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Article

Identifying critical migratory bottlenecks and high-use areas for an endangered migratory soaring bird across three continents

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Migrant birds face a number of threats throughout their annual cycle, including persecution, collision with energy infrastructure, and habitat and climate change. A key challenge for the conservation of migrants is the identification of important habitat, including migratory concentration areas, because species survival rates may be determined by events in geographically very limited areas. Remote-tracking technology is facilitating the identification of such critical habitat, although the strategic identification of important sites and incorporation of such knowledge in conservation planning remains limited. We tracked 45 individuals of an endangered, soaring migrant (Egyptian vulture *Neophron percnopterus*), over 75 complete migrations that traversed three continents along the Red Sea Flyway. We summarize and contextualize migration statistics by season and age class, including migration start, midpoint, and end dates, as well as linear and cumulative migration distance, migration duration and speed, and route straightness. Then, using dynamic Brownian bridge movement models, we quantified space use to identify the most important migratory bottlenecks and high-use areas on the flyway. These areas each accounted for < 5% of the overall movement range of the tracked birds, yet > 20% of all tracks passed through bottlenecks, and > 50% of the overall vulture time spent on migration fell within high-use areas. The most important sites were located at the southeastern Red Sea coast and Bab-el-Mandeb Strait (Saudi Arabia, Yemen, Djibouti), the Suez Canal zone (Egypt), and the Gulf of Iskenderun (Turkey). Discouragingly however, none of the area within the major migratory bottlenecks was protected and < 13% of the high-use areas were protected. This demonstrates a very concerning gap in the protected area network for migratory soaring birds along the Red Sea Flyway. Because reducing threats at migratory concentrations can be a very efficient approach to protect populations, our work

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provides clear guidelines where conservation investment is urgently needed to benefit as many as 35 migratory soaring-bird species that regularly use the Red Sea Flyway.

Keywords: migration, avian ecology, ornithology, conservation biology, conservation planning, protected area network, scavenger, phenology, endangered species, *Neophron percnopterus*, Egyptian vulture, flyway

Introduction

Approximately 19% of all bird species are migratory, of which 11% are threatened or near-threatened with extinction (Kirby et al. 2008). Migrant birds face a number of threats throughout their annual cycle, including persecution, collision with energy infrastructure, and habitat and climate change (Kirby et al. 2008). Conservation of migratory species is particularly challenging, because it may be ineffective if focused solely on one portion of the species' range (Runge et al. 2014). If species concentrate within small geographic areas during migration, impacts at these sites could have population-level effects (Runge et al. 2014). A key issue for the conservation of migratory birds, then, is the identification of important habitat throughout the annual cycle, including where individuals spend a lot of time (hereafter 'high-use areas') and/or concentrate during migration (hereafter 'bottlenecks') due to geographical, meteorological, or other factors (Limiñana et al. 2012, Runge et al. 2014, Horns et al. 2016). The increasing availability and miniaturization of remote-tracking technologies is facilitating a boom in the study of the full annual cycles of migratory birds, which allows the identification of such critical habitat (Bridge et al. 2011, Vickery et al. 2014). However, the incorporation of such knowledge in conservation planning remains limited (Runge et al. 2014, Dhanjal-Adams et al. 2017).

Migratory birds perform many valuable ecosystem services (Whelan et al. 2008), such as seed dispersal (Howe and Desteven 1979, Nathan et al. 2008), or control of agricultural pests (Kellermann et al. 2008, Philpott et al. 2009), and thus link spatially disparate ecological communities (Bauer and Hoye 2014). Detrimental effects that occur at any stage along the flyway and reduce the populations of migratory birds may therefore have ecosystem consequences across continents if migratory birds no longer fulfill their roles in these ecological communities. One guild of birds that has a keystone status (Mills et al. 1993) are scavengers like vultures, as declines in vulture populations can result in trophic cascades and mesopredator release (Ogada et al. 2012, Buechley and Şekercioğlu 2016a, b) and human rabies epidemics (Markandya et al. 2008). Vultures are the most endangered group of birds, with nine species Critically Endangered, three Endangered, and four Near Threatened (Buechley and Şekercioğlu 2016a, BirdLife International 2018). The long-distance migrations of some vulture species (Mandel et al. 2008, García-Ripollés et al. 2010) indicate that population declines could have negative consequences for ecosystems across continents connected by migrations.

One of the vulture species that exhibits regular intercontinental migrations is the Egyptian vulture *Neophron percnopterus*, a scavenger distributed across southern Europe, central and southern Asia, the Middle East and Africa (BirdLife International 2018). In 2007, the Egyptian vulture was uplisted from Least Concern to Endangered due to widespread population declines, range contractions and extinctions of populations caused by inadvertent poisoning, electrocutions, collisions with wind turbines, reduced food availability and persecution (Cuthbert et al. 2006, Virani et al. 2011, Ogada et al. 2015, Velevski et al. 2015). The Egyptian vulture has been the focus of considerable research and conservation effort, mostly in Europe (López-López et al. 2014a, Oppel et al. 2016a, b) and India (Cuthbert et al. 2006), with some studies illuminating the migration routes and winter ranges of birds (Meyburg et al. 2004, Ceccolini et al. 2009, García-Ripollés et al. 2010, López-López et al. 2014b, Oppel et al. 2015, Buechley et al. 2018). Nonetheless, little is known about the status and ecology of the species in central Asia, the Middle East, and north Africa, and there is little information on concentration areas during migration, which hinders conservation planning. Indeed one of the primary recommended actions for future research and conservation of the species is to identify migratory bottlenecks and high-use areas, and then work to mitigate threats therein (Oppel et al. 2015, Nikolov et al. 2016).

