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Article

Mining citizen science data to explore stopover sites and spatiotemporal variation in migration patterns of the red-footed falcon

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Abstract

Citizen science data have already been used to effectively address questions regarding migration, a fundamental stage in the life history of birds. In this study, we use data from eBird and from 3 additional regional citizen science databases to describe the migration routes and timing of the red-footed falcon *Falco vespertinus* in the Mediterranean region across 8 years (2010–2017). We further examine the seasonal and yearly variation in migration patterns and explore sites used during the species migration. Our results suggest that the autumn passage is spatially less variable and temporally more consistent among years than in spring and that birds migrate faster in spring than in autumn. The species seems to be more prevalent along the Central Mediterranean during spring migration, probably as a result of the clockwise loop migration that red-footed falcons perform. There was a high variation in annual median migration dates for both seasons as well as in migration routes across years and seasons. Higher variation was exhibited in the longitudinal component thus indicating flexibility in migration routes. In addition, our results showed the species' preference for lowlands covered with cropland and mosaics of cropland and natural vegetation as stopover sites during migration. Stopover areas predicted from our distribution modeling highlight the importance of the Mediterranean islands as stopover sites for sea-crossing raptors, such as the red-footed falcon. This study is the first to provide a broad-scale spatiotemporal perspective on the species migration across seasons, years and flyways and demonstrates how citizen science data can inform future monitoring and conservation strategies.

Key words: distribution modeling, eBird, Maxent, Mediterranean, opportunistic data, raptors

Twice every year, a vast number of birds move between the western Palearctic and Africa connecting the 2 continents and their different biomes (Berthold 2001). Birds travel between geographically distinct locations to take advantage of seasonally predictable resources thus supporting their reproduction and overall survival. Migration, therefore, is a fundamental stage in the life history of birds and is under strong selective pressure mainly driven by geographic and temporal variation of resource availability (Salewski and Bruderer 2007) or selection of optimal wind conditions for departure and traveling. Both drivers are particularly important when birds have to face large ecological barriers (Saino et al. 2010). Ecological barriers, such as the Mediterranean Sea, can shape the migration of species: large raptors migrate predominantly by thermal soaring and therefore migrate over land, converging through specific flyways (Porter and Beaman 1985), however, some smaller raptors such as falcons undertake long sea crossings to move between Europe and Africa (Agostini et al. 2015).

The red-footed falcon *Falco vespertinus* is a small migratory falcon that breeds in steppe habitats, from Eastern Europe across Central Asia and winters in southern Africa (Ferguson-Lees and Christie 2001). The species is mostly insectivorous and is considered a generalist predator opportunistically feeding on locally abundant species of Orthoptera and Coleoptera (Cramp and Simmons 1980; Chavko and Krištín 2017). Available information on the species migration is fragmentary and thus its migration routes are still unclear. Standardized counts and migration phenology studies in the past decades suggest that red-footed falcons breeding in Europe migrate on a broad front directly crossing the Mediterranean Sea in spring and they are presumed to do so during autumn migration without concentrating at bottleneck sites to the extent that many other raptors do (Galea and Massa 1985; Roth 2008). However, some reports suggest an autumn migration funneled through the Levant (Leshem and Yom-Tov 1996). More recently, information from tracking devices suggests that red-footed falcons return to the European breeding grounds via West Africa and the central Mediterranean thus creating a migration loop (Palatitz et al. 2018). Asian conspecifics also perform a clockwise loop migration, with birds flying through the Caspian Sea and the Middle East in their southbound migration, whereas spring migration happens farther west and involves crossing both the Sahara Desert and the Mediterranean Sea (Katzner et al. 2016). Although tracking studies can provide high-quality data for the migration routes of individual birds, sufficient resources are needed to obtain geographically wide datasets for many individuals. So far migration patterns of the red-footed falcon have not been examined in a broad geographic scale and there is no knowledge about either variation between autumn and spring migration at the population level or the species stopover sites and habitat use during migration.

Over the past decades, tracking devices, bird ringing, and standardized counts at migration bottlenecks have provided conclusive insights into the biology of birds, especially on their movements and migration routes with direct implications on conservation and management (Baillie 2001; Bairlein 2001; Hebblewhite and Haydon 2010). Citizen science, the involvement of the public in scientific research, has become increasingly important in conservation science as it provides an opportunity to use large numbers of observers to address issues over broad geographic areas and for long time periods. Such information would otherwise be impossible to collect due to time and resource constraints (Dickinson et al. 2010). Currently, one of the best known ornithological citizen science platforms is Cornell's eBird (www.ebird.org), which provides crucial information for bird migration studies. eBird is a large citizen science database that contains a large and growing volume of bird count data or "checklists" (Sullivan et al. 2009). Such opportunistic data have already been engaged to effectively address questions regarding patterns of species occurrence (Devictor et al. 2010), diversity patterns (La Sorte et al. 2014), bird distributions (Fink et al. 2010), migration (Supp et al. 2015) as well as population monitoring (Walker and Taylor 2017; Horns et al. 2018).

