



# High juvenile mortality during migration in a declining population of a long-distance migratory raptor

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Many populations of long-distance migrants are declining and there is increasing evidence that declines may be caused by factors operating outside the breeding season. Among the four vulture species breeding in the western Palaearctic, the species showing the steepest population decline, the Egyptian Vulture *Neophron percnopterus*, is a long-distance migrant wintering in Africa. However, the flyways and wintering areas of the species are only known for some populations, and without knowledge of where mortality occurs, effective conservation management is not possible. We tracked 19 juvenile Egyptian Vultures from the declining breeding population on the Balkan Peninsula between 2010 and 2014 to estimate survival and identify important migratory routes and wintering areas for this species. Mortality during the first autumn migration was high (monthly survival probability 0.75) but mortality during migration was exclusively associated with suboptimal navigation. All birds from western breeding areas and three birds from central and eastern breeding areas attempted to fly south over the Mediterranean Sea, but only one in 10 birds survived this route, probably due to stronger tailwind. All eight birds using the migratory route via Turkey and the Middle East successfully completed their first autumn migration. Of 14 individual and environmental variables examined to explain why juvenile birds did or did not successfully complete their first migration, the natal origin of the bird was the most influential. We speculate that in a declining population with fewer experienced adults, an increasing proportion of juvenile birds are forced to migrate without conspecific guidance, leading to high mortality as a consequence of following sub-optimal migratory routes. Juvenile Egyptian Vultures wintered across a vast range of the Sahel and eastern Africa, and had large movement ranges with core use areas at intermediate elevations in savannah, cropland or desert. Two birds were shot in Africa, where several significant threats exist for vultures at continental scales. Given the broad distribution of the birds and threats, effective conservation in Africa will be challenging and will require long-term investment. We recommend that in the short term, more efficient conservation could target narrow migration corridors in southern Turkey and the Middle East, and known congregation sites in African wintering areas.

**Keywords:** Balkan peninsula, feedback loop, Movebank, navigation, satellite telemetry, vulture.

Many populations of long-distance migrants are declining, and for most populations the causes of population declines are poorly understood (Berthold *et al.* 1998, Vickery *et al.* 2014). In recent

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years, however, there has been increasing awareness that events during migration or on wintering grounds can affect populations of migratory animals (Newton 2004, Studds & Marra 2005, Both *et al.* 2006). Identifying migration routes, stopover areas and wintering areas for migratory species that are declining is therefore necessary for designing effective conservation strategies that can address threats operating outside breeding areas (Wilcove & Wikelski 2008).

The decline of long-distance migrants has been most apparent for passerines and smaller-bodied birds but there is evidence that long-distance migratory raptors are also declining (Hoffman & Smith 2003). Among the four vulture species that breed in the western Palaearctic, the Egyptian Vulture *Neophron percnopterus* is the only long-distance migrant that travels to wintering regions in sub-Saharan Africa (Porter & Beaman 1985, Meyburg *et al.* 2004, García-Ripollés *et al.* 2010). Egyptian Vulture populations in Europe have been declining for decades but the reasons for population declines are still poorly understood and are likely to be a combination of several known threats such as poisoning, electrocution, landscape changes and direct persecution (Carrete *et al.* 2007, Mateo-Tomás & Olea 2010, Velevski *et al.* 2015). Owing to its long migration route and wintering areas in Africa, the Egyptian Vulture is exposed to a wide variety of natural and anthropogenic hazards along its flyway, and it is possible that factors operating outside the breeding areas are partially responsible for population declines in Europe (Grande *et al.* 2009, Ogada *et al.* 2012, Velevski *et al.* 2015). Recent evidence suggests that substantial mortality occurs during migration in raptors (Klaassen *et al.* 2014), and an area where high unnatural mortality occurs has been described for the eastern flyway of Egyptian Vultures (Angelov *et al.* 2013). However, to design and implement effective conservation measures we require a better assessment of where Egyptian Vultures migrate and winter, what proportion of mortality is caused by humans or human infrastructure, and where human-induced mortality that is amenable to management occurs.

We estimated the survival probability of juvenile Egyptian Vultures to quantify the extent of anthropogenic mortality. We tracked juvenile Egyptian Vultures using GPS satellite transmitters from the declining Balkan breeding population to delineate flyway corridors, and estimated the size

of winter movement ranges and the habitat preferred by juvenile birds. This information allowed us to assess where management to reduce human-induced juvenile mortality could be an effective conservation strategy for this endangered migratory raptor.

## METHODS

### Satellite tracking

We tracked 19 juvenile Egyptian Vultures from breeding areas in Bulgaria ( $n = 9$ ), Greece ( $n = 6$ ), the former Yugoslav Republic of Macedonia ( $n = 3$ ) and Albania ( $n = 1$ ) between 2010 and 2014. We captured juveniles in their nest at an approximate age of 65 days, and measured their tarsus, tail and head length using callipers. We then attached solar-powered 45-g GPS satellite transmitters (Microwave Telemetry; [www.microwavetelemetry.com](http://www.microwavetelemetry.com)) to the birds' backs using a Teflon ribbon harness in a backpack configuration. The entire transmitter equipment did not exceed 3% of the birds' body mass, and was unlikely to influence mortality of soaring migrants (Klaassen *et al.* 2014). The satellite transmitters were set to record the location of each bird with GPS accuracy every 2 h between 04:00 and 22:00 h every day over a period of several years. Data were downloaded via the ARGOS satellite system and deposited in Movebank ([www.movebank.org](http://www.movebank.org)).

