediterranean flyway where conservation measures could be implemented.

Mortality of Egyptian vultures from the Balkans has been found during migration in the Mediterranean (Oppel et al., 2015) and in Africa (Angelov et al., 2013; Oppel et al., 2015). The main threats for this species are accidental poisoning, electrocutions, direct persecution and collisions with electricity infrastructures (Nikolov et al., 2016; Saravia et al., 2016), operating at very large spatial scales (Velevski et al., 2015). The main cause for the population decline is too low survival of adult and immatures (Grande et al., 2009; Oppel et al., 2016; Velevski et al., 2014). Some of the mortality may happen on migration, but so far we do not know where concentrations occur. Birds may concentrate either at roosting areas, which we termed 'migration hotspots', or their flight paths may converge in space, which we termed 'migration bottlenecks'. Identifying the most important migration bottlenecks and hotspots and where immature birds roam for the four years before they start breeding is absolutely critical if we want to save that species. Those concentration areas can then be examined for any existing anthropogenic risks such as wind turbines, electricity infrastructure, and the general use of shooting and poisoning.

In this study we used satellite tracking data to identify areas used by a large proportion of the Egyptian vultures from the Balkan population during migration and examined the potential threats in those areas from human infrastructure. This information is critical to direct conservation measures in crucial regions where a high number of birds from the Balkan population may be at risk of mortality.

MATERIALS AND METHODS

Study area and population

The Egyptian vulture population of Balkan Peninsula consists of approximately 60 pairs and has been fragmented into several small population clusters mostly distributed in three countries: Bulgaria, Greece and the Former Yugoslav Republic of Macedonia (Velevski et al., 2015). However, the population may be linked to Turkish breeding populations in central Anatolia (Méndez et al., 2015), similar to other raptor species (Demerdzhiev et al., 2015). The population is migratory and the birds fly from their breeding grounds to their wintering areas in Sub-Saharan Sahel region via the Middle East (Meyburg et al., 2004; Oppel et al., 2015) but the corridors of migration are unknown. The species has been classified as 'Endangered' due to the rapid decline of the Indian population (Cuthbert et al., 2006) and long-term declines of European and African populations (Ogada et al., 2016). A combination of several threats seems to cause the population declines, such as poisoning, electrocution, landscape changes and direct persecution (Sanz-Aguilar et al., 2015; Saravia et al., 2016). Moreover, the threats seem to vary in different countries where the birds breed, migrate or overwinter. In the last three years the Bulgarian population has been stabilized but some of the conservation measures, such as nest guarding and supplementary feeding did not have the expected positive results on the populations. Generally, conservation measures on breeding grounds in the Balkans have been less successful than expected (Oppel et al., 2016), and there is an urgent need to investigate the other parts of the life cycle of Egyptian vultures to find the potential threats operating there.

Satellite tracking

Egyptian vultures were satellite-tracked in Bulgaria and Greece during a large conservation project (LIFE+ project "The Return of the Neophron", LIFE10 NAT/BG/000152) between 2010 and 2016. The project tagged 25 birds, but 11 juveniles did not complete any migration and were not included here (Oppel et al., 2015).

We pooled migration data from all trapping sites in the Balkans because birds from different sites were from the same population. We tagged adult birds on breeding grounds, in Bulgaria (n = 2) and in Greece (n = 1) between 2012 and 2015. Birds were captured with a manually-triggered net trap set at a feeding site. Two additional birds were found poisoned in Greece and tagged after rehabilitation. Juvenile Egyptian vultures were tagged in their nests at an approximate age of 65 days, in breeding areas in Bulgaria (n = 7) and Greece (n = 2) between 2010 and 2013.

All birds were equipped with solar-powered 45-g GPS satellite transmitters (PTT-100 45 gram Solar GPS, Microwave Telemetry Inc.; www.microwavetelemetry.com) attached to the birds using a Teflon® ribbon harness in a backpack configuration. The entire transmitter equipment, harness, metal ring and tag, did not exceed 3% of the birds' body mass, and was unlikely to influence mortality of soaring migrants (Klaassen et al., 2014; Sergio et al., 2015). The devices were programmed to obtain the location of each bird from GPS satellites every 2 hours every day over a period of several years. Data were downloaded via the ARGOS satellite system and deposited in Movebank (www.movebank.org), and erroneous locations (>500 km from previous location) were filtered manually.

Definition of migratory seasons

Because spring and autumn migrations can differ in length, duration and route, we conducted all analyses separately for spring and autumn migrations. These seasonal distinctions were somewhat arbitrary for immature birds that do not breed or establish territories and therefore may exhibit constant roaming behavior not clearly separable into distinct migration periods. We defined the autumn and spring migratory periods from the GPS locations fixes recorded for each individual and each year. Only the birds that completed at least one migration, i.e. the first autumn migration to Africa, were used for the analyses. All the locations corresponding to dates out of the periods defined as migrations were deleted.

The onset of the autumn migration was defined as the first day on which immature birds travelled >50 km and adult birds flew >150 km after the breeding season. The end of autumn migration was defined as the first day south of 22°N latitude when a bird reversed its course or remained stationary following the same approach as Oppel et al. 2015. This latitude was selected as it is the southern border of the Sahara, a major ecological barrier. The crossing of that desert represents a critical point of the migratory routes that the birds have to overcome to reach their wintering area in East Africa (Klaassen et al., 2014; Strandberg et al., 2009).

For non-breeding immature birds that returned to the Balkan Peninsula or Turkey without displaying territorial home range behavior over the summer, we manually determined the start of their subsequent autumn migration as the first day of directed movement away from the populations' breeding area. However, because these immature birds were not breeding and were therefore not closely tied to a central location, the movements we considered as migration may have in fact been exploratory movements that were impossible to distinguish from migration (Oppel et al., 2008).

Spring migration can differ considerably between adults and immatures, because immature birds do not return to breeding grounds for 2-4 years and start breeding at the age of 5-6 years. We therefore used different approaches to define the start and end of spring migration for adults and immatures.

For adults we determined the onset of spring migration manually by identifying the first sustained northward movement from wintering ranges into the Sahara. The end of spring migration was defined as the date when the bird reached its breeding territory and started a central-place movement behavior.