Furthermore, the Egyptian vulture is an excellent model species to identify migratory habitat for soaring birds generally. The species is an obligate soaring migrant which relies heavily on thermal and orographic uplift to migrate (Bildstein 2006, Mandel et al. 2008). Migratory routes of Egyptian vultures are therefore largely shaped by geographic features, and, in particular, avoidance of water crossings (García-Ripollés et al. 2010, but see Oppel et al. 2015), which are characteristics shared by many migrants (Bildstein 2006). Indeed, observed congregations of Egyptian vultures occur at many known migratory bottlenecks in the Middle East and eastern Africa (Welch and Welch 1988, Shirihai and Christie 1992, Oppel et al. 2014).

This study was located at the intersection of Europe, Asia, and Africa, in a region recognized as the Red Sea Flyway (UNDP 2006). The Red Sea Flyway is the second most important flyway for migratory soaring birds in the world and the most important route for Palearctic soaring birds migrating to and from Africa, yet it is perhaps the least studied major flyway in the world (UNDP 2006). Well over one million migratory soaring birds of at least thirty-five species regularly use this flyway, including ten species at risk of extinction (Supplementary material Appendix 1) (Welch and Welch 1988, UNDP 2006). Nearly the entire world population of Levant sparrowhawk *Accipiter brevipes* concentrates here on migration, as well as > 90% of the lesser spotted eagle *Aquila pomarina* population, ~60% of Eurasian honey buzzard *Pernis apivorus* and the endangered steppe eagle *Aquila nipalensis*, and ~50% of short-toed eagle *Circaetus gallicus*, booted eagle *Hieraaetus pennatus*, and white stork *Ciconia ciconia* populations (UNDP 2006, BirdLife International 2018). Furthermore, approximately 50% of the global population of the Egyptian vulture uses the Red Sea Flyway (UNDP 2006), making this arguably the most important region for research and conservation of this species.

In this paper we investigate the following questions: 1) where are the migratory bottlenecks and high-use areas for Egyptian vultures during migrations along the Red Sea Flyway?, and 2) do these areas receive any formal national or international protection for their value to migratory birds? To investigate these questions, we use data from 45 Egyptian vultures that were tracked over a period of eight years (2010–2017) across eastern Europe, the Middle East and north and east Africa, and that migrated along the Red Sea Flyway (Fig. 1). Using dynamic Brownian bridge movement models, we quantified space use along migration paths to identify the most important migratory bottlenecks and high-use areas on the flyway. We then evaluate the percentage of these key sites that are included in the protected area network and highlight gaps in protection. Because reducing threats at migratory concentrations can be a very efficient approach to protect populations, our work provides clear guidelines where conservation investment is urgently needed to benefit as many as 35 migratory soaring bird species, including the Egyptian vulture and nine other species at risk of extinction that regularly use the Red Sea Flyway (UNDP 2006).

Methods

Vulture capture and tagging

From 2010–2016, 45 Egyptian vultures were trapped and fitted with satellite transmitters in the Balkans (Bulgaria, Greece, Former Yugoslav Republic of Macedonia, and Albania), the Middle East (Turkey and Armenia), and Africa (Ethiopia and Djibouti). Tagging in the Balkans was completed in the LIFE+ project 'The Return of the Neophron'

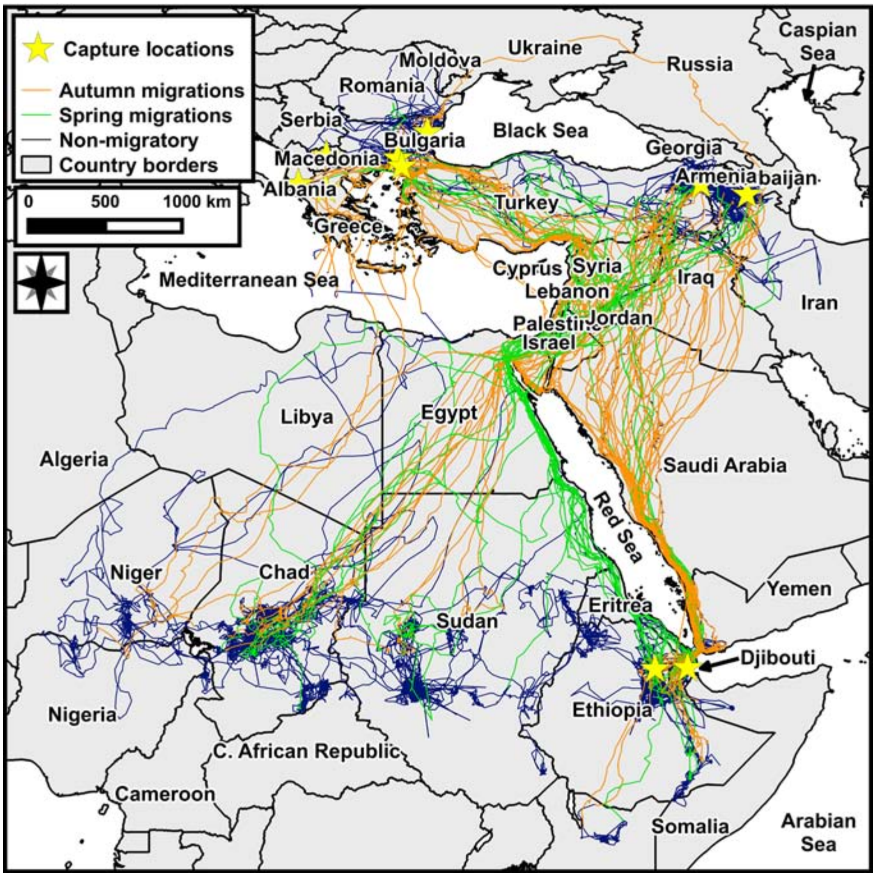

Figure 1. Overview map of the complete satellite tracking dataset from 45 Egyptian vultures. Individuals ranged across eastern Europe, the Middle East, and north and east Africa, with migration routes concentrating along the Red Sea Flyway. All labeled countries (n = 38) were visited by tagged individuals.