### Estimation of juvenile survival probability

If a satellite tag failed to transmit new data, or if data persistently indicated the same coordinates, local collaborators were mobilized to inspect the last known location, retrieve any carcass and determine the cause of death. If the last locations occurred over the sea, we assumed that a bird had died even if no carcass could be found. Depending on the cause of death, we classified mortality as human-induced (e.g. shooting) or natural (e.g. starvation, lost at sea, killed by natural predator). If a tag failed for unknown reasons and mortality could not be ascertained, we censored the data for the respective bird at the last month in which the tag was working and considered its fate 'unknown' following similar work on migratory raptors (Klaassen *et al.* 2014). To estimate monthly and annual survival probability of satellite-tagged birds

between fledging and 2 years of age, we used known-fate capture–recapture methods (Murray 2006). We assumed that monthly survival until the end of the first autumn migration (up to 3 months after fledging, August–October) was lower than subsequent survival (McIntyre *et al.* 2006, Demerdzhiev *et al.* 2014, Stoychev *et al.* 2014), and incorporated this temporal structure into survival models. Annual survival was estimated by multiplying the respective monthly survival estimates over the first and second year of life (Powell 2007).

We used a Bayesian framework for inference and parameter estimation with diffuse priors (0–1) for the poorly known survival probabilities during the first 2 years of life (Kéry & Schaub 2012). We fitted the survival model in program JAGS (Plummer 2012) called from R 3.0.1 (R Development Core Team 2014) via the package ‘R2jags’ (Su & Yajima 2012). We ran three Markov chains each with 200 000 iterations and discarded the first 50 000 iterations. From the remaining iterations we only used every third iteration for inference, and tested for convergence using the Gelman–Rubin diagnostic (Brooks & Gelman 1998). We present posterior estimates of parameters with 95% credible intervals.

### Analysis of migration and winter movement data

To characterize the migration strategy of juvenile Egyptian Vultures, we calculated the start and end time of migration, the distance migrated and the migration speed based on GPS location fixes for each individual. Start of autumn migration was defined as the first day on which birds travelled over 100 km, 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. Migration distance was the cumulative distance between all subsequent locations during the migration period, and migration speed was the migration distance divided by the number of days spent migrating (Alerstam 2003). The wintering period was defined as the time between the end of autumn migration and the onset of spring migration, and we used all locations from that time period to estimate a movement range for each individual. For the birds still alive after 2 years, the onset of spring migration was defined as the date when the first northward movement was initi-

ated that ultimately took the bird north of 22°N. The winter movement range was calculated as the minimum convex polygon of 100% of the winter locations to be comparable with a previous study (Meyburg *et al.* 2004), and the home-ranges were calculated as the 95% and 50% kernel utilization distribution (García-Ripollés *et al.* 2010). Besides individual home-ranges, we also calculated a population-level 95% and 50% utilization distribution including winter locations of all individuals to delineate the area in which conservation measures for the species would be most urgently required. We estimated areas of movement and home-ranges in the R package ‘adehabitatHR’ using the *ad hoc* method to determine the smoothing parameter (Calenge 2011).

### Analysis of mortality on migration

To understand the factors influencing juvenile Egyptian Vulture mortality on migration, we first classified birds as either ‘successful’ or ‘unsuccessful’ migrants depending on whether they successfully migrated to wintering areas in Africa or died en route. We then assessed whether the probability of successful migration was related to the origin of the birds, their fledging date, their onset of autumn migration, their travel speed, measurements of body size taken at the time birds were tagged, or environmental variables that are known to affect the initiation of migration and migration route of soaring raptors (Shamoun-Baranes *et al.* 2006, Dodge *et al.* 2014, Vansteelant *et al.* 2015). Because mortality was mostly a result of suboptimal navigation (see Results), we defined the decisive initial part of the migratory journey for each individual as the period from 3 days prior to the start of migration to the time the bird passed a gateway landmark beyond which it was highly unlikely to change the route to another flyway. We then extracted weather data (cloud cover, air pressure, wind direction, wind speed, thermal uplift, orographic uplift) for all locations during that time period using the track annotation system in Movebank (Dodge *et al.* 2013). To assess which of the 14 individual and environmental variables had the greatest influence on successful migration, we used an algorithmic random forest approach (Cutler *et al.* 2007, Oppel *et al.* 2009b, Fernández-Delgado *et al.* 2014). We used the R package ‘randomForest’ v. 4.6-7 in R 3.1.0 to construct this model (Breiman 2001, Liaw & Wiener 2002, R

Development Core Team 2014) using 66% of the data to construct each of 1500 classification trees with eight variables tried at each tree node. We report variable importance as the increase in node impurity after random permutation of the variable (Cutler *et al.* 2007, Grömping 2009), scaled to 100% for the most important variable.