For immatures, we considered a 'spring migration' as any movement that reached at least as far as Turkey (i.e. within the potential breeding range of the population), and thus excluded movements within Africa even when they resembled spring migratory behavior (e.g. crossing the Sahara, but turning back in Egypt or Libya). The start of spring migration for immatures was determined manually as the first date when the bird started a northward movement that led at least as far as Turkey. The end of spring migration was either defined as the date when the bird started a central-place movement behavior within the potential breeding range of the population (Balkan Peninsula, Turkey), or the date when the bird reached the closest distance to its nest of origin if the bird did not exhibit any stationary behavior throughout the summer.

Calculation of migration distance, duration and speed

For each bird and each migratory season we calculated different parameters describing the spatial and temporal extent of the migration. The days defining the onset and the end of the respective season were included (Oppel et al., 2008). Migration duration was the number of days between the onset and the end of the migration, i.e. number of days spent migrating. The migration distance was the cumulative distance between all subsequent locations during the travelling period, using the orthodrome which is the shortest path between two points on the Earth's surface (Gudmundsson and Alerstam, 1998), calculated as great-circle distance (using function 'spDistsN1' in R package 'sp'). Finally, migration speed was the migration distance divided by the duration (López-López et al., 2014).

Because the adult birds were difficult to catch and tag, the low sample size reduced the power of a robust statistical analysis comparing differences between seasons and age classes, and we therefore used only graphical representations to describe our results. We present all migration parameters as averages ± standard deviation separately for each age class and season. We used 'immature' as an age class describing the migration of all birds tagged as nestlings, as the progressive improvement of migratory performance with age could not be studied with our small sample size (Sergio et al., 2014).

Identification of areas where migration is concentrated

To identify areas where migratory vultures may be especially prone to mortality, we defined two complementary concepts. We defined ‘migration hotspots’ as those areas where birds of the Balkan population spent a lot of time, and ‘bottlenecks’ as those where a large proportion of the tracked population migrated through, without necessarily stopping.

We used the positional data from the transmitters that fell within any of the migratory seasons defined using the criteria listed above to calculate hotspots and bottlenecks along the flyway of the birds. Migratory GPS positions were interpolated to every five minutes, to have a fixed time interval between all locations and ensure that a bird’s presence was recorded in the smallest spatial unit used for analysis. This interpolation assumed straight-line travel at constant speed between two subsequent location fixes.

Firstly, to understand where birds spent more time on migration, i.e. where they are more exposed to potential threats, we determined hotspot areas using a method quantifying the time-in-area that has been used for other far-ranging birds to reflect the relative importance of a given region (Warwick-Evans et al., 2015). From all the migration positions, we created a regular grid with cells of 100 x 100 km using the function ‘makeGridTopology’ in package ‘trip’ (Sumner and Luque, 2015), because this grid cell size was a reasonable compromise between the continental scale of migration and the local scale at which threats can be assessed and mitigated. We also tested a grid size of 50 x 50 km, but results were superficially similar and increased the spatial complexity of area prioritization. The grid was anchored in the North-West by the northern most latitude of a nest in Bulgaria and by the western most latitude of a nest in Greece, and in the South-East by the Bab El Mandeb strait, the strait at the southeastern end of the Red Sea which is a known migration route from the Arabian Peninsula to Africa (Hilgerloh et al., 2011; Leshem and Yom-Tov, 1998; Welch and Welch, 1988). We calculated the amount of time in days spent by all tracked birds in every grid cell by adding up their individual residency times using the function ‘tripGrid’. Briefly, this function calculates the time for each bird by counting the number of locations included in each cell and summing the time of each step between two subsequent locations. We then selected the 5 % of grid cells with the largest amount of time spent as the most important ‘hotspots’ sites and depicted them on a map.

Secondly, using the same grid, we calculated the proportion of tracked migrations that passed through each cell in each season, by enumerating all the birds that passed through the cell and dividing that number by the total number of migrations in that season. This proportion of migration passing through a given cell in a season was used to identify ‘bottlenecks’. As the birds may fly along different corridors between autumn and spring, we expected differences between both seasons. Therefore, we highlighted the bottlenecks in each season and represented them on two different maps.

Finally, in order to prioritize areas for conservation, we combined these results to select the most important areas for both spring and autumn migration. We prioritized grid cells based on an index calculated as the weighted mean of the proportion of migrations passing through each cell in autumn and in spring. We considered the ten cells with the highest migration concentration index as the main bottlenecks where conservation measures should be focused.

Assessment of potential threats in important concentration areas

Based on the hotspots and bottlenecks defined above, we aimed to quantify the potential threats from existing human infrastructure existing in those concentration areas. The Egyptian vulture is vulnerable to electrocution due to its habit of perching on power lines for roosting where no tree is available (Angelov et al., 2013). Similarly, the species is exposed to collision with wind turbines (Carrete et al., 2009). We therefore enumerated wind turbines and electricity pylons in all hotspot and bottleneck grid cells to identify areas where migration was concentrated and a large number of potential threats exist. We obtained the location of all wind turbines in Eastern Europe and Africa from The Wind Power (Tournefeuille, France) on 17th of May 2016 but we could not get data concerning the Middle East.

RESULTS

The tracking data used to perform all the analyses were collected between 10th of August 2010 and the 16th of June 2016. The 14 birds (5 adults, 9 juveniles) contributed a total of 11251 locations during their respective migratory seasons, describing 12 spring (including 5 from adults) and 18 autumn migrations (including 6 from adults).

Calculation of migration distance, duration and speed

Generally the autumn migration started as early as the 20th of July and the birds arrived on their wintering ground as late as the 6th of November (Table 1). The departure and the arrival dates of the immatures ranged over two months, whereas autumn migration departure and arrival was much more constrained for adults (Table 1).

Spring migration started as early as the 1st of March and ended as late as the 23rd of July, but was equally poorly constrained for immatures as autumn migration, and two individuals roamed all summer and identifying an end of spring migration was arbitrary. Adult birds left their wintering grounds three weeks earlier than the immatures and reached the breeding area almost one month before them (Table 1). The adults were flying shorter distances in spring and had shorter duration of migration for both seasons compared to the young birds (Figure 1).

Among the adult birds there was no difference between the seasons for the duration and the speed of the migration but the distance migrated in autumn (5695 ± 382 km) was marginally shorter than in spring (4945 ± 265 km) (Figure 1). The only difference for the immatures was a longer distance travelled in spring with 9511 ± 2047 km, than in autumn where they flew 5807 ± 726 km (Figure 1). However, due to the small sample size for adult birds and the difficulty to objectively identify the end of 'migration' for continuously roaming immatures, a statistical comparison had no power to detect any differences.

