


Seasonal and daily activity patterns by Eleonora's Falcon *Falco eleonora* based on GPS telemetry: a contribution to the species' movement ecology at its breeding grounds

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Summary

Eleonora's Falcon *Falco eleonora* is a migratory raptor, well-known for its delayed breeding period. Owing to its great mobility, current information on its distribution pattern during the pre-breeding period is rather sporadic, mainly based on field observations and only one telemetry study. Likewise, the species' ranging activity during the breeding period has not been thoroughly investigated due to methodological limitations of the approaches implemented in previous studies, again amounting to only two telemetry studies in recent years. In this study we aimed to provide a comprehensive overview of the species' ranging activity at its breeding grounds based on telemetry. Utilizing GPS data from six adult females originating from the core of the species' breeding range we explored broad- and fine-scale activity patterns while at their breeding grounds. Our results indicated that during the pre-breeding period the falcons visited high biodiversity areas lying hundreds of kilometres away from their colonies, exhibiting site-fidelity, as shown for falcons from other breeding colonies in the past. During the breeding period the falcons roamed at an average distance of 17 km from their nesting sites, but their ranging activity could be observed up to 130 km. In accordance with the species' breeding biology, the falcons tended to perform longer trips as the nestlings became more independent. The temporal pattern of ranging activity fitted well with the diurnal variability of the autumn migration flux. Furthermore, nest attendance tended to decrease in windy conditions and as the season progressed, and to increase when southerly winds blew. Despite the low number of tracked falcons, our study set a reference basis for future studies highlighting the importance of specific (protected) areas during the pre-breeding period and providing the first assessment of the movement ecology of the species during the pre-breeding and breeding period in Greece.

Keywords: *Falco eleonora*, Aegean Sea, GPS telemetry, protected areas, nest attendance.

Introduction

One of the fundamental topics in ecological research deals with how, why, where and when organisms move. Movement ecology is an extensive field of research that addresses questions

related to the distribution pattern of organisms in space and time, the mechanisms involved, and the intrinsic and extrinsic factors underlying the observed patterns, providing insights on the interactions among individuals and their environment that are crucial for wildlife management (Nathan *et al.* 2008). The emergence of tracking technology has proven a valuable tool in this endeavour (Fancy *et al.* 1988, Cooke 2008), offering continuous monitoring of the movements of free-living animals across space and time. The miniaturization of tracking devices has undoubtedly broadened the horizons of ecology in recent years (Wilmers *et al.* 2015), contributing to various disciplines, such as behavioural, community and functional ecology (Börger *et al.* 2020). Birds, especially migratory species, have been the epicentre during this often-acclaimed golden era for tracking technology (Wilmers *et al.* 2015), that has led to the accumulation of voluminous tracking data through an increasingly large number of studies (López-López 2016).

Eleonora's Falcon *Falco eleonora* G^{éné}, 1839 is a fully migratory species that spends half the year (spring–autumn) in the Mediterranean basin, the Atlantic coast of Morocco and the Canary Islands and the other half (winter–spring) in Madagascar and surrounding areas (Walter 1979). Among birds of the Palearctic region, Eleonora's Falcon stands out for its delayed breeding season that coincides with the autumn migration of passerine and near-passerine birds (Walter 1979). Eleonora's Falcon is classified as 'Least Concern' according to the IUCN criteria (BirdLife International 2020) but is included in Annex I of the Birds EU Directive (EEC 2010).