(LIFE10 NAT/BG/000152). Twenty-nine birds were tagged in the Balkans, the majority of which were juveniles tagged in the nest prior to fledging (n = 21). Of the remaining eight birds, two adults and one immature (4th year) were captured with net traps at a feeding site, two adults were found poisoned in Greece and were tagged and released after rehabilitation, and three juveniles were released captive-born individuals. The University of Utah, USA, led tagging of fifteen birds in Turkey, Armenia, and Ethiopia. International Avian Research tagged one bird in Djibouti. Of these sixteen birds tagged in the Middle East and Africa, seven were adults and nine were immatures (2nd through 4th years). All birds in the Middle East and Africa were captured near municipal waste dumps, where they reliably congregate (Fazari and McGrady 2016), using padded leg-hold traps with weakened springs to minimize the risk of injury (Bloom 1987). All captured birds were measured, checked for overall health, and were in good physical condition when released. Permits were acquired for each country and year of capture.

In the Balkans, all birds were fitted with 45 g solar-powered Microwave Telemetry GPS transmitters, while birds in the Middle East and Africa were tagged with Microwave Telemetry, Ecotone Telemetry, North Star Telemetry, or DynaTrak GPS transmitters. All 45 units were attached as backpacks with 8 mm Teflon® ribbon, and could operate continuously for many years because the solar panel was sufficient to re-charge the battery. Transmitters weighed 24–45 g, accounting for < 3% of body mass, which is unlikely to have had adverse effects on individuals' survival probability or movement ecology (Klaassen et al. 2014). Six transmitters attached in the Middle East and Africa used the GSM network to relay GPS fix data. The other 39 units across both tagging regions used the Argos Satellite Data Collection Relay System (CLS America, USA). Two units in the Middle East and Africa recorded positions at a temporal resolution of one point per minute; all others recorded positions only up to once per hour. All data were automatically downloaded and incorporated into the Movebank database (<www.movebank.org>).

Processing GPS telemetry data

Telemetry data were censored to remove erroneous locations using the 'longest-consistent track' filter in Movebank (2016). To roughly standardize the temporal resolution of the data across all units, we excluded all but the first location point for each individual in each hour from the two units that recorded data at higher resolution.

Individual-level migration parameters

To identify concentration areas during migration, we first segmented the raw tracking data for each individual to extract data associated with long-distance migration. We identified migration parameters (migration start date, end date, duration, and distance) with a method based on net displacement (ND) (Fig. 2). ND measures the straight line distance between the first location (i.e. the trapping location) and all subsequent relocations for an individual animal (Bunnefeld et al. 2011, Beatty et al. 2013). We calculated daily ND values for each bird with the first relocation recorded each day. We specifically used one point per day because we were interested in broad scale movement patterns to define migration phenology.

We then fit a nonlinear model based on the three-parameter logistic growth model (Pinheiro and Bates 2000) to the ND values for each bird. The migration distance (δ), or the distance of migration between the winter and summer range, varied among migration events to account for individuals that returned to different wintering and/or summering areas each year (Bunnefeld et al 2011). In addition, the migration midpoint (θ), or the point at which half of the migration distance was completed, and scale parameters (φ), or the temporal duration of migration, also varied among migration events to account for heterogeneity in migration patterns among years and seasons. We identified the migration start date as $\theta - 3\varphi$ and the migration end date as $\theta + 3\varphi$ to correspond to approximately 5 and 95% of asymptotic height, respectively. Although previous researchers have used $\theta \pm 2\varphi$ (Beatty et al.

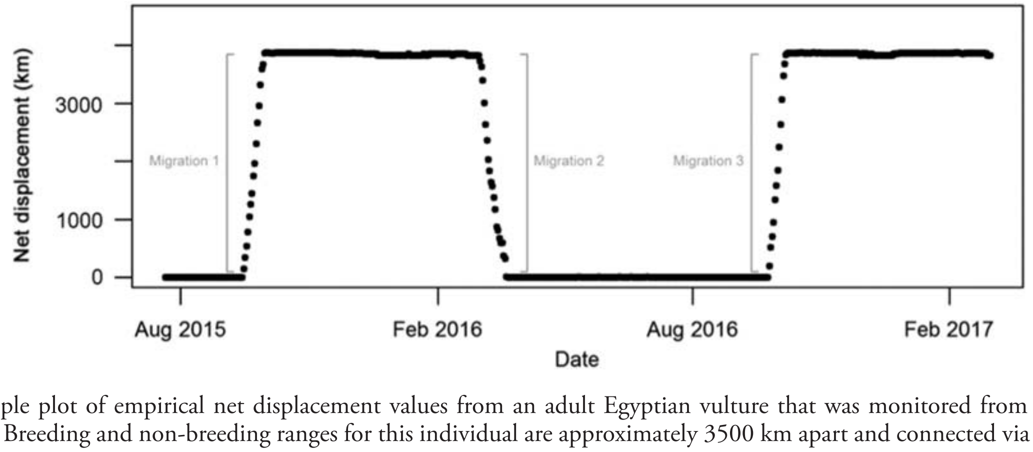

Figure 2. Example plot of empirical net displacement values from an adult Egyptian vulture that was monitored from August 2015 to February 2017. Breeding and non-breeding ranges for this individual are approximately 3500 km apart and connected via regular, seasonal migrations.

2013) or $\theta \pm \varphi$ (Bunnefeld et al. 2011), the objective of this study was to identify important areas throughout the full migration cycle. Consequently, we wanted to liberally define the migration period to include all potential information on bird movements during the migration period.