Two immature birds had particularly long duration of migration, both in spring: Dobromir, 96 days in 2014 and Sanie, 76 days in 2015 (Figure 1), when the average duration was around 55 days for immatures and 30 days for adults for spring migration. During that remarkable travel, Dobromir kept flying around the Black Sea without really stopping in particular place (Eastern route on the map, Figure 1) so the total distance covered was also notably high with 16684 km. Similarly, Sanie kept travelling across Syria and Turkey where the bird spent more than a month roaming among various places that could be potential breeding areas.

Identification of areas where migration is concentrated

Most birds stopped at random places along the route, and very few roosting places overlapped among individuals. As a consequence, there were very few 'hotspot' areas where the population as a whole spent much time. We identified only one major (~ 30-bird days) stopover congregation site in central Anatolia (Turkey, Figure 2), which is also known as a major breeding area for Egyptian vultures (Beypazari, Turkey). Two other hotspots were located in the North-West of Turkey and in the southern tip of the Sinai Peninsula. The fourth one, with approximately 17-bird days was located in southern Turkey and the fifth one on the border between south-east Bulgaria and Greece with 16-bird days.

In a general way, the bottlenecks were more concentrated in spring than in autumn (Figure 3), with 25 cells that were crossed by more than 50 % of all migrations compared to only 7 cells in autumn. The maximum percentage reached in spring was 91 % of migrations occurring in one area, around Suez (Egypt), against 83 % in autumn, around Iskenderun (Turkey). The most important areas where the Egyptian vultures passed through were located at the southern margin of the Mediterranean Sea in spring and at the northern margin of the Mediterranean in autumn (Figure 3). Plus, the routes appeared to be different between autumn, where the birds flew through the Bosphorus after which their tracks got very dispersed south of the Mediterranean for the crossing of the Sahara, and spring where birds followed a route along the Red Sea and then proceeded via the Dardanelles to reach their breeding quarters.

There were less migratory locations in spring than in autumn, respectively 12 against 18, and the adult birds' contribution to these bottlenecks was more important in spring (Figure 1). Indeed, the adults contributed 42 % for the spring tracks, but only 33 % for the autumn migration.

Among the ten most important bottlenecks we calculated from both autumn and spring migration, the first one was located in the Gulf of Iskenderun (South Turkey) and included more than 70 % of all the migrations (Figure 4). The second one was positioned around Suez (Egypt) and exactly 70 % of the migrations were passing through the area. In the eight other cells, 53 % to 66 % of all the migrations occurred there, concentrating more than 15 migrations in each of them. All highlighted areas were mostly around the eastern coast of the Mediterranean from Turkey to Egypt, through Syria, Lebanon and Israel, as well as in central Anatolia (Turkey), around Beypazari, an area that we already highlighted as a migratory hotspot for Egyptian vultures (Figure 2 and 4).

Assessment of potential threats in important concentration areas

We identified one registered wind farm located in the main hotspot in central Anatolia (Figure 2), which is also an important bottleneck, seven within the most important bottleneck areas and two were partially included in one of the cells (Figure 4). Six of them were in the area where the largest number of Egyptian vultures passed through around the Gulf of Iskenderun (Turkey), and the seventh one was located in the second most important bottleneck around Suez (Egypt). The number of wind-turbines in each wind-farm could be as little as 5 and as many as hundreds.

DISCUSSION

From 14 Egyptian vultures originating from the Balkan population tracked by satellite telemetry, we defined the onset and the end of the spring and autumn migrations. From our definition, we identified 30 migrations, 18 in autumn but only 12 in spring because some juveniles died during or after their first autumn migration to East Africa or had not initiated a spring migration by 2016 (Oppel et al., 2015).

Egyptian vultures are not breeding before they become 5-6 years old but they are travelling from their breeding ground to East-Africa just after fledging, and come back to Europe between 2 to 4 years after, travelling then for every season. These pre-breeding travels were called 'migrations' in our study. Nevertheless, some birds were not really stopping as they did not have a precise goal like the adults that were going back to their nest for breeding, and some immatures kept flying around Eastern-Europe and Turkey. The variability among immature routes was high and we had the case of one bird that was flying around the Black Sea during the summer without a stationary period, thus essentially merging spring migration and subsequent autumn migration into one extremely long round trip. Moreover, in spring some immatures were flying from their wintering ground to northern Egypt or northern Libya and then turning back south. All those movements seem to describe an exploratory behavior of the birds that could help them to recognize and learn from their environment before performing their first proper migration for the breeding season when they become mature. This could explain why we found a longer distance travelled by the immatures in spring than in autumn.

The migration distance and duration of immatures in spring were also higher than those of the adult birds in the same season. The adults were showing constant parameters between seasons in our results. Oppel et al. in 2015 have suggested that the immatures could be flying under the guidance of the adults for their first autumn migration that could explain the higher efficiency of the young birds during autumn than spring. The immature Egyptian vultures might learn the migration route from the adult (Mellone et al., 2011), to choose the safer one (Velevksi et al. 2014). Benefiting from the older, the young birds could correct their trajectory, save time and energy, avoid natural barriers, flying as much of their journey as possible overland (Newton 2008). Sergio et al. in 2014 described the progressive improvement of migratory performance with age, supporting our hypothesis of efficient migratory routes in terms of length and duration for the adults. This phenomenon has been previously reported for the Golden Eagle, another soaring bird (Miller et al., 2016). Improving migratory performances, they would increase their survival, breeding success and so their fitness and longevity (Sergio et al., 2014). Thus, it could explain why we observed shorter migratory distance and duration for the adults, and lower individual variability within adults than among immature birds. Plus, the adults were more consistent in terms of departure and arrival dates of migration, reinforcing the hypothesis that they may be more constrained by time, especially in spring for the breeding season (Miller et al., 2016). Becoming adults, the Egyptian vultures from the Iberian population seem to show consistent migration timing at the individual level in both seasons (López-López et al., 2014), that was also suggested for the Balkan population by our observations on five adult birds. To confirm this migration strategy at the population level, more tracking data on adult Egyptian vultures from the Balkan population are needed.

The Balkan population has declined from >500 to approximately 60 pairs since 1980 and has fragmented into several small population clusters (Velevski et al., 2015). Thus, the chances of the birds to fly under the guidance of adults for their first migration have severely decreased. This could explain why many birds died in the Mediterranean Sea (Oppel et al. 2015), trying to fly directly headed for their wintering quarters without any experience of navigating around that large open area of water.