### Habitat selection in wintering regions

To assess what habitats Egyptian Vultures select at the continental scale, we downloaded environmental data for all winter locations of tracked Egyptian Vultures using the track annotation system in Movebank (Dodge *et al.* 2013). Specifically, we downloaded information on land cover type (from GlobCover 2009; [http://due.esrin.esa.int/page\\_globcover.php](http://due.esrin.esa.int/page_globcover.php)), elevation ([https://lpdaac.usgs.gov/products/aster\\_products\\_table/astgtm](https://lpdaac.usgs.gov/products/aster_products_table/astgtm)), rainfall ([http://mirador.gsfc.nasa.gov/collections/TRMM\\_3B42\\_006.shtml](http://mirador.gsfc.nasa.gov/collections/TRMM_3B42_006.shtml)), primary productivity ([https://lpdaac.usgs.gov/products/modis\\_products\\_table/mod17a2](https://lpdaac.usgs.gov/products/modis_products_table/mod17a2)), and normalized difference vegetation index (NDVI, [https://lpdaac.usgs.gov/products/modis\\_products\\_table/mod13a1](https://lpdaac.usgs.gov/products/modis_products_table/mod13a1)) to characterize the habitats used by Egyptian Vultures. We combined land cover types into five discrete landscape types: cropland (including GlobCover classes 11, 14, 20 and 30), savannah (GlobCover classes 60, 130 and 110), grassland (GlobCover classes 120 and 140), desert (GlobCover classes 150 and 200), and other landscapes including all remaining GlobCover classes (urban, water, infrastructure, mesic vegetation).

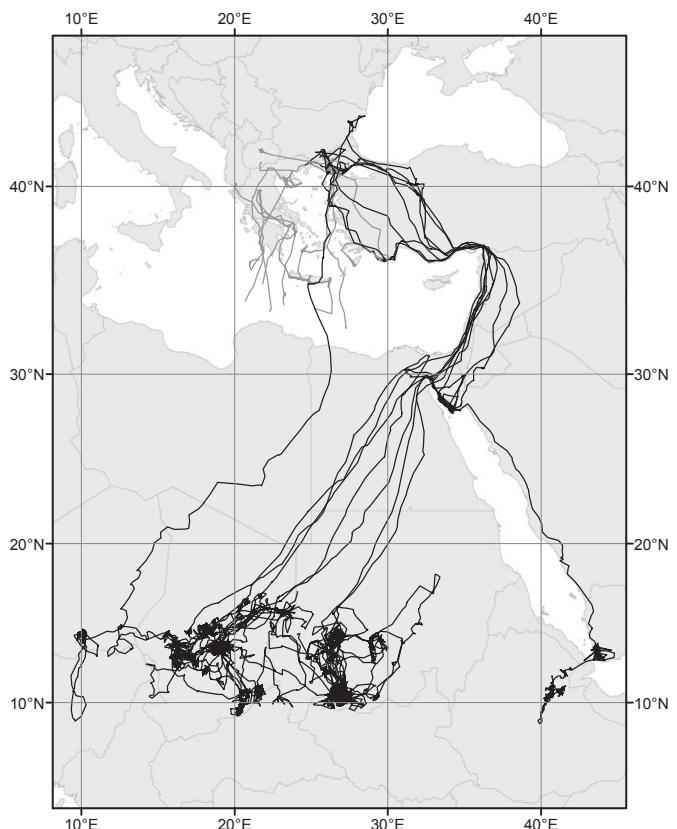
To assess which habitats were preferred by Egyptian Vultures, the habitat available to the birds had to be quantified (Jones 2001). Assessing what habitat is ‘available’ to a far-ranging species is a complex challenge, especially because several of our environmental variables vary not only in space but also over time (Arthur *et al.* 1996, Monserrat *et al.* 2013). We therefore quantified available habitat at the individual level, and used the environments encountered within the 100% minimum convex polygon movement range of all winter locations as ‘available’ (Trierweiler *et al.* 2013, López-López *et al.* 2014a). Environmental conditions at all locations that were within the 50% kernel core home-range of each individual were contrasted against available conditions to assess the habitat preferred by wintering Egyptian Vultures. We used the same algorithmic random forest

approach as described above to evaluate which of the five environmental variables best predicted whether a location was within the core home-range or not.