In this study, we use data from eBird as well as from 3 regional citizen science platforms to describe the migration routes and timing of the red-footed falcon across the Mediterranean region. We further aim to examine the seasonal and yearly variation in migration patterns and assess stopover sites used during the species migration. We expect red-footed falcons to migrate faster in spring than in autumn according to the optimal migration theory and to exhibit a loop migration in the region as indicated in previous studies. Because our study area is located at the beginning of autumn migration and at the end of the spring migration, we expect greater variation in the migration routes for spring migration and a greater variation in daily longitude rather than in latitude across years.

Materials and Methods

Data collection

We extracted observations of red-footed falcons from 2010 to 2017 from the eBird database. eBird's quality control process includes various metrics during data submission, automated data filters, and a large network of regional editors (Sullivan et al. 2014). We only included scrutinized eBird observation data collected under the "traveling count" and "stationary count" sampling protocols. Only complete checklists were used and casual single species observations were discarded. We subsetted the dataset to include observations only during the species migration (Ferguson-Lees and Christie 2001; Palatitz et al. 2018): from March to June for spring migration and from August to October for autumn migration. Only observations that occurred outside the species' breeding distribution (BirdLife International 2019) were kept for the analyses. Additionally, we complemented the eBird dataset with observations from citizen science platforms around the Mediterranean region: in Italy (https://www.ornitho.it), Greece (Ornithotopos; Hellenic Ornithological Society 2009) and Turkey (www.kusbank.org). Only observations that came with a precise location (within 1 km^2) were used. We used all the data as presence records only, making no attempt to infer abundance or absence.

Migration patterns

We used the number of reports submitted each day that included observations of red-footed falcons, hereafter mentioned as "frequency." We used frequency of red-footed falcon reports rather than abundance of red-footed falcons to avoid potential bias by sightings of large roosts or large-scale migration through known bottlenecks (Hurlbert and Liang 2012). For each migratory season (spring and autumn) we calculated the median date and interquartile range of the bulk of observations on the species migration over the Mediterranean region. The relationship between frequency of red-footed falcons in each flyway and migration season was explored by performing chi-square test on a 2×3 contingency table.

Regarding migration routes and timing, we calculated species mean daily locations and analyzed them under a General Additive Model (GAM) framework following Supp et al. (2015) and making use of the R code snippets provided therein. Specifically, we compiled red-footed falcon daily observations from our dataset for each Julian day in each year and calculated a mean daily location. For each year and migration season, the mean daily locations were fed to a GAM to separately fit the latitude and longitude of daily locations as a function of time (Julian day). Based on GAM fits we obtained predictions of daily latitude and longitude and combined them to obtain predicted daily locations on the population-level. To infer migration speed, we calculated the daily great circle distance traveled by the population (in km per day) between all consecutive daily locations from the GAM analysis (R package "spaa," function "geodist"; Zhang 2013). Then for each season, we took the median of the 5 fastest speeds (thus minimizing the effects of potential outliers) as the maximum population-level migration speed (*sensu* La Sorte et al. 2013). Finally, we fitted GAMs on the latitude and the longitude of predicted migration routes for each migration season to determine the amount of variance explained by both Julian day and different years.

Because red-footed falcons migrate on a broad front, citizen science observations might be influenced by subpopulations that behave differently (Sullivan et al. 2014), providing rather unrealistic estimates when calculated in the population level. To address such potential issues the previously described analysis pipeline was followed not only for the whole dataset but additionally for each of the 3 delineated flyways: the Central Mediterranean flyway including observations of the central Mediterranean and Italian peninsula, the Balkan flyway including eastern Mediterranean and the Balkan Peninsula, and the Eastern flyway including observations from Black Sea through Turkey and the Middle East (Supplementary Figure S1).