The definition of the season migration was particularly challenging, that is the reason why we had to set its onset and end manually in most of the cases that might be arbitrary and could have distorted our results. However, they represent a base that can be used for further studies and the season definition for immatures can be refined and completed with additional data.

Identification of areas where migration is concentrated

Using the birds' locations corresponding to the 30 described migrations, we highlighted important concentration areas. Our tracking data on Egyptian vultures highlighted only one particular hotspot along the migration route, in central Anatolia (Turkey) around Beypazari, a well-known breeding area (Sen, 2012) where most of the Egyptian vultures originating from the Balkans are migrating and immature birds have been prospecting. In that region, the birds were migrating through another breeding area, potential for genetic exchange, population connectivity. We need to consider Balkan and Turkish populations as connected because some immatures may actually start breeding there. The hypothesis has not been investigated yet; therefore more research on that eventuality is needed. The municipal rubbish dump of Beypazari was an important congregation site until early 2015 when it was closed due to sanitary concerns. Because this foraging site is no longer accessible to vultures, this measure may contribute to a decrease of visits of migratory birds to the region in the future.

The second most important hotspot was located at the southern tip of the Sinai Peninsula, where the narrowest strait is known to be crossed by a large number of migrants in spring and autumn (Hilgerloh et al., 2011). In autumn, Egyptian vultures seemed to fly to the southern part of the Sinai and then reverse their course to find their way to Egypt and enter the African continent mainly at Suez. The same behavior was previously observed in the southwestern part of the Sinai Peninsula but finally the Egyptian vulture crossed the Red Sea to reach Africa (Gradev et al., 2012). Thus, every bird demonstrating similar behavior in the southern part of the Sinai Peninsula might explain the observation of a hotspot, originating from the accumulation of time spent by each bird in the area.

As the tagging has been performed in the breeding area of the birds, places where they also came back, there was one highlighted hotspot among the 5 most important which is actually corresponding to this breeding area and not to a migratory hotspot and will not be consider here.

Finding stopover hotspots, as you would do for migrating waders, waterfowl, or storks, is unlikely to be a very suitable conservation strategy for the Egyptian vulture. Being full migrant, broad-winged raptors, it has been shown that the Egyptian vultures are stopping unfrequently trying to reach their wintering or breeding areas as fast as possible without using specific stopover sites (Porter & Beaman 1985; Oppel et al. 2015). Moreover, we had the case of some identified 'hotspots' that were actually the result of a single bird staying for a long time in a same area (Dobromir in northeast of Iraq), rather than lots of birds using the same place. The result of one bird roosting in one place for ten days or ten birds stopping in that area for one day would have shown the same result on the map. Generally, the Egyptian vultures halt for several hours only during the night to roost on trees or electric pylons but do not spend a lot of time in stopover sites during the day, so we did not consider the area in Iraq as a hotspot.

The bottlenecks appeared to be far more meaningful than hotspots, and we found interesting ecological patterns here. Autumn migration proceeded via Bosphorus and then got very diffuse south of the Mediterranean Sea. In contrast, spring migration partially focused along the Red Sea coast that may be explained by strong winds in Sahara (Liechti, 2006; Strandberg et al., 2009) and followed a route by the Dardanelles to the breeding grounds. The birds were mostly crossing the Sahara in autumn and flying along the Red Sea coast in spring, being in accordance with García-Ripollés et al. (2010) who observed the same phenomenon for Egyptian vultures from Spain migrating to West Africa. It is possible that some birds have been drifted or had to turn back because of strong winds. For example, in spring 2016 two birds migrating across the Sahara stopped and migrated south, then east, back-tracking from their intended directional movement and waited 2-5 days before continuing their travel to their breeding grounds. At the same time, a strong north-northeast wind (50-60 km/h) was recorded at the nearest weather station, which is consistent with the hypothesis that strong headwinds affected the progress of the birds. Then, in autumn the Egyptian vultures were flying southward until they reached the Mediterranean at its northern end and we observed the same phenomenon in spring when birds were flying northward until they reached the Sea at Suez Canal. In both seasons, the birds had to fly a detour around this huge natural barrier, following the coast and describing a clear route used by a large number of individuals in spring. During autumn the tracks were more dispersed before and after the concentration area at the initial meeting point with the Mediterranean. The routes' difference between seasons can be slight or pronounced with the autumn route lying consistently east or west of the spring one, and could be explained by environmental conditions, especially for soaring birds that are dependent on wind conditions (Newton, 2007). Indeed, this phenomenon called 'loop migration' may find its origin in the selection of wind regimes by the birds (Nilsson et al., 2013) or wind drift (Klaassen et al., 2010, 2011), where spring and autumn routes differ significantly. In our case, the autumn route was first east of the spring one in the northern part of the flyway, before changing after the Egyptian vultures reached the Mediterranean and became west of the spring route in the south, when the individuals entered Africa. These observations of loop migration are in agreement with studies on the migration of other raptor species in the same region (Agostini et al., 2012; Meyburg, Paillat, & Meyburg, 2003) and also in Spain (García-Ripollés et al., 2010; Mellone et al., 2013).

The bottleneck areas were more concentrated in spring rather than in autumn. Interestingly, the proportion of adult birds contributing to spring migration description was higher in our data than for autumn migration (Table 1). Immature birds initiate a dispersal process that first involves first departure from the natal population, exploratory movements, temporary settlements and then a return to the natal population as shown for the Spanish Imperial Eagle (Ferrer, 2008). Compared to the adults, immatures birds in general seem to be naturally more dispersed, wandering over extensive feeding sites, settling for variable duration in appropriate areas or perform long travels prospecting for potential breeding territories, especially when approaching the age of first breeding (Reed et al., 1999). Becoming adults at about 5 years old, they abandon their wandering and communal lifestyle in search of breeding territory they will have to defend and keep for years like most of the long-lived bird species (Grande et al., 2009). In the same way as the Spanish Imperial Eagle whose dispersal process can last the entire immature period, the behavior of immature Egyptian vultures may also differ radically from that of territorial adults (Ferrer, 2008).