### RESULTS

Of the 19 juvenile Egyptian Vultures tracked from Eastern Europe, one bird died near its natal territory before starting to migrate, nine (47%) died on their first migration and nine (47%) successfully completed their first autumn migration to Africa. All eight birds that migrated around the eastern Mediterranean via the flyway through Turkey and the Middle East survived their migration and arrived in sub-Saharan Africa or the Arabian Peninsula, whereas only one of the 10 birds that attempted to take a more direct route survived crossing the open Mediterranean (Fig. 1). The other nine birds using this route perished either at sea after unsuccessful attempts to cross the Mediterranean ( $n = 7$ ) or on islands in the Mediterranean ( $n = 2$ ). We did not record any mortality on migration across the Sahara desert. The average monthly survival probability over the first 3 months (August–October, autumn migration) was lower than after the first autumn migration had been completed (Table 1). After migration, two birds were killed by people in wintering areas in Chad and Niger, and two birds died due to unknown reasons in Sudan. Annual survival probability for Egyptian Vultures was very low during their first year of life and increased during their second year (Table 1). Of the 10 cases where the cause of death could be ascertained, only two were induced by humans (shooting in Africa), whereas the remaining eight were due to natural mortality.

Of 14 individual and environmental variables used to predict whether juvenile birds successfully completed their first migration, the longitude of origin was the most influential (variance explained by random forest model = 97.8%, Table 2). All juveniles tagged in nests west of 22°E died on migration, whereas only three of 12 birds from further east suffered the same fate (Fig. 2). Tarsus length, departure time and head length were the next most important variables in the model (Table 2) but indicated only marginally higher survival for birds with intermediate body size and departing at later dates (Fig. 2). All weather-related variables had relatively little influence on



**Figure 1.** Map of juvenile Egyptian Vulture autumn migration and winter movements for 19 birds tracked from breeding areas in the Balkans in 2010–2014. Black lines indicate birds with successful autumn migration, while dark grey lines reflect birds that did not survive their first autumn migration.

**Table 1.** Mean monthly and annual survival probability ( $\pm 95\%$  credible intervals) of juvenile Egyptian Vultures estimated with a known-fate model based on 19 satellite-tracked individuals. The period August–October encompasses the first autumn migration and therefore has different survival probability.

	Mean 95% credible interval
Monthly survival (Aug–Oct)	0.750 (0.620–0.860)
Monthly survival (after Oct)	0.958 (0.916–0.986)
Annual survival (year 1)	0.297 (0.146–0.480)
Annual survival (year 2)	0.611 (0.347–0.845)

whether birds chose the safer route and migrated successfully (relative importance < 10%). However, the single bird that successfully crossed the Mediterranean enjoyed a significantly higher tailwind component during the days of the crossing (mean meridional wind velocity =  $-3.47 \text{ m/s}$ ) than the birds that perished en route ( $-1.98 \text{ m/s}$ ,  $P < 0.001$ ).

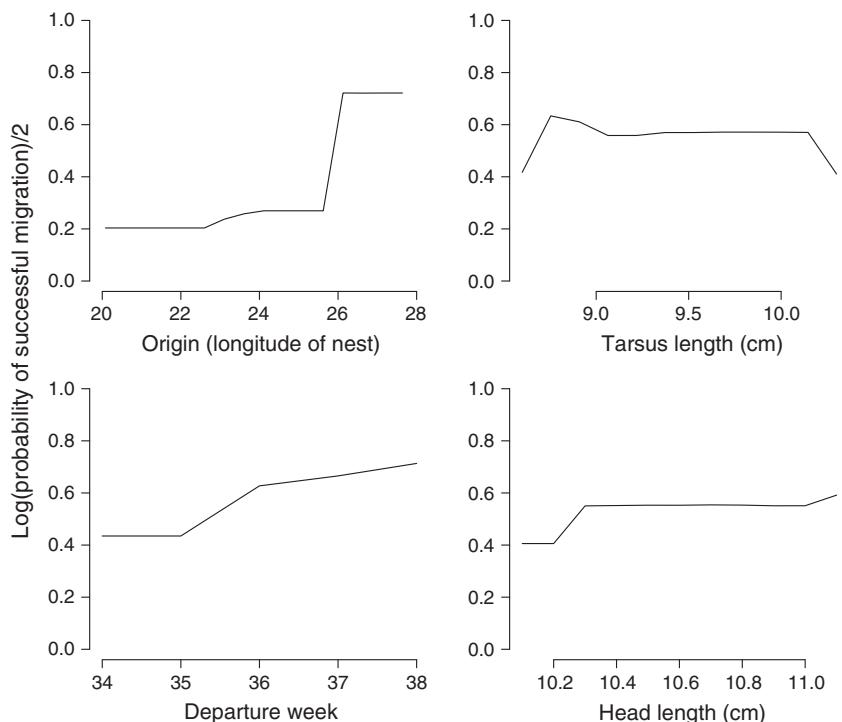
Birds that migrated successfully arrived in wintering regions between 24 September and

7 November. The average distance travelled on migration was 5275 km, and migration took on average 35 days with a mean migration speed of 172 km/day (Table 3). The maximum sustained flight speed of any bird occurred during a 4-h interval on 18 September 2012 in southern Turkey and northern Syria, when one vulture flew with an average speed of 81 km/h assisted by tailwind (6.7 m/s). The longest distance travelled by a bird in a single day was 507 km on 21 September 2013, between southern Egypt and northern Sudan.