We conducted further visual inspection of empirical ND data and migration parameters from fitted models to validate migration events (Fig. 2). Our criterion for a validated migration event involved a bird moving from traditional wintering grounds to summering grounds or vice versa. We identified several immature birds that wandered widely throughout north Africa, including long distance movements during the migratory season. We identified such forays as non-migratory movements and excluded them from further analyses. In addition, several vultures initiated a migration event, but did not complete the migration because they either died or the transmitters failed during migration. For these individuals, we included their migration paths in use and bottleneck analyses, but do not make any inferences on migration parameters. We performed all operations in R (R Core Team), using the nls function and the adehabitatLT package (Calenge 2017).

Using complete migration trajectories, we extracted the following migration parameters: 1) migration start, midpoint, and end date; 2) migration duration (days); 3) linear distance between migration start and end points (km); 4) cumulative distance traveled between migration start and end points (km); 5) migration speed (cumulative distance/duration); and 6) migration straightness (linear migration distance/cumulative migration distance). Straightness provides an estimate of route efficiency (López-López et al. 2014b).

Identifying high-use areas and migratory bottlenecks

Egyptian vultures are diurnal soaring migrants that rest each night during migration. At the population level, the areas that would be most important for conservation activities are those where one or more individuals spend a lot of time during migration (high-use areas) or where multiple individuals migrate through a relatively narrow area where they may be exposed to certain threats (bottlenecks). We used dynamic Brownian bridge movement models to analyze space use and corridors during migration, which allowed us to quantify the use of geographic areas by the tracked population. The Brownian bridge movement model is based on a probabilistic model of the movement path between relocations (Horne et al. 2007). This model uses the time between successive points, the uncertainty inherent in the location coordinates, and an uncertainty component that describes how much the animal's trajectory deviated from a straight-line movement (Brownian motion variance, σ^2_m), within a random walk framework to estimate the probability of use of a given geographic area (Horne et al. 2007). The Brownian bridge movement model is particularly useful for delineating migration tracks of animals because it produces a probabilistic estimate of the path of migration between points, and facilitates identification of migration corridors (Sawyer et al. 2009, Fischer et al. 2013).

The dynamic Brownian bridge movement model (dBBMM), which we use here, is a further refinement of the Brownian bridge movement model that identifies distinct movement patterns (e.g. active migration versus temporary stationary periods) and assigns a variable Brownian motion variance along the movement path, given that an animal's behavior varies predictably between distinct patterns (Kranstauber et al. 2012). This classification is accomplished by searching over temporal 'windows' of the data to identify changes in the amount of displacement between points. The dBBMM accurately distinguishes between temporary roosting sites with local movements and long-distance movement corridors, and is thus ideal for evaluating avian migrations for species that do not fly non-stop, such as diurnal soaring raptors (Palm et al. 2015). The output of the dBBMM is a utilization distribution (UD), which summarizes the area and relative intensity of use (Worton 1989). We used the UDs resulting from the dBBMM to identify high-use areas and bottlenecks throughout the study area.

We used the migration start and end dates as identified from the individual-level net displacement models (including all points from the first and last day of each migration segment) and calculated UDs for each individual and migration based on the dBBMM in the move package (Kranstauber and Smolla 2013) in R (R Core Team). We set the grid size for all UD calculations to a 10 × 10 km resolution, which provided relatively high resolution mapping over the very large extent of Egyptian vulture migrations (across 3 continents), while maintaining computational efficiency. We set the window size and margin, which control the Brownian motion variance parameter, at 25 and 9 subsequent hourly locations respectively, which corresponded to a window size of approximately one day (Kranstauber et al. 2012, Palm et al. 2015). This choice was based on the biological rhythm of a diurnal soaring migrant such as the Egyptian vulture, where daily movements are interspersed by nocturnal rest periods of ~8 h, and these window and margin sizes should thus identify changes in σ^2_m both within and across days over the course of each migration trajectory.

To identify high-use areas, we weighted each individual UD by the migration duration, by multiplying all pixels in the UD by the number of days spent on that migration trajectory (Palm et al. 2015). This effectively converted the proportional UD to a common curency (number of days) that could be used across migratory journeys of different duration. We then summed all individual UDs to create a global UD for all tracked individuals over the entire study area, and normalized it so that the cumulative pixel values summed to 1 (Sawyer et al. 2009, Palm et al. 2015). The resulting UD provided an estimate of the proportional use of each 10 km^2 grid cell by all tracked individuals over the entire study area. We then identified the 50, 75, and 99% probability densities of the UD (i.e. the area in which location distribution predicts the vultures spent *x*% of time). Following Palm et al.

(2015), we assumed that the 50% probability were high-use areas and the 75% probability were moderate use areas. The 99% probability effectively represents the range map for all Egyptian vultures tracked in this study.

To identify migratory bottlenecks, we summed the number of migration routes – as identified from the 99% probability densities for each individual migration trajectory – that overlapped in each 10 km^2 grid cell over the entire study area (Sawyer et al. 2009). We then divided this by the total number of migration routes in the study to produce a raster where each cell had a value indicating the proportion of all migration tracks that passed through it. As many as 35% of all migration tracks intersected any given 10 km^2 grid cell. We assumed that areas with 10–20% of migratory paths were migration corridors (of medium importance), and > 20% were migration bottlenecks (of high importance). To visualize how migratory bottlenecks differed between seasons, we subset the data by season and repeated the above processes.

We used all migration paths in both use and bottleneck analyses, including those of incomplete migrations (e.g. when a bird died on migration), because we deem all trajectories to contribute important information about the migration ecology of the species. Furthermore, 16 of 45 birds were tracked for more than one migration event and each migration trajectory was included because birds used different migration paths between seasons and years. However, although individuals contributed up to seven migration trajectories, this constituted just 7.7% of all migration tracks, and therefore no individual had an overly large influence on the location of high-use areas or bottlenecks.