During the past 15 years, research on Eleonora's Falcon has benefited from tracking technology advances. In particular, the first satellite telemetry study was considered a breakthrough in research on the species' by revealing the migration route Eleonora's falcons undertake twice each year between their breeding and wintering grounds (Gschweng *et al.* 2008). Since then, an increasing number of telemetry (mostly satellite) studies have been carried out, unveiling important aspects of the species' ecology during the migratory (López-López *et al.* 2009, 2010, Mellone *et al.* 2011, Kassara *et al.* 2012, Mellone *et al.* 2013b, Hadjikyriakou *et al.* 2020b) and wintering period (Gschweng *et al.* 2012, Mellone *et al.* 2012a, Kassara *et al.* 2014, Kassara *et al.* 2017, Hadjikyriakou *et al.* 2020a). Still, to date the movement ecology of the species during the pre-breeding and breeding period remains largely unexplored. Indeed, there have been only three satellite telemetry studies up to now: Mellone *et al.* (2013a) and Gangoso *et al.* (2020) in Spain and Mellone *et al.* (2012b) in Morocco. Despite the small sample size of the tracked falcons and the rather large sampling interval owing to technical limitations of the equipment available in earlier years, telemetry studies have provided the first evidence of site fidelity, reported on the land cover composition where the species occurred during the pre-breeding period (Mellone 2013a), and revealed important information on the ranging behaviour of the species during the breeding period, highlighting the importance of inland areas for foraging (Mellone 2012b). Thanks to recent advances in tracking technology, Gangoso *et al.* (2020) were able to explore in detail the influence of wind regime on food availability and subsequently on the foraging activity of the falcons using smaller devices that also collected fixes at a higher sampling frequency. However, apart from these studies, the species' whereabouts and behaviour while at its breeding grounds has been mainly reported through field-based studies.

In particular, the extensive reviews by Ristow and Wink (1992-1994) and Ristow (2010) indicate that during the pre-breeding period Eleonora's Falcons are common across southern Europe, occurring several kilometres away from their breeding colonies (Ristow and Wink 1992-1994, Ristow *et al.* 2010) in search of insects, their main food source during this period of the year (Ristow 2004). However, this information is based on field observations and ring recoveries, offering little insight on the origin of the observed birds and, overall, on the species' habitat requirements during the pre-breeding period. The birdwatching community has actively contributed with field observations that are publicly available through the eBird database (eBird 2020), but apart from the aforementioned limitations, these observations tend also to be spatially biased in favour of popular and easily accessible birdwatching sites. Furthermore, there have also been a few field-based studies reporting on the species' distribution (e.g. Besson 1982, Xirouchakis 2005, Mas 2006) and activity patterns (Kassara *et al.* 2019) prior to the onset of the breeding period.

On the contrary, Eleonora's Falcon breeding distribution and population size is well-documented owing to systematic field surveys undertaken during the past 15 years (e.g. Dimalexis *et al.* 2008, Del Moral 2008, López-Darias and Rumeu 2010), confirming that the islands and islets of the Aegean Sea are the core of its breeding range, hosting c.85% of the global breeding population (Dimalexis *et al.* 2008) which is 14,550–14,750 pairs (BirdLife International 2020). Among numerous field studies on the breeding biology (e.g. see Ristow and Wink 1985 and references therein), the use of radar and optical rangefinders have provided detailed information on the altitude (Xirouchakis and Panuccio 2019), flight patterns (Hedenström *et al.* 1999) and path metrics of the falcons' hunting excursions (Rosén *et al.* 1999). Still, despite the fine-scale description of the falcons' movements, the timeframe of these studies was rather short, while the detection range of the hunting falcons was limited to the vicinity of the studied colonies.

In this study we used GPS technology to explore the spatiotemporal patterns of the ranging activity of Eleonora's Falcons from the core of the species' breeding range, namely the Aegean Sea, to (a) identify intensively used areas during the pre-breeding period and (b) determine which factors influence nest attendance during the breeding period. Therefore, we aimed to increase our knowledge regarding the movement ecology of Eleonora's Falcon taking advantage of the continuing improvements in tracking technology, and ultimately offer a comprehensive overview of the falcons' ranging activity throughout their stay at their breeding grounds.

Materials and Methods

Animal capture and handling

Capturing and tagging activities took place on the Antikythira island (Figure 1a) using mist nets during the breeding period (first week of September 2015 and 2016). Following standard bird survey techniques, the captured individuals were ringed with a metal ring, and biometric measurements, including body weight, were recorded. The tagged falcons were all females of breeding age (Ristow *et al.* 1983b), i.e. after second calendar year.