Juvenile Egyptian Vultures remained in wintering regions for at least 1.5 years and did not attempt spring migration in the year after their first arrival in Africa. During this time, winter movement ranges were large and included multiple centres of activity, in which birds remained for several weeks before exploring alternative areas. The average core 50% utilization distribution was  $28\,000 \text{ km}^2$ , but ranged from < 5000 to

**Table 2.** Relative importance and mean value of environmental and individual variables differentiating between successful and unsuccessful migrants. Relative variable importance was calculated using a permutation procedure based on a random forest model distinguishing between locations of successful and unsuccessful migrants.

Variable	Unsuccessful migrants	Successful migrants	Relative importance (%)
Longitude of origin (degrees)	22.9095	26.2785	100.00
Tarsus length (cm)	9.23	9.25	63.84
Departure day	4 Sept	8 Sept	58.89
Head length (cm)	10.43	10.58	44.66
Latitude of origin (degrees)	40.7606	41.8385	43.60
Tail length (cm)	20.77	20.84	43.21
Fledging date	15 Aug	17 Aug	42.59
Wind direction (d)	197.79	123.48	16.54
Wind speed (m/s)	3.51	3.77	8.85
Air pressure (mbar)	974.18	984.19	6.15
Cloud cover	0.14	0.13	4.95
Thermal uplift	0.70	0.84	2.78
Travel speed (m/s)	6.39	7.87	0.57
Orographic uplift	0.22	0.26	0.00



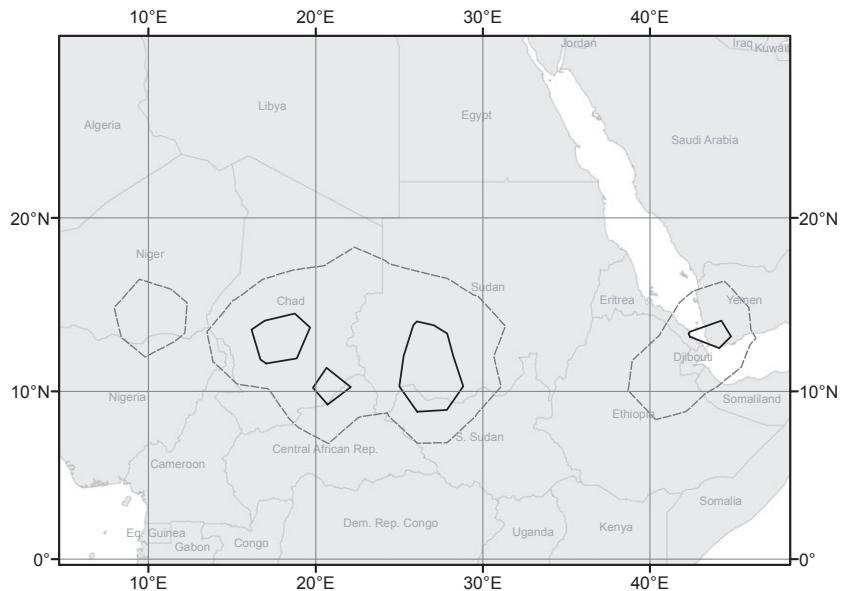
**Figure 2.** Partial dependence plots for the four most important variables predicting whether juvenile Egyptian Vultures tracked from breeding areas in the Balkans in 2010–2013 successfully completed their first autumn migration. The y-axis is half the logit of the predicted probability of a bird successfully completing migration. Tarsus and head length were measured when birds were tagged as nestlings, approximately 1 week prior to fledging.

> 90 000 km<sup>2</sup> among individuals (Table 3). Winter movement ranges (100% minimum convex polygon) were more than an order of magnitude larger (> 310 000 km<sup>2</sup>), with similarly large varia-

tion among individuals (Table 3). Wintering regions ranged from southwest Yemen to Nigeria, with core wintering areas in southern Chad and Sudan (Fig. 3).

**Table 3.** Mean (with standard deviation and range) dates of onset and completion of autumn migration, migration duration, speed, and distance of juvenile Egyptian Vultures migrating from breeding grounds in the Balkans to wintering grounds in sub-Saharan Africa. Wintering home-ranges were based on 50% and 95% kernel utilization distributions, and movement ranges were based on 100% minimum convex polygon (MCP). Unsuccessful migrants did not survive autumn migration and the end of their migration is therefore truncated in the Mediterranean Sea.

	Successful migrants				Unsuccessful migrants			
	Mean	sd	Min.	Max.	Mean	sd	Min.	Max.
Start autumn migration	8 Sept	6.6	30 Aug	19 Sept	4 Sept	5.0	28 Aug	13 Sept
End autumn migration	13 Oct	13.6	24 Sept	7 Nov	14 Sept	7.1	7 Sept	26 Sept
Duration of autumn migration (days)	35.0	16.0	17.0	61.0	10.3	6.5	4.0	24.0
Migration distance (km)	5275	930	4093	6733	1193	491	515	2205
Migration speed (km/day)	172.3	57.0	110.4	256.8	138.5	79.1	73.6	323.8
Winter home-range (50% kernel, km <sup>2</sup> )	27 137	28 327	4797	94 134				
Winter home-range (95% kernel, km <sup>2</sup> )	211 777	189 896	53 457	653 398				
Winter movement range (100% MCP, km <sup>2</sup> )	310 180	282 644	53 086	818 908				



**Figure 3.** Map of 50% (solid line) and 95% (broken line) utilization distributions of nine juvenile Egyptian Vultures tracked with satellite transmitters from breeding areas in the Balkans in 2010–2014 during their first 1.5 years in sub-Saharan Africa.