The higher concentration of the bottlenecks in spring may be explained by a faster migration, with birds spending less time en route, supported by the few hotspots we described earlier, and so they flew the shortest distance back to their breeding ground. In this sense we observed shorter migration distance and duration for adult birds, present in larger proportion in our data on spring migration than during autumn but still not reaching the half of the sample size. For different raptors species, during spring migration the aim of adult individuals is to reach the breeding area and start reproduction early to reduce competition, get a better territory and so increase their breeding success (Osprey, *Pandion haliaetus*: Alerstam, Hake, & Kjellén, 2006; Osprey and Western Marsh-harrier, *Circus aeruginosus*: Mellone et al., 2012; Nilsson et al., 2013). However, the hypothesis of time-minimization strategy for breeding has been refuted in studies on Egyptian vulture, that reveals being faster in autumn (García-Ripollés et al., 2010; López-López et al., 2014) or showing same travel speed and duration in both seasons (Mellone et al., 2012). Our results are consistent with the second case because adult birds revealed a slightly shorter migration in autumn than in spring but no difference in terms of duration or travel speed between the two seasons. The autumn migration could be faster because soaring conditions are better, e.g. hotter air mass than in spring. In their study, Lopez-Lopez et al. in 2014 explained the lower duration of migration in autumn for Egyptian vultures by more favorable factors (tailwind and day length) experienced in the same time by the birds in that season. Another study from García-Ripollés et al 2010 mentioned prevailing north-east to south-west dominant tail-winds that could explain the faster autumn migration. The difference of speed between the seasons combined with our previous observations of different routes followed, i.e. crossing the Sahara in autumn and flying along the Red Sea coast in spring, could suggest an adjustment of adult birds' behavior when they encounter unfavorable landscape or meteorological conditions by speeding up their flight (García-Ripollés et al., 2010).

The wind has been mentioned several times as a modeling factor for the migration routes of birds (Klaassen et al., 2011) and might be one of the most important selective agents shaping the loop migration (Agostini et al., 2012; Alerstam, 1979; Klaassen et al., 2010; Newton, 2007).

The most important bottlenecks were selected using an index calculated with data from autumn and spring. To prioritize areas for conservation we kept the ten cells with the highest average of tracks passing through it. The most important bottleneck was located around the Gulf of Iskenderun (Turkey), the eastern tip of the Mediterranean, including also Belen Pass a mountain pass located in south-central Turkey. This region is known to concentrate important raptor migrations in autumn, along the coast at the northern extent of the gulf and at higher altitudes across the mountains (Meyburg et al., 2004; Oppel et al., 2014; Sutherland and Brooks, 1981). The second important bottleneck was positioned further south, around Suez (Egypt), with other bottlenecks located in-between across Syria, Lebanon and Israel, route previously observed to be followed by Egyptian vultures from the same population (Gradev et al., 2012) and other soaring birds (Leshem and Yom-Tov, 1998). Suez is known to be crossed by migratory raptors and small birds, primarily in spring but in rather small numbers in autumn (Meyburg et al., 2003). In autumn, the case of one Lesser Spotted Eagle migrating south of the Sinai Peninsula and reversing its course, flying back north to enter Africa via Suez was evoked by Meyburg et al. in 2002, referring to the observations we made about the hotspot in the southern tip of the Sinai Peninsula. Few birds were crossing the Red Sea at Bab-El-Mandeb Strait and most of them bypassed it, consequently they were travelling between the Mediterranean and the Red Sea through Egypt and Israel. However, the area around Eilat (Israel), a well-known migratory bottleneck for raptors (Meyburg et al., 2003; Oppel et al., 2014; Shirihai and Christie, 1992), was not highlighted as such with our data but another region on the border between Egypt and Israel appeared to be more significant in terms of birds' tracks concentration. Shirihai and Christie in 1992, following counts started earlier (Porter and Beaman, 1985), reported high numbers of raptors passing through the same area, in the northern valleys of Israel, around Kfar Kasem. Then, further observations in 1998 reported two important migratory routes across Israel, between the coast and Kfar Kasem due to the topographical structure of the country (Leshem and Yom-Tov, 1998), for soaring birds that did not travel through Eilat.

The area around Beypazari, previously highlighted as a hotspot, also appeared as an important bottleneck. Including between 53% to more than 70 % of all the migrations we defined, the coasts around the Gulf of Iskenderun, the regions around Suez and Beypazari should then be investigated as a priority for potential threats. Generally, Turkey is widely known as a gateway for millions of western Palaearctic migratory birds to attain their wintering quarters in Africa (Porter and Beaman, 1985). Turkish territory was also a significant roaming area for the tracked immature birds, especially one bird (Sanie) that travelled for more than one month through the country, stopping for short time in different areas. Besides, the Balkan population of Egyptian vultures may be supported by the different populations in Turkey (Méndez et al., 2015) as it has already been suggested for other species suspecting immigration episodes that are difficult to measure empirically (Demerdzhiev et al., 2015).

Assessment of potential threats in important concentration areas

We found ten wind farms in the identified important migration concentration areas. The area around Beypazari, central Anatolia, contained one wind farm close to Ankara. Six were enumerated in the main bottleneck around the Gulf of Iskenderun and one in the southern tip of the Sinai. Data about the Middle East were not accessible and explain why no wind-farm was represented on the map. Also, it seemed that some wind-farms were missing from the list we obtained, therefore we need people to work on-site, within the identified congregation sites to obtain more locations and more accurate positions of wind turbines, because not all wind turbines are automatically a threat unless they are situated in areas that vultures use for soaring or gliding.

In Spain, studies have described the negative effects of wind-farms on the population growth rates of the Egyptian vultures (Carrete et al., 2009; García-Ripollés and López-López, 2011) by causing additional mortality of adult birds. Another study described four main effects that wind-farms can have on birds, namely collision, displacement due to disturbance, barrier effects and habitat loss (Drewitt and Langston, 2006). The power lines are also an important threat for birds of prey, causing electrocutions and collisions (Loss, 2016). Therefore, the mapping of the potentially dangerous pylons, especially low-voltage ones (Arkumarev et al., 2014), in regions where birds congregate along with their insulation should be consider in the next conservation projects. Global energy demand being increasing around the world, the electricity infrastructures are expanding. It should be a priority to resort to long-term solutions and use non-lethal installations if we want to reduce the electrocution induced mortality of vultures and large raptors. Indeed, the insulation of dangerous pylons is an inadequate temporary solution because of the material weathering over time (Angelov et al. 2012).