Habitat use and stopover niche modeling

We extracted all observations on migration that were noted by users as species stopovers (birds displaying foraging activity) across all the abovementioned platforms. These data (61 observations) were used to compare the frequency of the most commonly used habitat type between seasons using chi-square tests. The global land cover map GlobCover version 2.3 (ESA 2010) was used to map habitats. GlobCover uses satellite image data to map land cover in raster format at 300 m resolution. The map was overlaid with a hexagonal grid (1×1 km) and for each observation, the main habitat was assigned, based on the main cover type (mode of pixels) within each cell. Additionally, to further assess habitat selection we modeled the red-footed falcon's ecological niche using Maxent, which requires presence-only data to develop a predictive model (Phillips et al. 2006). Overall, 51 locations contributed to the development of the model. Maxent was run using a maximum of 500 iterations, 10 replicates and converge threshold of 1×10^{-5}, although the maximum number of background points was set to 10,000. The discriminatory ability of the model was evaluated using the area under the receiver-operated characteristic curve (AUC). AUC ranges from 0.5 (performance not better than random) to 1 (perfect fit). Additionally, the True Skill Statistic (TSS) scores were calculated (Allouche et al. 2006) and the model was classified as having moderate performance (≥ 0.5), fair performance (≥ 0.3), and poor performance (< 0.3). Maxent produces a logistic output for every grid cell, ranging between 0 and 1, reflecting relative occupancy probability. We considered as "suitable" areas for the species those cells for which probability of presence was >0.5 and as "very suitable" those with values >0.75 (Limiñana et al. 2012). As predictive variables of the potential stopover distribution of the species, 19 bioclimatic variables related to temperature and precipitation in raster format with 30-s resolution (roughly equivalent to 1 km^2 cells) were downloaded from WorldClim–Global Climate Data (http://www.worldclim.org). These data are a set of climate layers from 1970 to 2000 that represent information derived from monthly temperature and rainfall obtained from weather stations and then interpolated for illustrating the average value of surfaces with a spatial resolution of 1 km^2 (Hijmans et al. 2005). Keeping in mind the biology of the species, the bioclimatic variables were tested for collinearity using the R package "usdm" (Naimi 2015). We kept variables that showed a correlation <0.7 and a Variance inflation factor < 10 resulting in 6 climatic variables. In addition to the climatic variables, we included the land cover layer, 2 topographical variables (slope and elevation), and distance to roads (Table 1). All environmental variables used were resampled at a resolution of ~1 km^2 to the WGS84 geographical coordinate system.

Results

Our final dataset consisted of 1,361 observations (number of reports) covering 7 autumn migrations (2010–2016, $n = 225$ observations) and 8 spring migrations (2010–2017, $n = 1{,}136$ observations). All over the Mediterranean region, autumn migration occurs from mid-September to early October peaking in late September whereas, in spring, migration occurs from late April to mid-May with a peak in early May (Figure 1). There was a high variation in annual median migration dates for both seasons (standard deviation [SD] for autumn = 18.1 days, SD for spring = 13.3 days, Supplementary Table S1). Differences in migration timing among flyways are more evident in autumn; birds migrating through the Central Mediterranean and Eastern Flyways reach their peak at mid-to-late September, although in the Balkans the median date was found to be in early October with the main passage lasting until mid-October (Figure 1). The chi-square test examining differences in the frequencies of red-footed falcons in each flyway relative to the migration season was significant ($\chi^2 = 145.3$, df $= 2$, $P < 0.0001$). Further examination of combinations that contributed to the overall significance of the test showed that red-footed falcons migrate more frequently through the eastern flyway in autumn whereas in spring birds migrate mainly through the central Mediterranean (Supplementary Figure S2), thus confirming the species' loop migration.

Analysis of migration speed both in the complete dataset and for each flyway separately showed that red-footed falcons migrate faster in spring than in autumn and specifically twice faster (Table 2). The GAMs indicated that birds migrate on a wider front and in a larger time period during spring as opposed to the more concentrated autumn migration (Figure 2). Variance in the migration routes was better explained by both year and Julian day especially for autumn whereas the variance in latitude was much better explained by Julian day and year than in longitude (Table 3, Supplementary Figure S3).

During migration red-footed falcons used mostly areas associated with crop productions, either rainfed croplands (26.2% of locations) or mosaics of mostly cropland along with natural vegetation (26.2% of locations). Additionally, areas mostly covered by natural vegetation (mosaics of grassland/shrubland with cropland at lesser extent; 14.8% of locations) were also frequently used. Other

Table 1. Variables used in the ecological niche model and contribution of each one to the model for migration stopovers of red-footed falcons in the Mediterranean

Variable	Source	Percentage contribution
Land cover	Globcover (ESA 2010)	18.7
Isothermality (BIO3)	BioClim (Hijmans et al. 2005)	0.9
Temperature annual range (BIO7)		22.1
Mean temperature of wettest quarter (BIO8)		4.5
Mean temperature of warmest quarter (BIO10)		1.8
Annual precipitation (BIO12)		24.3
Precipitation seasonality (BIO15)		2.3
Slope (degrees)	Derived from Digital elevation model (DEM) from http://srtm.csi.cgiar.org/	3.4
Elevation (m)		13.7
Distance from roads (decimals)	Shapefile of world roads and railroads (www.esri.com)	8.3