GPS-GSM-UHF tags (SKUA-L GPS-GSM-UHF tracker, 15g, Ecotone Telemetry Inc.) were attached as backpacks with a harness, weighing in total 17g. These tags operate on two separate modules, GPS-GSM and GPS-UHF. GPS fixes are stored in memory until a GSM network or a base station is in range for data retrieval. The UHF link allows collection of many more GPS fixes than GSM, but it is restricted by the availability of a nearby base station. In our case a hand-held base station was used to download UHF data while the falcons were present on Antikythira island. Thus,

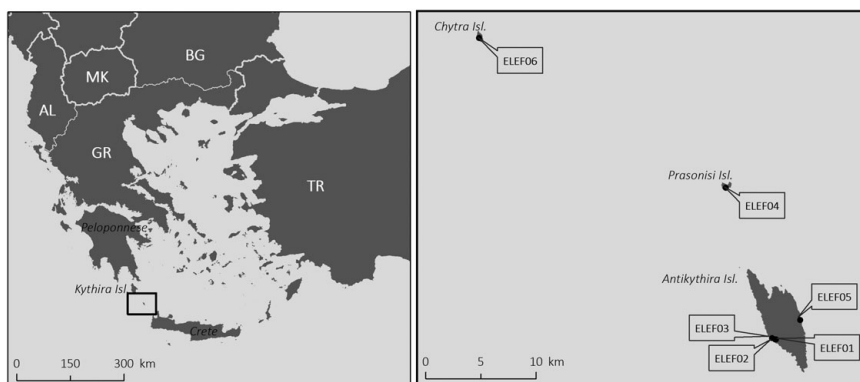


Figure 1. Location of (a) the study area and (b) the nesting sites occupied by the 6 GPS tracked Eleonora's Falcons (Map projection: Greek Grid - epsg: 2100).

the retrieved UHF data covered only a small part of the falcons' movements during the breeding and/or pre-breeding period. GSM data and UHF data consisted of GPS fixes programmed to be stored every 2 hr and every 15 min, respectively.

Bird handling took place in a concealed, shady location, to ensure minimal disturbance to the remaining falcons that were present in the area, as well as to minimise stress for the captured falcons. The tagging procedure lasted c.30 min per falcon. The falcons were released immediately after handling. While still in sight, the behaviour of the tagged falcons was observed through binoculars. No signs of aberrant behaviour were detected.

GPS data preparation

After removing duplicate records, we classified the UHF and GSM data into (a) 'day-time' and 'night-time' using nautical dawn and dusk hours and (b) 'at nest' and 'away from nest' to distinguish between movements related to ranging activity and movements related to nest attendance, nest defence and other social interactions, by considering a 100-m radius around each nest. We were not able to locate the nests of the tagged falcons in the field, except for ELEFO5, due to the geomorphology and/or remoteness of the nesting locations. The coordinates of the nest sites for the remaining falcons were first estimated based on visual inspection of the GSM data received during the breeding period (from August until October) and were subsequently verified by calculating the revisitation pattern of the trajectory of each individual (for detailed methodology see Appendix S1 in the online supplementary material). GSM data were further classified into 'at sea' and 'over land' considering a 50 m buffer to the coastline to account for the positional accuracy of the GPS fixes.

Breeding period

We used GSM data to explore the seasonal variability in the distance of the ranging activity of (a) all tagged falcons following their release and until departure from their colony and (b) of two of them (ELEFO2, ELEFO5) during the breeding period (see definition below) for which we continued to receive data in subsequent years. For these two falcons we could not define the exact date of the onset of the breeding period, so we hereafter use the term "breeding period" to refer to the period between egg-laying and departure from the colonies. The onset of the incubating period was estimated as the day the falcons started remaining exclusively at their nests.

Brooding is carried out by the females, thus we hypothesized that as the nestlings become older and less dependent on parental care, their mothers would be able to perform longer trips in search of food. After excluding ELEFO5 (year 2017) and ELEFO6 (year 2016) due to the very small sample size (Table S1), we modelled the distance from their nesting sites as a function of day (scaled values of Julian date) using Generalized Mixed Additive Models (GAMMs) considering the breeding event as random factor. Based on the results of the model validation (i.e. testing for normality and homoscedasticity of the residuals) with diagnostic plots we decided to log-transform the response variable in the final model structure. We also estimated the bearing of the GSM data relative to the location of the nest of each falcon to investigate whether there was directionality in the ranging activity of the falcons and estimated moonlight conditions (i.e. the illuminated fraction of the moon) to investigate whether visibility influenced night-time ranging activity. We additionally analysed the time budget of ranging activity at sea and over land using contingency tables following the classification scheme of Mellone *et al.* (2012b) for diurnal periods to obtain comparable results.