The habitat in core ranges in which juvenile vultures spent 50% of their time differed from the habitat encountered in winter movement ranges. Our random forest model explained 81.9% of the variation in the data and successfully classified locations as core wintering locations. Elevation and landscape type were the most important variables distinguishing core locations from those available in movement ranges (Table 4). Vultures primarily inhabited medium elevations up to 500 m above sea level in savannah, desert or cropland habitats (Fig. 4).

Highly productive habitats, with high general primary productivity (GPP) or normalized difference vegetation index (NDVI), were rarely used in core home-ranges (Fig. 4). GPP, rainfall and NDVI were ubiquitously low in all areas encountered by Egyptian Vultures during winter (Table 4).

## DISCUSSION

Juvenile Egyptian Vultures from the Balkan Peninsula suffered high mortality during their first

autumn migration, with monthly survival probabilities lower than those of other long-distance migratory raptors (Klaassen *et al.* 2014) and an annual survival probability that is unlikely to be sufficient for stable populations (Grande *et al.* 2009). However, none of this migration mortality was caused by human interference or infrastructure, and we speculate that the causes of migration-related mortality in juvenile Egyptian Vultures may be an indirect consequence of declining populations.

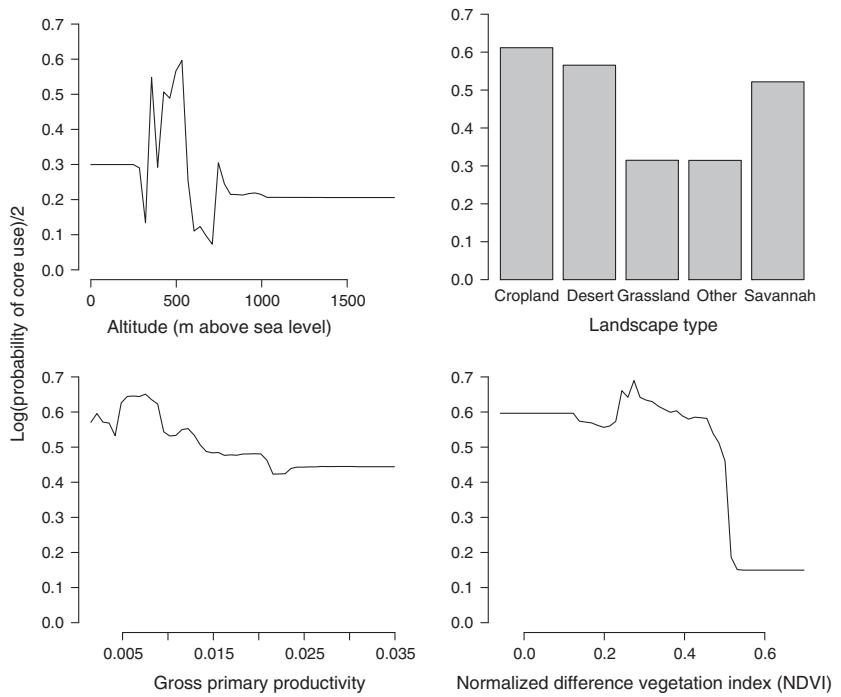
Mortality on migration can occur due to a variety of causes. For juveniles on their first autumn migration, unfavourable weather conditions are known to affect flight performance and may lead to mortality (Thorup *et al.* 2003, Liechti 2006, Strandberg *et al.* 2009). Alternatively, mortality may be a consequence of poor body condition, late fledging or departure date, or low travel speed that ultimately forces individuals to use a shorter but riskier migration route (Newton 2010, Sergio *et al.* 2014). For our sample of juvenile Egyptian Vultures there was some indication of wind facilitation (a strong tailwind may have facilitated successful crossing of the Mediterranean by one bird) but we found no evidence that unsuccessful migrants experienced adverse weather conditions that affected the ultimate fate of their migration. Like-

wise, the patterns in our data were not consistent with the expectation that smaller or later departing birds were more vulnerable. We found that birds that departed later were in fact more likely to migrate successfully than were birds departing earlier, and that differences in body size between successful and unsuccessful migrants were biologically insignificant (Table 2). In contrast, the longitude of origin was the most important predictor variable separating successful from unsuccessful migrants, and this geographical pattern could not be explained by environmental or other individual variables. We therefore conclude that juvenile birds from more western breeding areas are at higher risk of dying during their first autumn migration, and suggest that the currently low population size of Egyptian Vultures may provide an explanation for this pattern.