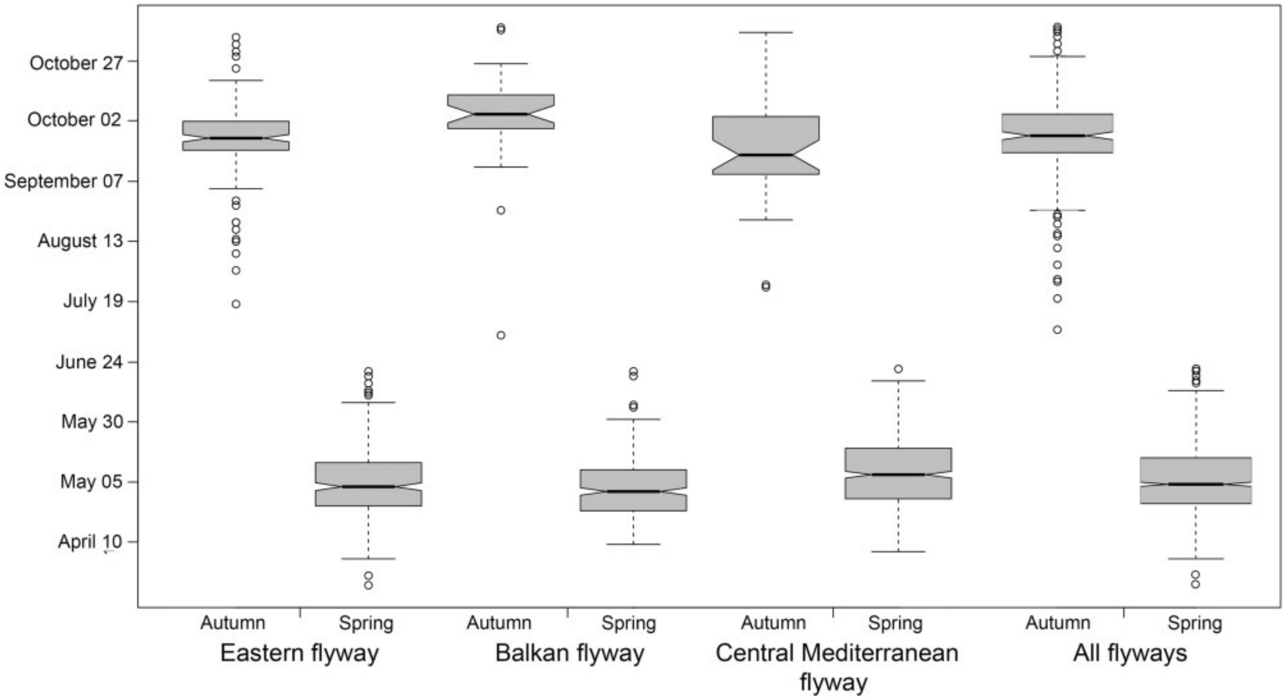

Figure 1. Boxplots of red-footed falcon migration dates for both autumn and spring between 2010 and 2017 for each flyway and across the complete dataset.

habitats accounted for <10% of the recorded locations (Supplementary Table S2). Habitat use did not differ between seasons ($\chi^2_{11} = 17.684$, $P = 0.089$). The Maxent model predicting suitable stopover areas for the red-footed falcon had a high discriminative ability (AUC = 0.866 ± 0.067; Supplementary Figure S4) and a TSS score (TSS = 0.531) indicating moderate performance. Of the 10 variables used to build the model, 5 were the most important ones (contributing a combined total of 87.1% to the model): annual precipitation (BIO12), annual temperature range (BIO7), land cover, elevation and distance from roads, accounting for 24.3, 22.1, 18.7, 13.7, and 8.3% contribution to the final model, respectively (Table 1). The probability of presence of red-footed falcons in stopover sites was higher in semi-arid areas with annual precipitation values ranging from 650 to 700 mm and small annual temperature ranges. Sites covered mainly by grasslands, cropland or mosaics of grassland and shrubland close to urban areas seem to increase the probability of occurrence for the species. Additionally, the model indicated a high probability of presence in lowland areas (<200 m) and in a small distance from roads, <10 km (Figure 3). Suitable areas (probability of presence > 0.5) for the species in the modeled region occurred in all flyways, from southern Italy to coastal areas in the Balkans and from Bosporus throughout the Levant. Very suitable stopover sites for the species (probability of presence > 0.75) were located mainly in islands (Malta, Sicily, Crete, and Rhodes) but also in some additional mainland locations in Western Italy, Attica region in Greece, Bosporus, and Israel (Figure 4).