Finally, we investigated ranging activity at a finer scale using the UHF data received for 2–5 weeks following the release of the falcons (Table 1). In particular, we explored the effect of wind conditions on the likelihood of ranging activity on an hourly interval as a function of Julian date and wind conditions, i.e. wind speed and wind direction, using GLMM models with a binomial family. Breeding event was a random factor in the model. Wind direction was classified into four

Table 1. Summary of GPS data for six female Eleonora's Falcons while at their breeding grounds. In parenthesis, the number of fixes received, and the number of fixes used for data analysis.

Tag	Tagging Year	Nesting site location	GSM data coverage	UHF data coverage
ELEFo1	2015	Antikythira island (west cliffs)	5/9 - 27/10/2015 (249/239) 11/5 - 19/5/2016* (56/56)	9/9 - 24/9/2015 (439/391)
ELEFo2	2016	Antikythira island (west cliffs)	7/9 - 17/10/2016 (247/243) 8/5 - 19/10/2017 (1237/1219) 26/4 - 24/10/2018 (1207/1183) 29/4 - 21/10/2019 (450/421)	6/9 - 18/10/2016 (1875/1131) 8/5 - 30/5/2017 (1723/0) 26/4 - 11/5/2018 (189/0)
ELEFo3	2015	Antikythira island (west cliffs)	5/9 - 27/10/2015 (330/318)	5/9 - 18/9/2015 (343/280)
ELEFo4	2015	Prasonisi islet	5/9 - 24/10/2015 (341/334)	5/9 - 29/9/2015 (1084/1011)
ELEFo5	2016	Antikythira island (east cliffs)	5/9 - 13/10/2016 (85/78) 16/5 - 6/10/2017* (843/830)	19/9 - 6/10/2016 (207/148)
ELEFo6	2016	Chytra islet	13/9 - 16/10/2016 (40/39)	-

* end of data transmission

categories (north [315, 45], east [45,135], south [135, 225] and west [225,315]) and category 'south' was used as a reference level. The number of UHF data fixes received within an hour was used as weight.

Pre-breeding period

For ELEFo2 and ELEFo5 we explored space use patterns after their arrival at the breeding grounds and until the onset of the breeding period, using dynamic Brownian Bridge Models (Kranstauber *et al.* 2012) to delineate the 2D area (50% and 95% utilization distribution) used by the two falcons. We tested visually the effect of various windows and margin sizes on the resulting utilization distributions and concluded by using a margin size of seven fixes and a window that corresponded to 7–10 days (window size: ELEFo2 2017 and 2018 = 91 fixes, ELEFo2 2019 = 29 fixes, ELEFo5 2017 = 75 fixes). We also plotted the average daily distance from their respective nests against Julian date to define the time period corresponding to visitation to core activity areas (50% utilization distribution). In addition, we used the Corine 2018 dataset (CLC2018 v20; <https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download>) and a digital elevation model (EUDEM v1.1.; <https://land.copernicus.eu/imagery-in-situ/eu-dem/eu-dem-v1.1?tab=metadata>) to describe landscape characteristics within the corresponding core areas. We also used the Natura 2000 (Greece, Bulgaria), Important Bird Areas (Greece, Bulgaria; hereafter IBAs) and Key Biodiversity Areas (Turkey; hereafter KBAs) database to estimate the respective overlap with high biodiversity areas.

Spatial analyses and map production were carried out in ArcGIS 10.1 (ESRI 2012), while model-building and further computations were performed in R.3.6.2 (R Core Team 2019). The 'lmerTest' package (Kuznetsova *et al.* 2017) was implemented for the creation of GLMM models, the 'piecewiseSEM' package (Lefcheck 2016) for the computation of marginal and conditional R^2 following Nakagawa and Schielzeth (2013) and the 'emmeans' package (Lenth 2019) for the estimation of the marginal means for the categorical variable wind direction using Tukey post-hoc tests. The 'suncalc' package (Thieurmél and Elmarhraoui 2019) was used to estimate sunlight hours and moonlight conditions. The 'mgcv' package (Wood 2011) was implemented for the creation of GAMM models. Dynamic Brownian Bridge Models were built using the package 'move' (Kranstauber *et al.* 2020), while weather data were kindly provided by the National Observatory of Athens, Institute of Environmental Research and Sustainable Development, on an hourly time interval.