The Balkan population of Egyptian Vultures has decreased from > 600 pairs to < 70 pairs over the past three decades (Velevski *et al.* 2015). Egyptian Vultures frequently use communal roosts near places with abundant food sources (Cramp & Simmons 1977, Donázar *et al.* 1996, López-López *et al.* 2014a), and such roosts can act as information centres where juvenile birds can link up with more experienced migrants to follow established migratory routes (Maransky & Bildstein 2001, Bijleveld *et al.* 2010, Mellone *et al.* 2011). However, with the currently low population densities, communal roosts have fewer birds or have disappeared altogether (Grubač *et al.* 2014), and the probability of a juvenile bird encountering a migrating group of experienced birds may be low compared with years when population density was higher. The difficulty in finding experienced migrants may force inexperienced juveniles to follow their migratory instincts to reach Africa by heading in a southerly direction, as has been found in other soaring migrants (Chernetsov *et al.* 2004). Such a strategy is riskier for birds from western breeding areas, where the shortest route will lead the birds either via the Peloponnese or via islands in the Aegean Sea across a > 250-km stretch of open water to the coast of northern Africa, an exceptional strategy for a large raptor that may only be viable in very favourable wind conditions (Bildstein 2006, Agostini *et al.* 2015). In contrast, birds from more eastern breeding populations reach Turkey via the Bosphorus or the Dardanelles when heading in a southerly direction. To avoid the hazardous route over the Mediterranean, the

**Table 4.** Mean proportion of habitat types and environmental variables at winter locations within the core 50% utilization distribution, compared with locations within winter movement ranges of wintering juvenile Egyptian Vultures in Africa. Wintering home-ranges were based on 50% kernel utilization distributions, and movement ranges were based on 100% minimum convex polygon (MCP). Relative variable importance was calculated using a permutation procedure based on a random forest model classifying locations as core range locations. GPP: general primary productivity.

	Core range	Winter movement range	Relative importance
Elevation	478 ± 167	538 ± 193	100
Habitat			
Cropland	22.2%	10.9%	62.1
Savannah	43.3%	15.1%	62.1
Desert	25.8%	34.7%	62.1
Grassland	8.7%	39.2%	62.1
Other	0.0%	0.1%	62.1
GPP	0.009 ± 0.004	0.008 ± 0.004	41.2
NDVI	0.23 ± 0.07	0.20 ± 0.07	32.8
Rainfall	0.022 ± 0.26	0.032 ± 0.31	3.5



**Figure 4.** Partial dependence plots for the four most important variables predicting environmental conditions in core wintering home-ranges of juvenile Egyptian Vultures tracked from breeding areas in the Balkans in 2010–2014 during their first 1.5 years in sub-Saharan Africa. The y-axis is half the logit of the predicted probability of a location being in the core use area.

birds from more western breeding areas would require an initial departure towards a non-intuitive northeasterly direction to migrate around the northern coast of the Aegean Sea. Such a detour might be facilitated by following experienced birds, as has been suggested for other soaring migrants detouring around the Mediterranean (Mellone *et al.* 2011, Panuccio *et al.* 2012).

Although there is no evidence that social facilitation or reliance on experienced migrants is a crucial element for successful migration of juvenile Egyptian Vultures, several migration patterns that can be observed in the region are consistent with the proposition that juveniles may benefit from following adult birds along a flyway through continental Turkey. First, adult and juvenile migration phenology matches temporally, with a peak for both age groups between 8 and 24 September in southern Turkey (Sutherland & Brooks 1981, Oppel *et al.* 2014). Secondly, of 68 juvenile Egyptian Vultures observed on autumn migration in southern Turkey in 2014, 48% were accompanied by conspecifics, 29% were in flocks of other species and only 23% migrated independently (Doga Derneği unpubl. data). Thirdly, very few adult

Egyptian Vultures migrate across islands in the Aegean Sea but a larger number of juveniles do (17 juveniles vs. six adults observed between 2007 and 2014; Hellenic Ornithological Society (HOS) unpubl. data, Lucia *et al.* 2011, Panuccio *et al.* 2013). Finally, two adult birds tracked with satellite transmitters from western Greece in 2012 and 2014 migrated around the Aegean Sea and via Turkey (Bulgarian Society for Protection of Birds, HOS unpubl. data). Although none of these observations provides conclusive evidence for the importance of experienced co-migrants, the circumstantial evidence suggests that adults do not routinely migrate across the Mediterranean and that most juveniles observed along the successful flyway through southern Turkey migrate in the company of conspecifics or other species. We encourage more research on tracking adult migration from the Balkans and the recording of flock composition of juvenile migrants along raptor migration monitoring stations in Greece, Turkey and Israel.

If we accept that guidance by experienced migrants may play an important role in juvenile navigation, the absence of a sufficient number of

experienced migrants may force an increasing number of juveniles to migrate independently. Such a pattern, paired with the more complicated migratory route from western breeding areas, may have led to the distinct geographical pattern of mortality that we found in our data. The potential lack of guidance by experienced conspecifics during the first autumn migration may therefore act as a positive feedback loop that accelerates population declines of migrants once a critically low population density has been reached that forces inexperienced birds to migrate independently.