Discussion

Regarding the species migration phenology, our results showed, on the one hand, little differences in median dates for spring migration among flyways, a result that is in accordance with previous reports

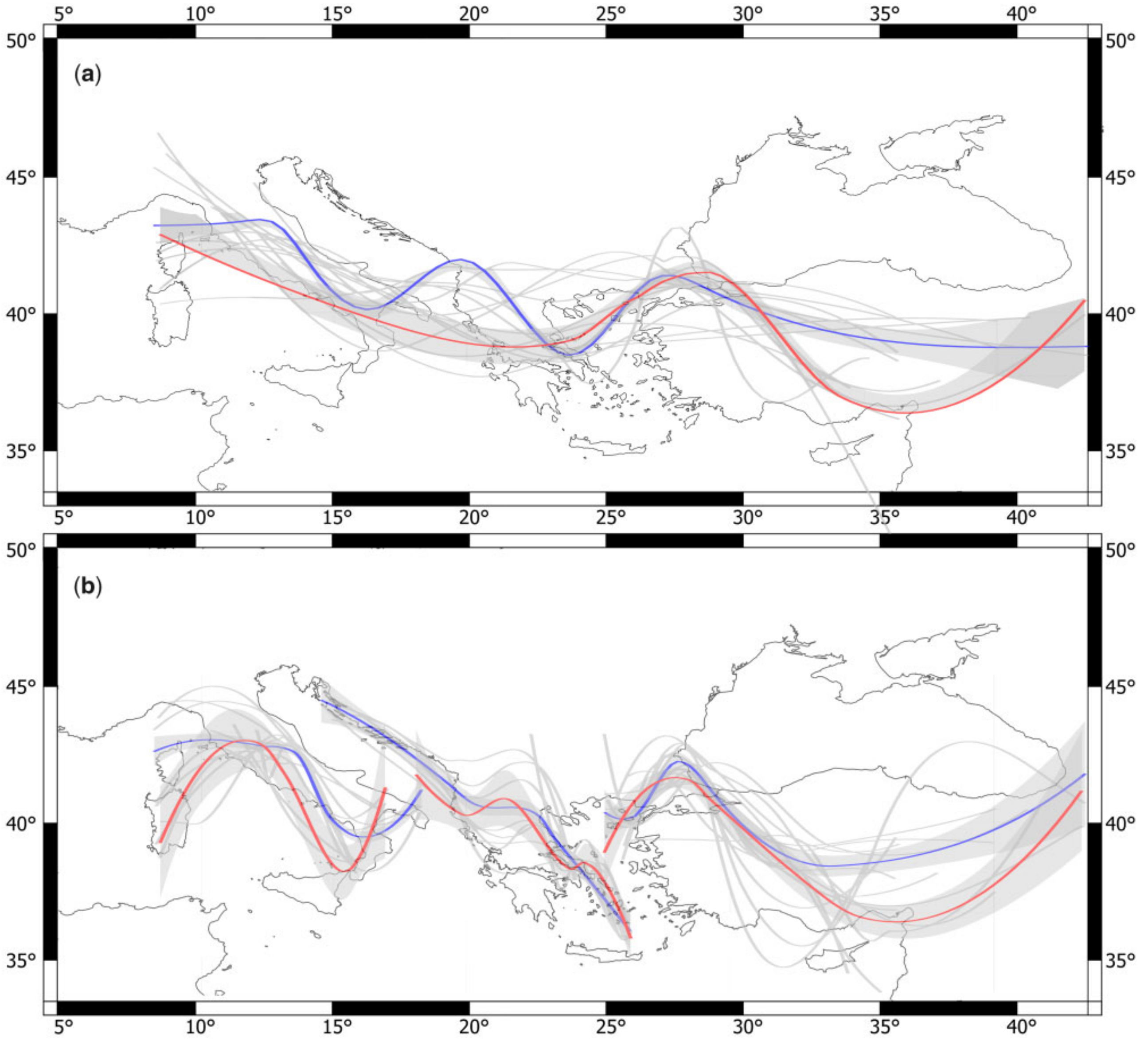

Figure 2. Migration routes of red-footed falcons in 2010–2017 (gray lines) and mean routes for autumn (red) and spring (blue) along with 95% confidence intervals for (a) all flyways and (b) each delineated flyway (from left to right: Central Mediterranean, Balkan and Eastern flyway).