Results

All tagged falcons nested in the wider area of the Antikythira island (Figure 1b, Table 1). In particular, three falcons nested on the west cliffs of Antikythira island (south of the capture site; ELEFo1, ELEFo2 and ELEFo3), one falcon on the east cliffs of Antikythira island (ELEFo5), one falcon on Prasonisi islet (7 km north of Antikythira island; ELEFo4) and one falcon on Chytra islet (3 km south of Kythira island and 32 km north-west of Antikythira island; ELEFo6).

Breeding period

For the two falcons that were tracked in multiple years, ELEFo2 and ELEFo5, their movement pattern suggested that the incubating period began rather late in 2017 (25 and 17 August, respectively), whereas in 2018 and 2019 ELEFo2 started incubating on 6 and 9 August, respectively.

During the breeding period most of the received GPS data (75%) indicated attendance to the nesting sites. Ranging activity occurred at an average distance of 16.77 km (SD = 26.14) while most of the ranging activity occurred at 24.71 km, with the exemption of ELEFo6 that stayed close to its nesting site (Figure 2, Table S1). However, there were large gaps in data collection for ELEFo6 (sampling frequency: mean = 20 hr, max = 116 hr) compared to the rest of the falcons, probably resulting in underestimation of its true movement pattern. Still, for the remaining falcons there was a substantial inter- and intra-individual variability in the ranging distance (Table S1). Accounting for these differences, the GAMM results indicated that the ranging distance increased during the breeding period ($F_{\text{Julian date}} = 20.96$, $df = 3, 308$, $P < 0.01$) but not in a linear way; from the middle of September until the middle of October it progressively increased, while earlier during the breeding period and until departure it remained rather stable (Figure S2). However, until the beginning of September ranging distances were available only for one falcon (ELEFo2), yet from multiple breeding events (2017, 2018, 2019), hence the larger confidence intervals (Figure S2). Furthermore, the bearing of the GSM data related to ranging activity also varied among and within individuals, indicating lack of directionality in most cases (Rayleigh's uniformity test, $P < 0.05$) (Figure 3). Night-time ranging activity was rather uncommon, occurred close to the nesting sites and was apparently not influenced by moonlight conditions (mean = 0.374, SD = 0.264, range = 0.134–0.561; Table S3).

The time budget analysis suggested that at-sea ranging activity occurred mainly in the morning and at night, while inland ranging activity occurred in the afternoon ($\chi^2 = 77.622$, $df = 1$, $P = 0.001$; Fig. S1). The longest trip was performed by ELEFo2 that overnighted on Antimilos islet, c. 130 km NE of Antikythira island. Inland movements were mostly over Antikythira island and only on a few occasions over Kythira island (Figure 3). Moreover, during the 2017 breeding period ELEFo5 made three night-time visits to the cliffs where ELEFo1, ELEFo2 and ELEFo3 nested.

Furthermore, the likelihood of ranging activity increased during the season, as well as at hours when stronger winds blew (i.e. northern or eastern ones; Table S4), while decreased when southern winds prevailed (Tables 2 and S2). All falcons left their colony after the 3rd week of October, but only three of them continued to transmit GSM data for the subsequent months (ELEFo1) and/or years (ELEFo2, ELEFo5; Table 1).

Pre-breeding period

ELEFo1 arrived at its nesting site on 11 May (year 2016), but data transmission ended abruptly eight days later while visiting a hilly, cultivated area in western Crete (Figure 4). Judging by the battery voltage and the recorded ambient temperature during the last days of transmission we excluded the possibility that the tag was not charging properly or was lying on the ground, while we were unable to locate the falcon during an on-site visit in the area a few days later.