The boundaries of the cells were set arbitrarily when the grid has been was defined in the analysis and they changed according to the anchor points used. We emphasize that the borders of the grid cells should not be used to delineate where the protection measures for the conservation of Egyptian vultures have to be undertaken on the ground, but rather as a coarse indication of the region with important congregation areas. To refine the crucial sites where we have to focus our conservation efforts, we need more information about the birds' migration routes and behaviors, especially concerning the adults from ground-based observations or very high resolution telemetry. Then the important regions where birds stop or fly through should be targeted for the research of threats at a local geographic scale for better results. Knowing that some areas are located in different countries and on borders between two or more countries, such actions will require substantial international coordination, efforts and resources (Velevski et al., 2014).

Finally, collisions and electrocutions with power lines and crash with wind turbines cannot be eliminated but they can be reduced, and the effects of wind-farm project can be assessed considering all the aspects of that threat concerning resident and migratory bird species (BirdLife International, 2015; http://migratorysoaringbirds.undp.birdlife.org/en/).

CONCLUSION

The Egyptian vultures from the Balkans have longer and more arduous migration than the birds from the Iberian population. The huge natural barrier which is the Mediterranean enforces a detour, which leads to migration bottlenecks at the northern (autumn) and southern (spring) margins of the Mediterranean. Some threats (windfarms) already exist in these bottlenecks, others (hunting) are likely, and more work on the ground is needed to identify and mitigate threats. Communication and data exchange will be necessary between conservation organizations especially as the Egyptian vultures are crossing many different countries during their travel. This work provides direction where future research and conservation efforts should be conducted along the Egyptian vulture flyway.

Table 1: *Summary of the migrations parameters for each bird, age class and year, ordered by season (ad = adult Egyptian vulture, im = Egyptian vulture tagged at nestling and progressively became adult).*

Name	Season	Age	Year	Start	End	Duration (days)	Distance (km)	Travel speed (km/day)
Lazaros	autumn	ad	2012	01/09/2012	26/09/2012	25	5713	229
Aoos	autumn	ad	2015	04/09/2015	27/09/2015	23	5302	231
Castor	autumn	ad	2014	22/08/2014	18/09/2014	27	4568	169
Castor	autumn	ad	2015	11/08/2015	09/09/2015	29	4307	149
Boris	autumn	ad	2015	14/09/2015	30/09/2015	16	4634	290
Jenny	autumn	ad	2015	14/09/2015	03/10/2015	19	5149	271
Spartacus	autumn	im	2010	13/09/2010	20/10/2010	37	4905	133
Levkipos	autumn	im	2012	09/09/2012	17/10/2012	38	5704	150
Arda	autumn	im	2012	18/09/2012	15/10/2012	46	5361	117
Volen	autumn	im	2012	05/09/2012	27/09/2012	22	4469	203
Dobromir	autumn	im	2012	02/09/2012	25/10/2012	53	6538	123
Dobromir	autumn	im	2014	27/07/2014	28/09/2014	63	7715	122
Dobromir	autumn	im	2015	22/08/2015	23/09/2015	32	5525	173
Svetlina	autumn	im	2012	07/09/2012	06/11/2012	60	6733	112
Iliaz	autumn	im	2012	19/09/2012	07/10/2012	18	4089	227
Paschalis	autumn	im	2013	08/09/2013	25/09/2013	17	4366	257
Sanie	autumn	im	2013	18/09/2013	11/10/2013	23	5307	231
Sanie	autumn	im	2015	20/07/2015	08/09/2015	50	8969	179
Lazaros	spring	ad	2013	08/03/2013	31/03/2013	23	5565	242
Aoos	spring	ad	2016	16/03/2016	18/04/2016	33	6335	192
Castor	spring	ad	2015	07/03/2015	05/04/2015	29	5625	194
Boris	spring	ad	2016	01/03/2016	20/03/2016	19	4459	235
Jenny	spring	ad	2016	16/03/2016	16/04/2016	31	6314	204
Volen	spring	im	2014	29/04/2014	25/06/2014	57	9959	175
Dobromir	spring	im	2014	18/04/2014	23/07/2014	96	16684	174
Dobromir	spring	im	2015	30/04/2015	15/05/2015	15	4789	319
Dobromir	spring	im	2016	01/05/2016	30/05/2016	29	6015	207
Iliaz	spring	im	2016	17/03/2016	09/05/2016	53	7306	138
Sanie	spring	im	2015	04/05/2015	19/07/2015	76	12587	166
Sanie	spring	im	2016	13/04/2016	02/06/2016	50	9236	185