Table 2. Mean (SD) for migration speed for each season and flyway across the 8 years of the study

Flyway	Autumn (km/day)	Spring (km/day)
Central Mediterranean flyway	31.2 (10.32)	84.5 (15.16)
Balkan flyway	38.2 (6.36)	83.6 (17.82)
Eastern flyway	46.9 (5.44)	83.8 (14.72)
Complete dataset	108.57 (4.55)	214.69 (14.76)

Table 3. Mean migration variance (2010–2017) explained by Julian day and year, separately for latitude and longitude in both migration seasons

Flyway	Autumn		Spring	
	R^2 lat	R^2 lon	R^2 lat	R^2 lon
Central Mediterranean flyway	0.94	0.77	0.42	0.51
Balkan flyway	0.89	0.96	0.77	0.63
Eastern flyway	0.79	0.82	0.43	0.68
Complete dataset	0.51	0.57	0.69	0.74

that state that migration is occurring from late April to mid-May in the region (Handrinos and Akriotis 1997; Corso 2001; Premuda et al. 2008), with some variation among years. On the other hand, during autumn migration, our results imply a rather late median date for autumn migration through the Balkans, compared with other flyways, with the main passage being from late September to mid-October, peaking on October fifth. One of the main factors that may shape the differences in the migration phenology of the species is the premigratory concentrations that occur in Central Europe (Palatitz et al. 2015). Such effects of premigratory gatherings on migration patterns have been described in other gregarious

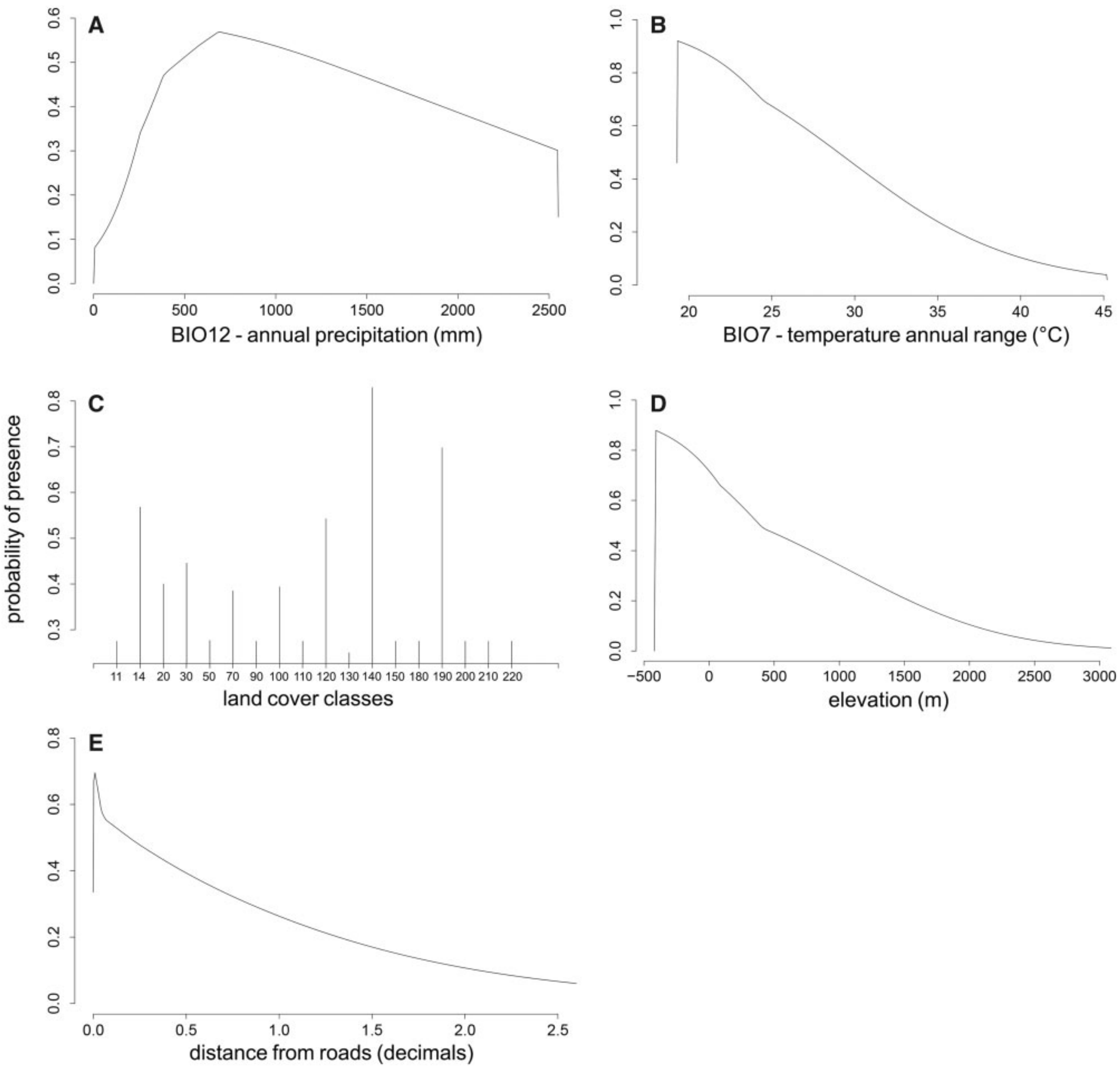

Figure 3. Relationships between the 5 most influential environmental variables (**A–E**) and the probability of occurrence for red-footed falcons in stopover sites during migration. (**C**) 14 = Rainfed croplands; 120 = Mosaic grassland (50–70%)/forest or shrubland (20–50%); 140 = Closed to open (>15%) herbaceous vegetation; 190 = Artificial surfaces and associated areas. (**D**) Elevation exhibits negative values because the study area includes the Dead Sea (−430 m).