Conservation gaps and priorities

Because inadequate protection of important migration routes is a recognized deficiency for long-distance migrants (Runge et al. 2014), we calculated the area and percentage of Egyptian vulture use areas that fell within existing protected or recognized areas of importance. In this analysis, we included both protected areas (PAs) (The World Database of Protected Areas (IUCN and UNEP-WCMC 2012)), obtained from protectedplanet.net (22 Feb., 2017), and Important Bird Areas (IBAs) (BirdLife International 2018). The PA database includes sites that are designated or proposed nationally and under regional and international agreements (IUCN and UNEP-WCMC 2012). IBAs are recognized for their importance for birds, but do not provide any formal protection unless they are inscribed as protected areas in national legislation (BirdLife International 2018). We used a geographic information system (GIS, using QGIS, <www.qgis.org>) to visualize results.

Data deposition

Data will be made available upon request from Movebank Program IDs 9651291 and 15869951.

Results

Individual-level migration parameters

Of 45 total tracked vultures, two from the Balkans died prior to migrating and two tagged in Ethiopia and Djibouti never migrated out of Africa. Of the 41 remaining migratory individuals, there were 22 juveniles, 8 sub-adults (2nd through 4th years) and 11 adults at the time of marking. Individual-level net displacement models identified 75 complete migration events, and 17 incomplete events. Incomplete migration events were associated with either mortality or transmitter failure during migration. Of the 41 individuals, 23 were tracked for just one migration event; two were tracked for two migrations, 10 for three, three for five, one for six, and two for seven. As Egyptian vultures aged over the course of the study, our sample included complete migration events from 22 first-year birds (juveniles), eight second-year, 12 third-year, seven fourth-year, and 38 adult birds (5+ years).

Collective Egyptian vulture migrations spanned a large time frame in both spring (27 Feb.–28 Jun.) and autumn (23 Jul.–26 Nov.), wherein individuals traveled between 3302 and 11 974 km over the course of 12 to 95 d (Table 1). The linear distance between migration start and end points was similar for immatures (first through fourth year vultures, mean = 3289 km) and adults (5+ year old vultures, mean = 3332 km), but immatures migrated less efficiently (mean straightness = 0.58) for longer cumulative distances (mean = 6212 km) than adults (mean straightness = 0.69; mean cumulative distance = 5001 km; Table 1).

High-use areas and migratory bottlenecks

Egyptian vultures tracked in this study had a large overall range across eastern Europe, the Middle East and north and east Africa, encompassing nearly four million km^2 (99% probability UD, Fig. 3a). Moderate-use areas (75% probability UD) were mainly concentrated along the eastern Mediterranean and Red Sea coasts. High-use areas (50% probability UD) were highly concentrated along the southeastern Red Sea coast (Saudi Arabia and Yemen), the Sinai Peninsula (Egypt), southern Israel, the Gulf of Iskenderun (Turkey), the Anatolian Plateau west of Ankara (Turkey), and the Bosporus Strait (Turkey). High-use areas encompassed just 4.7% of the overall range. Most birds did not spend more than a night at any given stopover site, and therefore high-use areas primarily represent areas that were used by several individuals during migration.

Similarly, migration corridors (areas with between 10 and 20% of all migration tracks) were concentrated along the coasts of the eastern Mediterranean and Red Sea (Fig. 3b). Migration bottlenecks (areas with > 20% of migration tracks) were very concentrated in a very small area representing just 0.6% of the overall range, and were located at the Gulf of Iskenderun (Turkey), the Suez Canal zone (Egypt), and the southeastern Red Sea coast and Bab-el-Mandeb Strait (Saudi Arabia, Yemen, Djibouti). There was a striking difference in

Table 1. Mean (inter-quartile range) of migration parameters for Egyptian vultures by season and age class (immatures < 5 yr, adults ≥ 5 yr). The migration midpoint is the date on which half the migration distance was reached, and migration start and end are the days on which migration initiated and concluded. Linear distance (km) is the maximum linear distance between summer and winter ranges, while cumulative distance is the summed linear distances between each successive point in the migration trajectory. Migration duration (d) is the number of days spent on migration, and migration speed (km d^{-1}) is the cumulative migration distance divided by the migration duration. Straightness is the ratio between the linear and cumulative distance. Only parameters from complete migration trajectories were included.

	Immature		Adult	
Migration parameter	Spring ($n=13$)	Autumn ($n=24$)	Spring ($n=13$)	Autumn ($n=25$)
Start date	22-Apr (06-Mar–25-May)	02-Sep (23-Jul–06-Oct)	18-Mar (27-Feb–16-Apr)	07-Sep (09-Aug–05-Oct)
Midpoint date	10-May (05-Apr–09-Jun)	21-Sep (27-Aug–14-Oct)	31-Mar (09-Mar–23-Apr)	18-Sep (31-Aug–17-Oct)
End date	28-May (02-May–28-Jun)	09-Oct (09-Sep–26-Nov)	12-Apr (20-Mar–03-May)	30-Sep (20-Sep–13-Oct)
Duration (days)	35 ± 16 (14–60)	37 ± 22 (13–95)	25 ± 9 (15–47)	23 ± 10 (12–50)
Linear distance (km)	3274 ± 488 (2636–4110)	3298 ± 374 (2762–4235)	3460 ± 374 (3078–4206)	3265 ± 341 (2758–3825)
Cumulative distance (km)	6966 ± 2002 (5014–10471)	5803 ± 2126 (3558–11974)	5304 ± 997 (3797–7395)	4843 ± 959 (3302–6409)
Speed (km d^{-1})	218 ± 58 (149–358)	189 ± 60 (81–288)	223 ± 49 (157–350)	231 ± 60 (115–361)
Straightness	0.50 ± 0.12 (0.30–0.72)	0.62 ± 0.16 (0.24–0.84)	0.67 ± 0.13 (0.42–0.85)	0.70 ± 0.15 (0.45–0.91)

the bottlenecks between spring and autumn, with the major bottlenecks located along the southeastern Red Sea coast (Saudi Arabia and Yemen) in autumn, and the northwestern Red Sea coast (Egypt and Israel) in spring (Fig. 4).