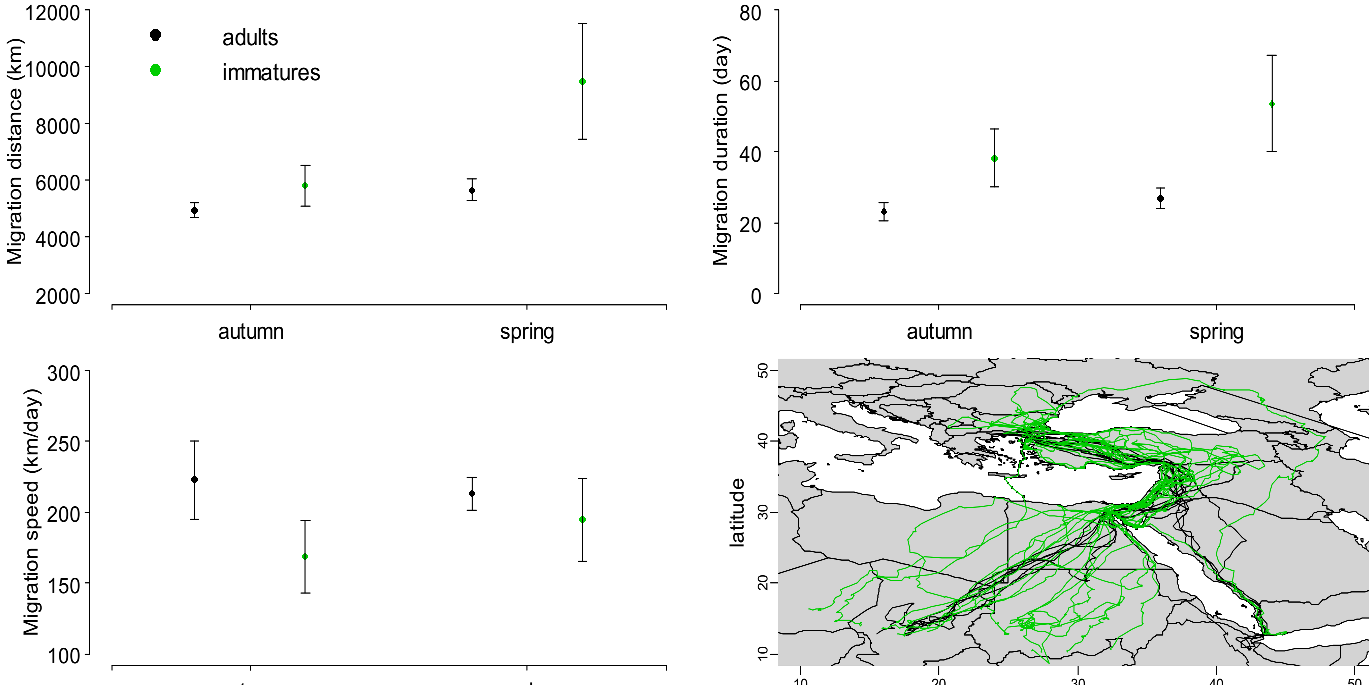

Figure 1: *Description of the average (± standard deviation) distance, duration and speed of migration for adult and immature Egyptian vultures during autumn and spring migrations. The map is describing all the 30 tracks of immatures (19, green) and adults (11, black) used for the analyses.*

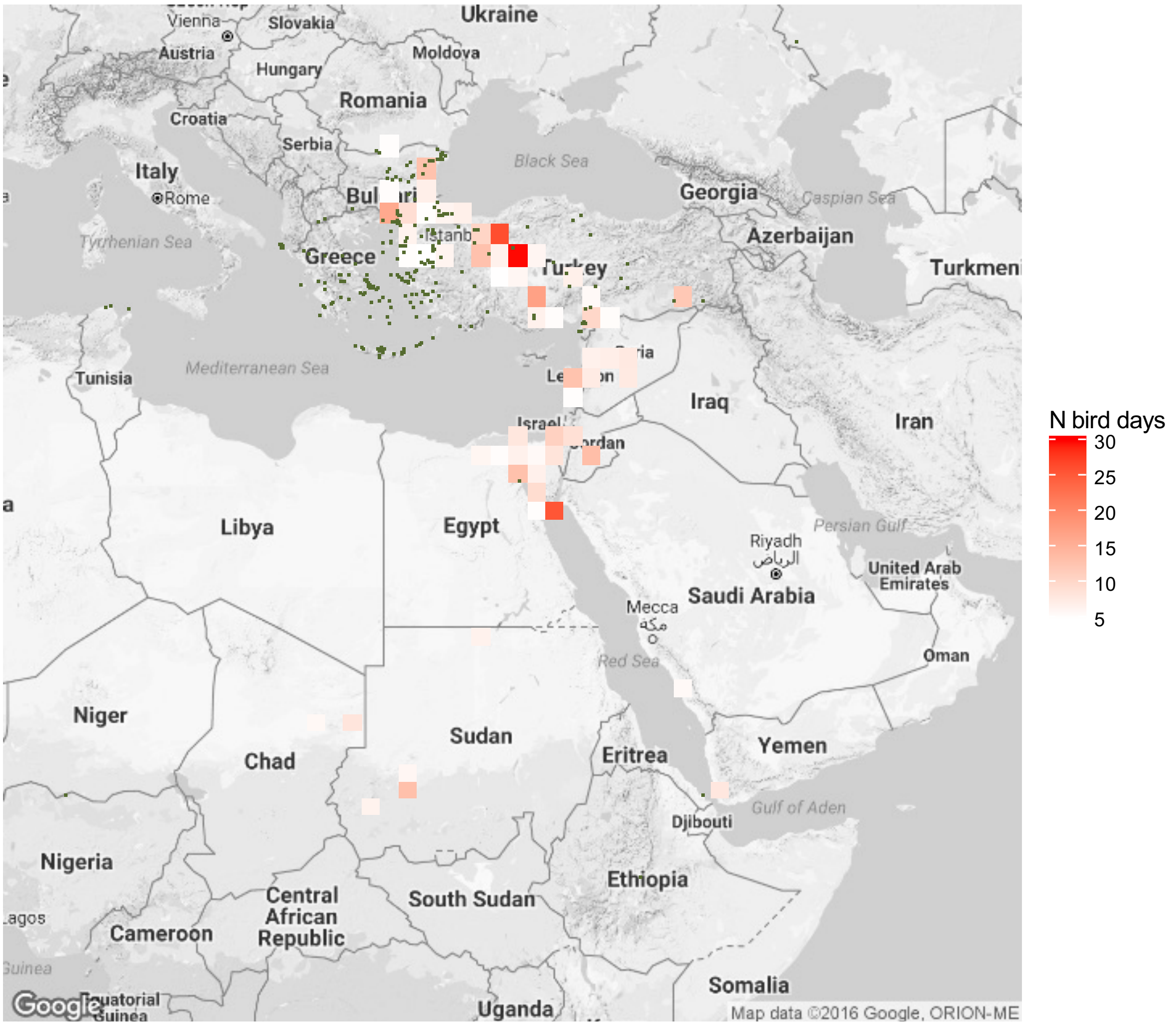

Figure 2: *Migration hotspots, i.e. areas where the 14 tracked Egyptian vultures from the Balkan population spent a lot of time during migration, calculated from 30 travels. Dark green dots mark wind-farms registered by The Wind Power©.*