falcons such as the lesser kestrel *Falco naumanni* (Bounas et al. 2016). Most red-footed falcons leave the premigratory roosts in Hungary during late September (Fehérvári et al. 2014; Palatitz et al. 2015) and they could subsequently migrate over the Balkans. The use of the Balkan flyway and the crossing of the Mediterranean Sea by individuals breeding in Hungary are further corroborated by both ringing recoveries (Handrinos and Akriotis 1997) and telemetry data (Palatitz et al. 2018).

Studies so far suggest that red-footed falcons perform a loop migration. From the available red-footed falcon observations we found that the species seems to be more prevalent along the central Mediterranean region during spring migration with much fewer observations taking place in autumn. Conversely, during autumn there is a higher prevalence in the eastern Mediterranean region. Such a pattern is most probably a direct consequence of the species loop migration. Numbers of migrating red-footed falcons could be further inflated by Asian birds, as their southbound routes pass through the Caucasus, into Turkey and the Middle East but during spring they migrate through the Mediterranean Sea. The fact that most of the species global population occurs in Asia (BirdLife International 2019) could explain such high spring prevalence, that is, if most of the population exhibits similar clockwise loop migration. This is further corroborated by Leshem and Yom-Tov (1996) that report greater numbers of red-footed falcons in autumn than in spring in Israel. Our modeling results, however, failed to provide any clear evidence of loop migration in the Mediterranean region. This is a potential limitation of the analysis that arises mainly because of the spatial extent of the study (only the Mediterranean

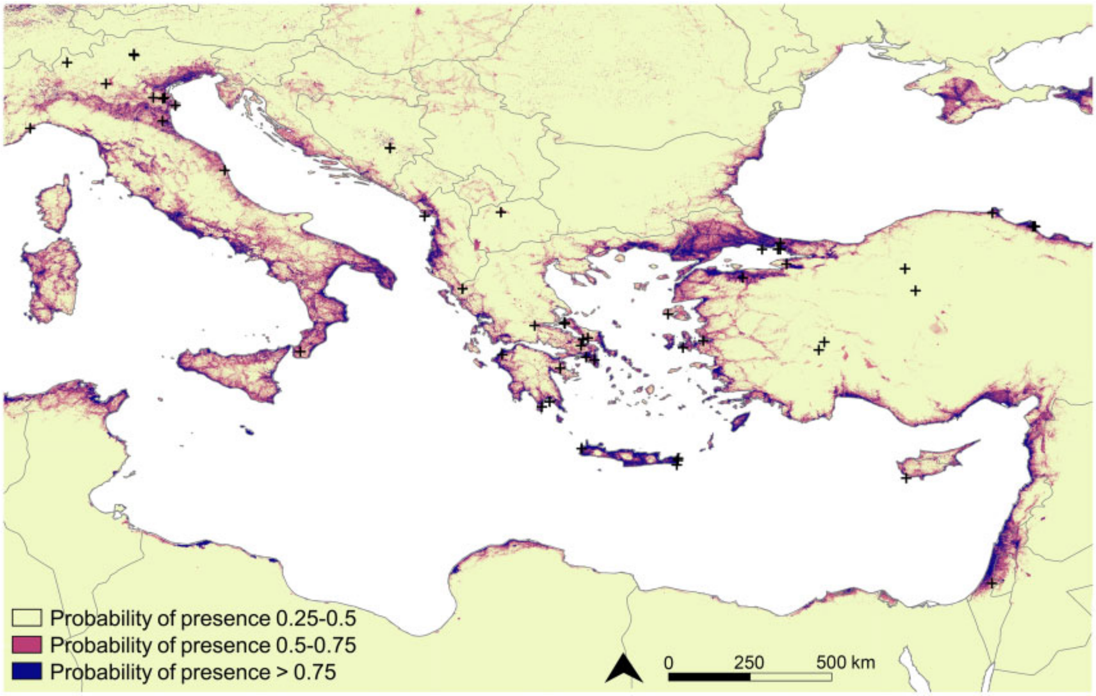

Figure 4. Probability of stopover presence for red-footed falcons migrating across the Mediterranean. Black crosses show the data used in Maxent modeling.

region) as well as due to the handling of the dataset; in spring the migratory flow can be much more broader compared with autumn and because the GAMs were fed with daily mean locations, they failed to distinguish the loop migration at the population level. Despite that, our results regarding the migration routes suggest that the autumn passage occurs on a narrower front and in a more concentrated period with most observations coming from the eastern flyway. Indeed such pattern has previously been reported for Israel with the species passage being concentrated into a short period between late September and mid-October (Alon et al. 2004). In addition, red-footed falcons have been seen migrating in high numbers in autumn at the Bosporus (Fülöp et al. 2014) and the Black sea (Iankov et al. 2007). Regarding spring migration, our results showed that it occurs in a wider front with birds using different migration routes in a wider time period.