Conservation gaps and priorities

Overall, 9.3% of the entire range of the tracked Egyptian vultures in this study was in protected areas (Table 2). A higher proportion of moderate (11.7%) and high-use areas (12.6%) were in protected areas, indicating that Egyptian vultures are disproportionately utilizing the protected area network during migration. However, only 8.3% of migration corridors and none (0.0%) of the migration bottlenecks fell within protected areas, demonstrating an important shortcoming in the protected area network for migratory soaring birds along the Red Sea Flyway. Important Bird Areas (IBAs), which are recognized for their importance but do not receive any formal protection, covered an additional 6.7% of high-use areas and 13.1% of migration bottlenecks, and could provide a framework for increasing protection of migratory birds along the Red Sea Flyway (Table 2). A list of the most important protected areas and Important Bird Areas (IBAs) for Egyptian vultures is available as Supplementary material Appendix 2.

Discussion

Our approach identified key migration concentration areas along the Red Sea Flyway, and revealed that only a very small proportion (< 13%) of these important areas are currently protected. We also showed that Egyptian vultures migrating through those concentration areas disperse over very large breeding and non-breeding ranges across Europe, Asia, and Africa.

Migratory bottlenecks and high-use areas

The high-use areas that we identified (Fig. 3) provide valuable information on where Egyptian vultures collectively spent more time during migration, and were more dispersed over the study region than bottlenecks. However, migratory high-use areas (Fig. 3a) overlapped extensively with migratory bottlenecks (Fig. 3b), because most birds did not rest for extended periods on migration, and areas where multiple migrations passed through a small area emerged as relatively high-use areas. Migrants can be exposed to anthropogenic threats even in areas where they do not rest or forage, for example through collision with wind turbines or power lines, or through direct persecution, which is rampant around the eastern Mediterranean (Brochet et al. 2016). Thus, targeted conservation actions within relatively small areas could be highly effective and cost efficient if threats to soaring migratory birds can be reduced or eliminated in those areas.

The most important migratory bottlenecks identified in this study are situated in three main areas: 1) the southeastern Red Sea coast including the Bab-el-Mandeb Strait (Saudi Arabia, Yemen, Djibouti), 2) the northern tip of the Gulf of Suez (Egypt), and 3) the area around the Gulf of Iskenderun (Turkey) (Fig. 3b). Additional important migratory corridors occur at the Bosporus and Dardanelles Straits (Turkey), the Anatolian Plateau west of Ankara (Turkey), southern Israel, and central and northern Jordan. These bottlenecks are a reflection of the locations at which birds were tagged in our study, and additional migratory bottlenecks likely exist elsewhere for other source populations from central Asia, or for other soaring migrants along this flyway (Verhelst et al. 2011).

The high-use areas and migration bottlenecks were not used equally during spring and autumn migration: migration bottlenecks occurred at geographic barriers where birds encountered a water barrier they were unwilling to cross (Agostini et al. 2015). These geographic barriers funneled birds to different areas in spring and autumn. For example, the Egyptian vulture population in the Middle East exhibited a clockwise migration strategy where most individuals migrated southwest in the autumn through the Arabian Peninsula until they encountered the Red Sea coast, which they followed south until they crossed into Africa via the