The annual juvenile survival of Egyptian Vultures that we found in eastern Europe is much lower than that in populations in Spain (Grande *et al.* 2009), perhaps a consequence of the more challenging migratory journey. The juvenile birds we tracked travelled on average about 2000 km more, and took on average 22 days longer to reach their wintering grounds than adult birds from Spain (López-López *et al.* 2014b). The longer time spent on migration may be due partly to an inherently slower migration speed of juvenile (< 180 km/day) than adult (> 250 km/day) Egyptian Vultures (Meyburg *et al.* 2004, García-Ripollés *et al.* 2010, López-López *et al.* 2014b) but the longer and more complex journey around the eastern Mediterranean is the most likely explanation of why juvenile mortality may be higher in the Balkans than in Spain.

Mortality after the first migration was much lower than during migration, and was comparable with estimates from other long-distance migratory raptors (Klaassen *et al.* 2014). Of the four birds that were lost in Africa, two were evidently shot by humans for superstitious reasons and for market trade. There is significant concern over local market trades for vulture parts affecting raptor populations in Africa (Thiollay 2006, Virani *et al.* 2011, Ogada *et al.* 2012) but the mortality resulting from this threat was comparatively low in our sample. However, given the high migration mortality, any non-natural mortality of birds is likely to be additive and will affect the small remnant populations in Eastern Europe. Although there is currently very little information about survival probabilities of adult birds in Eastern Europe, the low juvenile survival probability estimated here is likely to contribute to population declines.

Juvenile Egyptian Vultures used very large movement ranges during their first 1.5 years in

Africa, which were considerably larger than home-ranges used by adult birds tracked from Spain and wintering in western Africa (Meyburg *et al.* 2004, García-Ripollés *et al.* 2010, López-López *et al.* 2013). The larger range size is likely to be due to the longer period spent on wintering areas (1.5 years for juveniles, but only 6 months for adults) during which the birds used multiple centres of activity. In addition, juvenile Egyptian Vultures may explore several areas in wintering regions to track resource availability and build knowledge of alternative wintering areas with sufficient food sources that will benefit them in future years (Bennetts & Kitchens 2000, Oppel *et al.* 2009a, Trierweiler *et al.* 2013). The areas encountered during the entire wintering period were generally arid and with very low primary productivity. Vultures appeared to spend more time in savannah and croplands than in grasslands or the desert, a pattern that is consistent with previous findings for this species (Meyburg *et al.* 2004, García-Ripollés *et al.* 2010). These areas are likely to be inhabited by semi-nomadic livestock herders or resident subsistence farmers whose livestock carcasses may provide valuable and predictable food sources (Kendall *et al.* 2014). The Vulture's preference for arid and desert landscapes may also explain why we did not record any mortality on flights across the Sahara, which is a major barrier that incurs significant mortality in other species of long-distance migrants (Strandberg *et al.* 2009, Klaassen *et al.* 2014).

Given the broad wintering distribution of Egyptian Vultures breeding in eastern Europe, and the large number of direct potential threats to both juvenile and adult birds (Ogada *et al.* 2012, Angelov *et al.* 2013, Velevski *et al.* 2015), continental-scale policies and implementations will be required to increase significantly the survival probabilities of these migratory birds on their wintering grounds. In addition, campaigns to engage local communities in areas in which large congregations occur would be useful (Arkumarev *et al.* 2014). Our evidence for human-induced mortality, which exclusively occurred in sub-Saharan Africa, is a concern for declining populations. However, due to the diffuse occurrence of the documented threats, enormous efforts and a long-term investment would be required to change human behaviour over large spatial scales. More research on adult survival of this species and the social and economic significance of the vulture trade in

Africa is urgently needed to identify areas where conservation management would be feasible to reduce mortality sufficiently to benefit populations in Europe.

In comparison with the widespread distribution in Africa, we found that the successful migratory route from Eastern Europe was extremely narrow while traversing southern Turkey and the Middle East (Fig. 1). These flyway bottlenecks in Turkey (Sutherland & Brooks 1981, Oppel *et al.* 2014), Israel (Leshem & Yom-Tov 1996) and Egypt (Hilgerloh *et al.* 2011) are well known from ground observations of migrating raptors. Our satellite tracking study, combined with previous data (Meyburg *et al.* 2004) and unpublished data of two adult birds, indicates that a high proportion of the eastern European Egyptian Vulture population migrates through the bottleneck in southern Turkey (Oppel *et al.* 2014). Although we did not record direct mortality during migration along this migratory route in our study, there are significant concerns over potential threats to raptors throughout this flyway (Leshem & Yom-Tov 1996, Sekercioglu *et al.* 2011, Stoychev *et al.* 2014), and ensuring safe passage for European raptors to their wintering areas in Africa by replacing poorly insulated power lines or limiting industrial infrastructure such as wind turbines may be a more immediately effective conservation strategy than addressing the multitude of threats operating over vast geographical areas in wintering regions in Africa (Vickery *et al.* 2014). In the long term, however, more work is also needed on African wintering grounds to emphasize the biological and economic significance of vultures and work towards facilitating the long-term survival of these scavengers across the African continent.

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