ELEFo5 arrived at its nesting site on 16 May (year 2017) visiting Kythira, Peloponnese and central Greece until the start of the 2017 breeding season. Its signal was lost on 6 October due to technical failure, as since then we have been able to observe the falcon with the tag correctly attached on its back

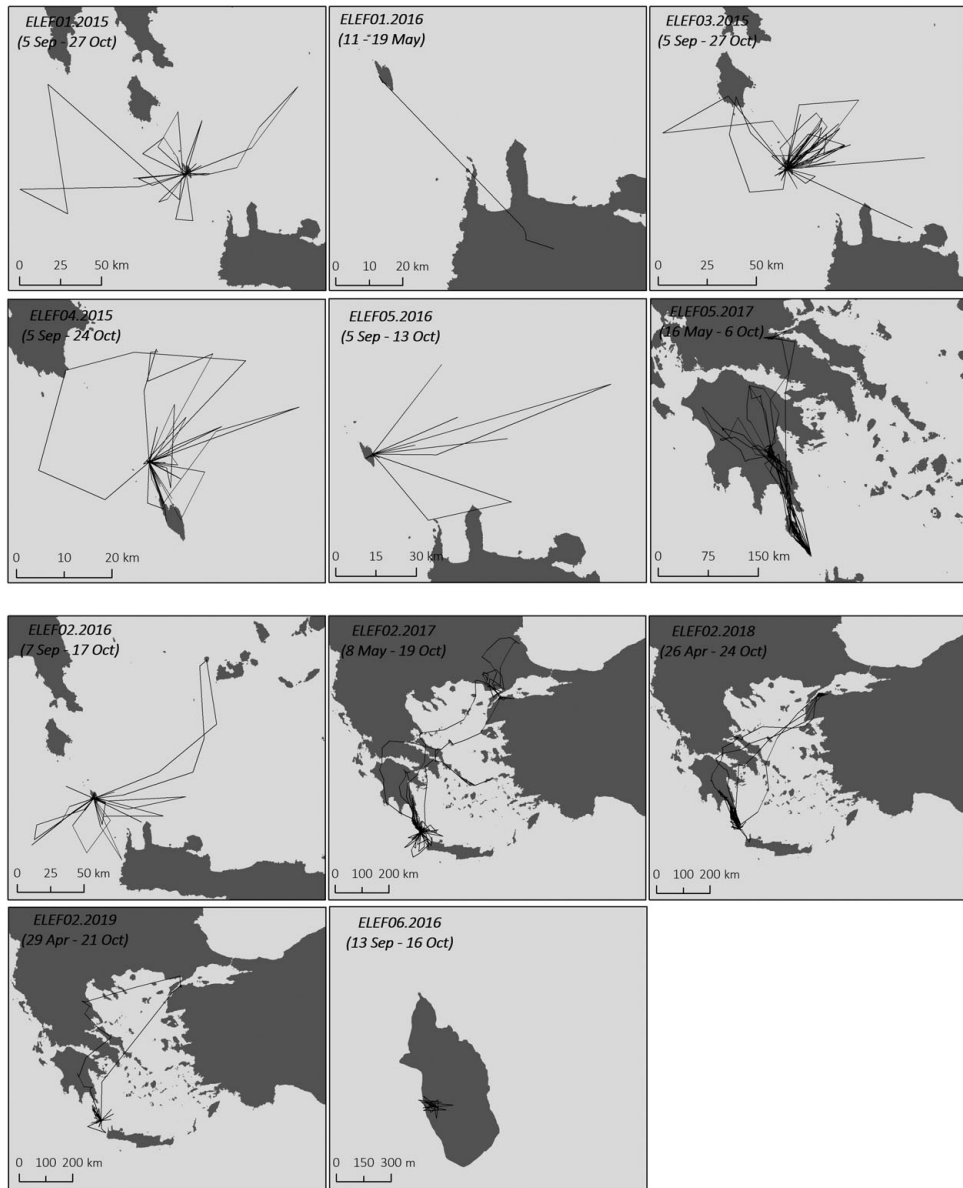


Figure 2. Distribution pattern of movements of six falcons while at their breeding grounds, including multiple years for some of them, based on GSM data (Map projection: Greek Grid – epsg: 2100).

on multiple occasions on Antikythira island, locate its nest and monitor its breeding performance in subsequent years (2018–2019; ABO unpublished data). Space-use analysis results suggest that apart from the surroundings of its nesting site, another core area of activity was located on Mt Parmonas (Peloponnese), c.160 km to the north, where the falcon spent approximately 30 days, but intermittently (Figure 4b). It consists of a mountainous area dominated by forests and shrubs (Table 3), which is also part of the Natura 2000 network (GR2520006; Table 4).