It is apparent in all flyways examined that birds migrate faster in spring than in autumn (Table 2) over the Mediterranean region. In fact, mean migration speed values calculated in our analysis turned to be very close with those reported from tagged red-footed falcons (Palatitz et al. 2018). Such a pattern has also been described for the closely related Lesser Kestrel (Sarà et al. 2019). Usually, birds travel faster in spring to optimize arrival for breeding whereas the slower autumn migration could depend on feeding opportunities or sex and age-related differences in the timing of migration (Alerstam 2011; Nilsson et al. 2013). However, deviations from the rule of faster spring migration exist and differences have been mainly attributed to stopover duration and environmental conditions faced during migration (Kölzsch et al. 2016; Carneiro et al. 2019). On the individual level, some tracked red-footed falcons have been found to perform a faster autumn migration (Palatitz et al. 2018) but our results on the population level suggest a faster spring migration. Additional work is needed to further illuminate the species migration speed patterns and how they are shaped. We should further stress that our analysis examined the migration speed of the species only over the Mediterranean region and not the total migration speed, therefore, these results should be handled with caution and not generalized for the overall migration speed of the species.

Regarding variance in migration routes, we demonstrate that longitude was less explained by both Julian day and year than latitude. This might indicate flexibility in the longitudinal component thus allowing red-footed falcons to adjust their location in an east–west axis to either track ideal resource opportunities or weather conditions. Weather and/or resource tracking have been proposed to be the main selective pressures that shape the variation in migration routes and timing and have been attributed as the main causes for the irruptive migration of the species (Hanžel 2015; Golawski et al. 2017). Our approach confirms a high annual variation in migration routes and timing reported for the species in the eastern Mediterranean (Handrinos and Akriotis 1997; Alon et al. 2004) while it additionally detects similar patterns across all flyways, especially during spring migration.

After climatological variables, the land cover was the most important variable predicting the most suitable stopover areas for the red-footed falcon. After all, the species is rather opportunistic, migrating using a "fly and forage" strategy and thus it is more likely to depend on feeding opportunities during migration. Our results showed a species preference for lowlands covered with cropland and mosaics of cropland and natural vegetation that presumably hold a high number of insects that birds can feed on (Benton et al. 2002). It has been reported that, at least during spring migration, the species can be found in any sizeable piece of open farmland including arable or open cultivated land (such as vineyards, alfalfa, etc.) with few scattered trees (Handrinos and Akriotis 1997). Species distribution models generated from eBird occurrence data may be used as the first step toward targeted field surveys or conservation planning. However, our stopover distribution model should be interpreted as a basic reference point as lowland agricultural areas and associated climate, that are deemed as suitable stopover sites for the species are extensively present throughout the Mediterranean and Anatolia region thus making it challenging to focus any conservation actions during the species migration. However, our results confirm the importance of the Mediterranean islands as stopover sites for sea-crossing raptors (Agostini and Panuccio 2010; Panuccio 2011).

Finally, spatial biases in citizen science datasets should be considered in this study: urban areas, as well as distance from roads variable, seem to also contribute (albeit with low percent contribution) in predicting suitable stopover areas for the species. Citizen science projects are prone to providing data that are spatially biased toward more densely populated, easily accessible habitats, and sampling efforts in different habitats may not reflect actual species occurrences (Geldmann et al. 2016) and additionally, potential bias might be taxa specific (Tiago et al. 2017). Thus birdwatchers that provide the observations may be more likely to report birds in areas closer to roads and possibly at places that provide better opportunities for birdwatching. The analysis of patterns in the distribution of observations deriving from citizen scientists or at least considering the influence of potential biases in the interpretation of opportunistically collected data is a basic step toward improving the quality and informativeness of such datasets. Nevertheless, the species seems not to actively avoid roads and urban areas.

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Author Contributions

A.B., C.B., and M.P. designed the study; C.B., M.P., S.B., T.B., K.E.-Y., P.I., and C.I. collected the data; A.B. and M.S. analyzed the data. A.B. wrote the paper, with input from all other authors.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

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