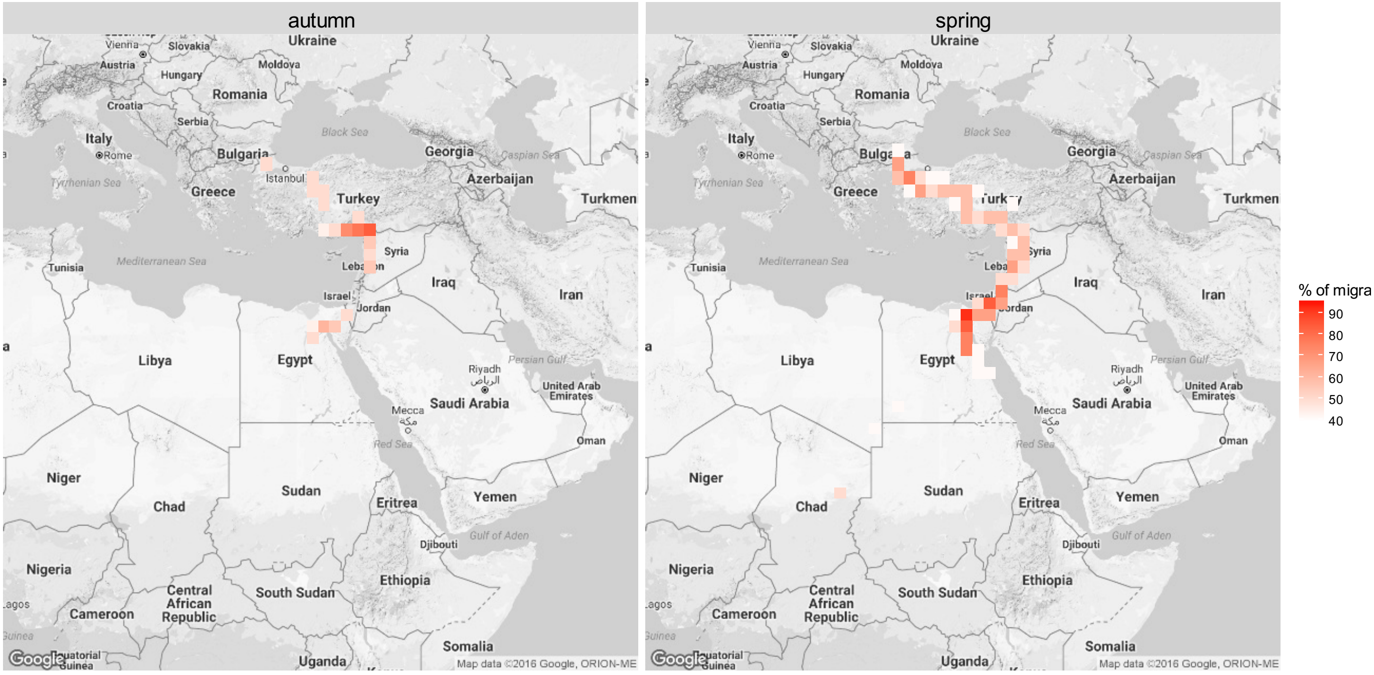

Figure 3: *Migration bottlenecks, i.e. areas where a large proportion of the tracked Egyptian vultures from the Balkan population migrated through, differentiated between spring and autumn migrations.*

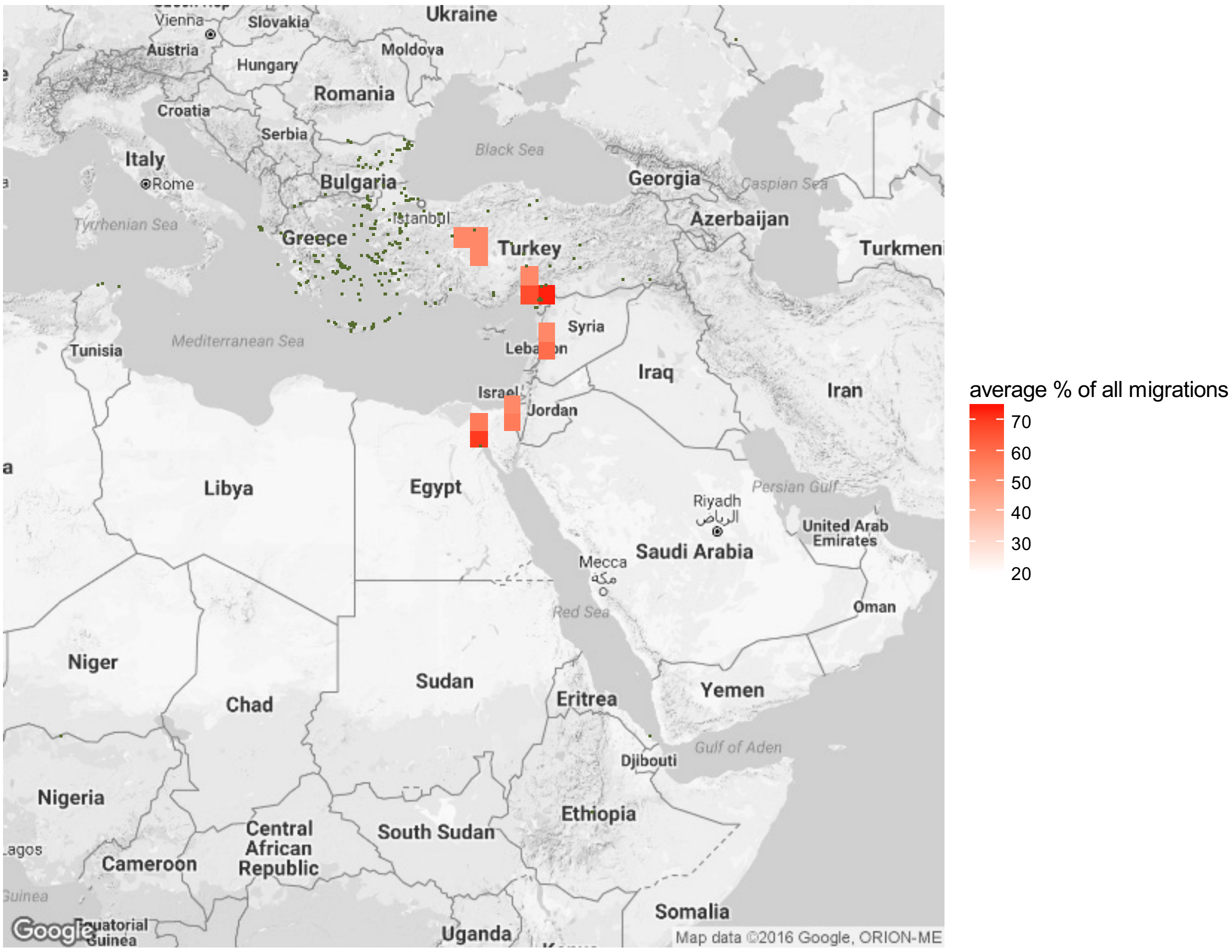

Figure 4: *Ten most important bottlenecks calculated as the weighted mean of the proportion of migrations passing through each cell in autumn and in spring. Windfarms locations obtained from The Wind Power© are represented by dark green points*

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