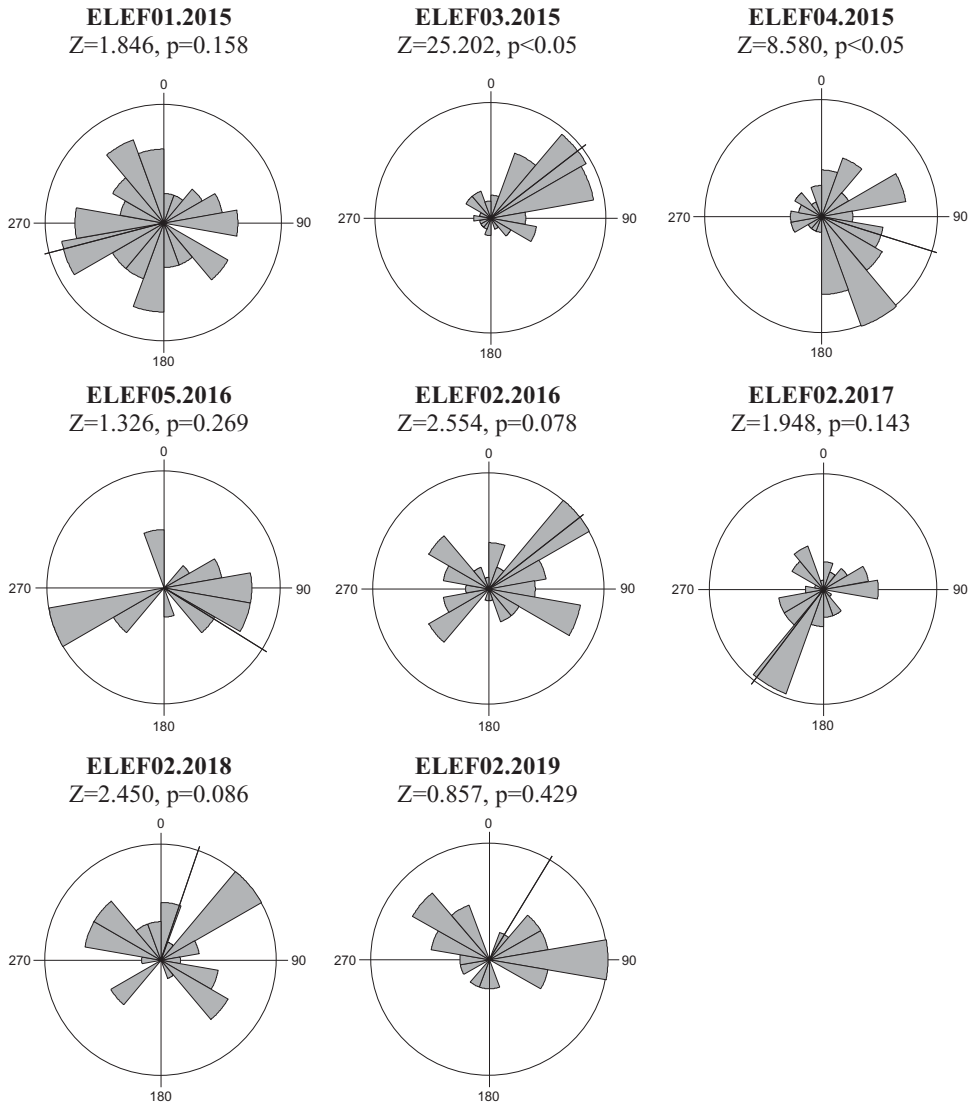


Figure 3. Rose plot histograms of the ranging activity relative to the location of the nesting site for five falcons. The black line indicates the mean vector of the bearings. The statistic of the Rayleigh uniformity test (Z) is given along with the p-value.