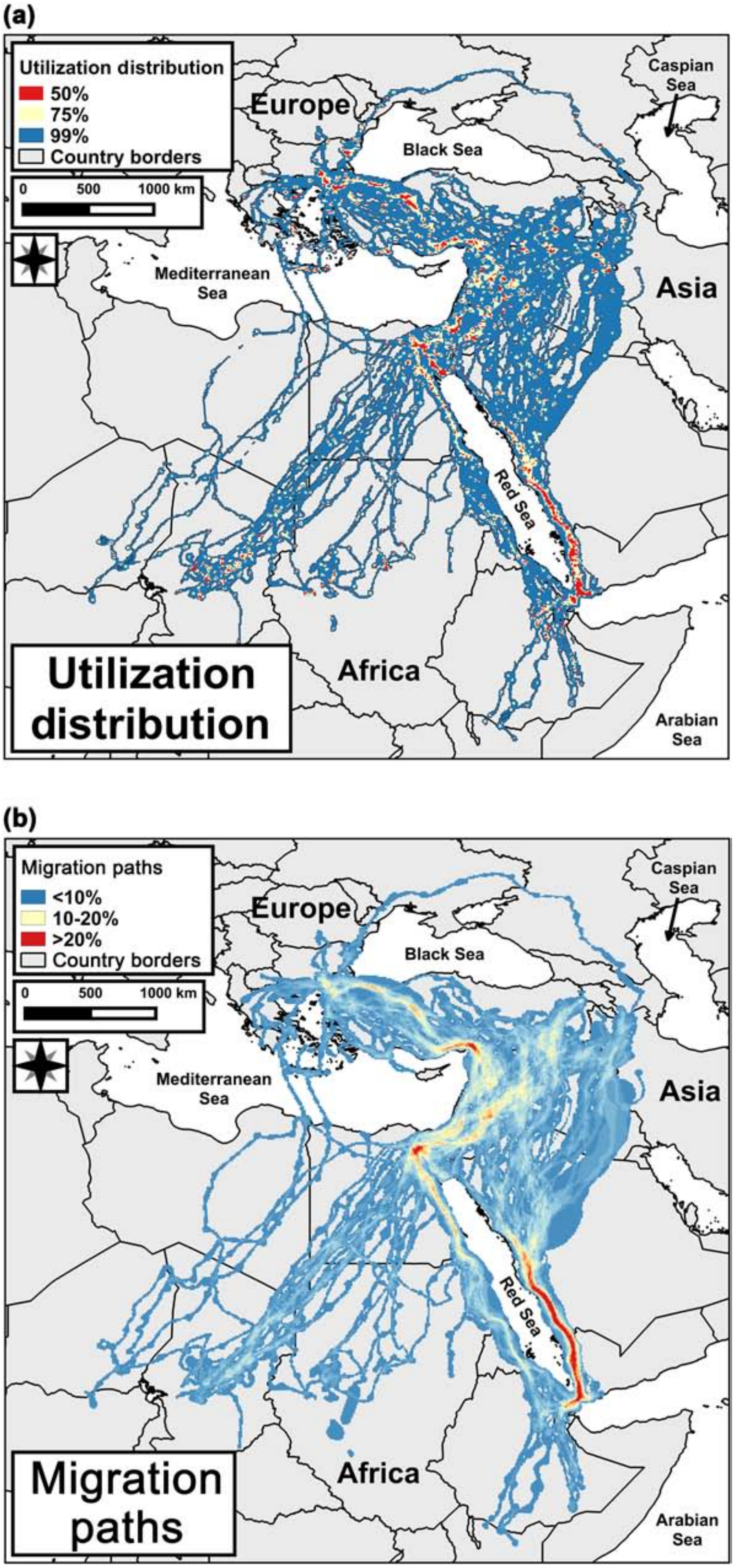

Figure 3. (a) Utilization distributions (UDs) and (b) migration paths for all individuals and seasons in the study. For UDs, blue indicates low use areas (99% probability UD), yellow indicates moderate use areas (75% probability UD), and red indicates high-use areas (50% probability UD). Migration paths (areas with < 10% of all migration paths) are blue, corridors (10–20% of all migration paths) are yellow, and bottlenecks (>2 0% all migration paths) are red.

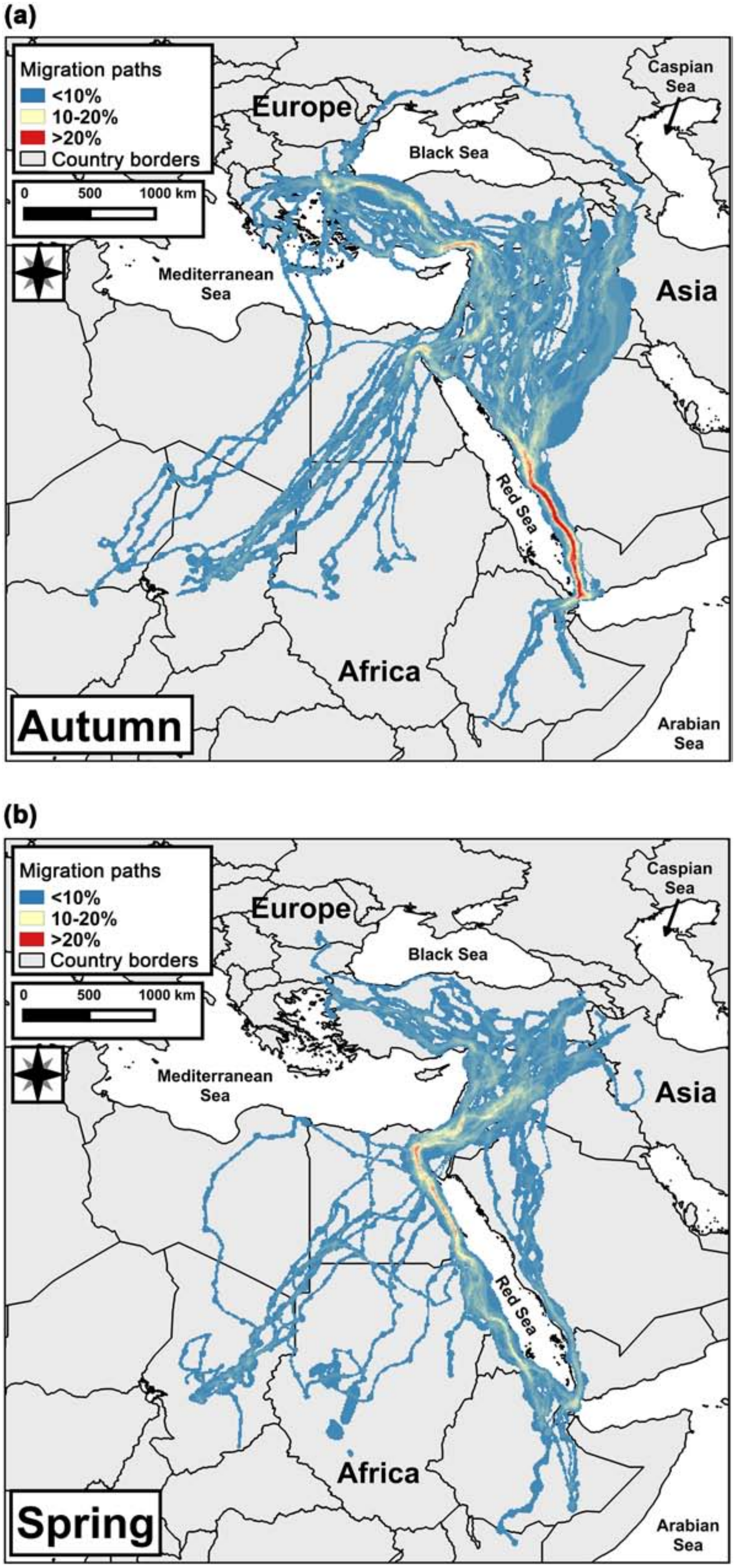

Figure 4. An overview of migration paths (areas with < 10% of all migration paths), corridors (10–20% of all migration paths), and bottlenecks (> 20% all migration paths) for all individuals in the study, split between spring and autumn seasons. Note the very different migratory bottlenecks between the two seasons.

Table 2. Summary of the total area (km²) of Egyptian vulture use areas, and the percentage of each use category that fell within protected areas (PAs) and Important Bird Areas (IBAs). 'PAs + IBAs' shows the total area within both PAs and IBAs. 'Low use' is the 99% probability utilization distribution (UD), 'moderate use' is the 75% probability UD, and 'high use' is the 50% probability UD. 'Migration corridors' include areas where 10–20% of all migration paths intersected, and 'migration bottlenecks' include areas where > 20% migration paths intersected.

Layer	Total area	% PAs	% IBAs	PAs + IBAs
Low use	3 754 800	9.3%	4.4%	13.7%
Moderate use	689 200	11.7%	5.9%	17.6%
High use	177 800	12.6%	6.7%	19.2%
Migration corridors	124 600	8.1%	6.0%	14.1%
Migration bottlenecks	23 100	0.0%	13.1%	13.1%

narrow Strait of Bab-el-Mandeb. In spring, the same birds typically migrated northeast, and followed the opposite shore of the Red Sea via North Africa and the Sinai Peninsula (although some birds also returned via Bab-el-Mandeb in the spring). This behavior led to strong geographic differentiation between the migratory bottlenecks and corridors between spring and autumn. Migratory bottlenecks in spring were located along the western Red Sea coast, the Sinai Peninsula, southern Israel, and northern Jordan/southern Syria, whereas in autumn, the major bottlenecks were located along the eastern Red Sea coast, the Straight of Bab-el-Mandeb, and the Gulf of Iskenderun (Fig. 3b).

Similar clockwise migration patterns have been observed in Egyptian vultures in west Africa (López-López et al. 2014b), and in many other raptor species (Bildstein 2006, Klaassen et al. 2010). However, individuals tagged in the Balkans did not exhibit this pattern, likely because their northbound migrations were inhibited by the Mediterranean Sea, forcing them to follow roughly the same route in autumn and spring via the Sinai Peninsula and eastern coast of the Mediterranean Sea. Overall, migration routes for all tracked individuals were straighter in autumn than spring, but whether different route choices between seasons are a consequence of visual navigation processes via landlines (e.g. the Red Sea coast), or whether typical wind patterns over the Sahara and the Arabian peninsula make certain migration strategies more efficient will require additional research (Vansteelant et al. 2017).

Egyptian vultures showed high migration timing plasticity, with a wide range of migration start and end dates (Table 1), and the timing of migration passage through major bottlenecks spanned on average about one month (Supplementary material Appendix 3). In spring, adult Egyptian vultures initiated migration on average one month (mid March) before immatures (mid April), likely driven by the desire to occupy territories and breed (Kokko 1999). In autumn, however, migration times of adults and immatures were similar, possibly as a consequence of juveniles benefitting from more efficient navigation when following adults (Mellone et al. 2011, Agostini et al. 2017).

Conservation prioritization

By overlapping existing protected areas (PAs) and Important Bird Areas (IBAs) with migratory use areas and bottlenecks, we identified conservation gaps for the species during migration. Overall, only 11.7% of moderate use and 12.6% of high-use areas during migration fell within the protected area network. But, as compared to 9.3% protection across the entire range, this indicates at least some level of focused protection of these important use areas. Discouragingly however, none (0.0%) of the area within migratory bottlenecks and only 8.1% of the area within migratory corridors was protected (Table 2). This demonstrates a very concerning gap in the protected area network for Egyptian vultures, as well as the numerous other soaring birds that utilize the Red Sea Flyway and that are known to concentrate at bottlenecks with the Egyptian vulture (Welch and Welch 1989, Hilgerloh et al. 2011, Oppel et al. 2014).

In addition to those areas that fall within the protected area network, Important Bird Areas (IBAs) recognize an additional 6.7% of high-use areas, 6.0% of migratory corridors, and 13.1% of migratory bottlenecks for their importance to birds (Table 2). However, IBAs in central Asia, the Middle East and north and east Africa are often in unfavourable condition, with the majority having high to very high threat scores and low to negligible conservation actions taking place (Horns et al. 2016, BirdLife International 2018, Buechley et al. 2018). While IBAs are not formally protected, the IBA network along the Red Sea Flyway could provide a platform by which to conserve migratory birds if measures are taken to officially protect these sites. However, simply designating areas as protected does not guarantee protection or effective conservation measures (Leverington et al. 2010). For effective conservation of the Egyptian vulture and other migratory soaring birds along the Red Sea Flyway, we encourage increased support for conservation efforts in high-use areas and migratory bottlenecks. Our quantitative determination of migratory bottlenecks corroborates extensive evidence on the importance of certain sites for migratory soaring birds, and underscores the importance of conducting research, monitoring and conservation for soaring migrants at three sites in particular: 1) the southeastern Red Sea coast and the Bab-el-Mandeb Strait (Welch and Welch 1988), 2) the Suez Canal zone (Hilgerloh et al. 2011), and 3) the Gulf of Iskenderun (Sutherland and Brooks 1981, Oppel et al. 2014).

As a first step, we recommend investigation and monitoring of threats to birds at these major bottlenecks. The types of major threats along the flyway are more or less well known (Nikolov et al. 2016), but there is little information about the magnitude and spatial distribution of these threats. This data will be crucial for undertaking focused and effective conservation measures on the Red Sea Flyway. Furthermore, we recommend initiation and/or continuation of regular counts of bird migrations at these bottleneck sites (using the periods we summarize from tracked birds, see Supplementary material Appendix 3). Such data can provide information on the populations and trends of species (Bildstein 2006), and are particularly valuable where information on the breeding and/or wintering populations is sparse (Dunn and Hussell 1995), which is the case for most species using the Red Sea Flyway (UNDP 2006). Indeed, observations at the migratory bottlenecks identified here may enable estimating and monitoring populations of as many as 35 species of migratory soaring bird that use the Red Sea Flyway, including the Egyptian vulture and nine other species at risk of extinction (Supplementary material Appendix 1; UNDP 2006).

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Supplementary material (Appendix JAV-01629 at <www.avianbiology.org/appendix/jav-01629>). Appendix 1–3.