Contrary to ELEF01 and ELEF05, ELEF02 did not visit its nesting site upon return from its wintering grounds until 17 May 2017, but instead spent a few days on islets of the Aegean Sea, central Greece, and the Peloponnese. After a brief visit to its colony, from the end of May until the beginning of July it wandered in the SE Balkans and NW Turkey, c.600 km away from its nesting site, whereas from July on it performed shorter trips to SE Peloponnese, Kythira island and Crete. Apart from the surroundings of its nesting site, another nine core activity areas were identified, among which the largest one was located in Çanakkale region (Figure 4a), a KBA site (Table 4), where it spent c.30 days (Figure 4b). Overall, the core activity areas consisted of lowland areas, mainly heterogeneous agricultural areas and shrublands (excluding marine waters) (Table 3).

Table 2. GLMM results regarding the likelihood of ranging activity as a response to Julian date, wind speed and wind direction based on UHF data.

Model terms	Coefficient	Standard error	P-value
intercept	-2.174	0.316	0.000
Julian date (scaled)	0.385	0.089	0.000
Wind speed (scaled)	0.116	0.054	0.031
Wind direction-North	0.634	0.240	0.008
Wind direction-East	0.741	0.206	0.000
Wind direction-West	0.923	0.206	0.000

R^2 fixed factors = 0.033, R^2 random factors = 0.038

ELEFo2 departed on 19 October from its colony and returned on 26 April 2018 (Figure 4a). This time it spent one month in the vicinity of its colony before heading to the Peloponnese, central Greece and Evia island. It visited NW Turkey again staying there for approximately 30 days, although this period also included a brief return of just two days at its colony in late June (Figure 4b). From the first week of July until the start of the 2018 breeding season it performed short excursions to SE Peloponnese, Kythira island and Crete (Figure 4). Apart from the surroundings of its nesting site, another three core activity areas were identified, yet of smaller total extent, of which Çanakkale region was again the largest. They comprised lowland areas, mainly forested, heterogeneous agricultural areas, shrublands and pastures (excluding marine waters) (Table 3).

Once more ELEFo2 began its southbound journey on 24 October and returned on 29 April 2019. As in the previous year, it stayed in the vicinity of its colony until late May and then spent a few days in the Peloponnese, central Greece and Evia island, before revisiting Çanakkale region where it stayed for three weeks, i.e. until the end of June (Figure 4b). In the following days it visited Kythira and Crete until the onset of the 2019 breeding season, which ended on 21 October (Figure 4a). Apart from the surroundings of its nesting site, Çanakkale region was the second largest core area used by the falcon. The composition of the land cover within the core activity areas consisted of forested and seminatural areas (excluding marine waters) (Table 3).

Discussion

In this study we present for the first-time detailed information on the ranging activity of Eleonora's Falcons originating from the south Aegean Sea during the pre-breeding and breeding period. Our key findings are largely in accordance with the species' biology and ecology and with previous studies. We found that upon arrival at the breeding grounds and until the onset of the breeding period female Eleonora's Falcons exhibit a widespread distribution pattern, visiting high biodiversity regions in insular and continental areas, which they tend to revisit in subsequent years. During the breeding period we found that female Eleonora's Falcons expand their ranging activity as the nestlings become more independent, are more likely to leave their nesting sites in windy conditions that are related to increased food availability, mostly autumn bird migrants but also insects (Xirouchakis *et al.* 2019), and that they are active both during daytime and night-time.

Breeding period

Our findings indicate that most of the ranging activity of the tracked female Eleonora's Falcons occurred at a distance of 25 km from their nesting sites (average 17 km) with the exception of one falcon that stayed close to its nesting site; however its respective sampling interval was rather infrequent, which probably led to an underestimation of its true ranging capacity. Ranging activity was most likely related to hunting birds as it mainly occurred over the sea in the morning and at night, in line with the diurnal variability in the abundance of the autumn migrant flux (Ristow *et al.* 1983a). Inland trips were no exception, mostly performed in the afternoon over Antikythira

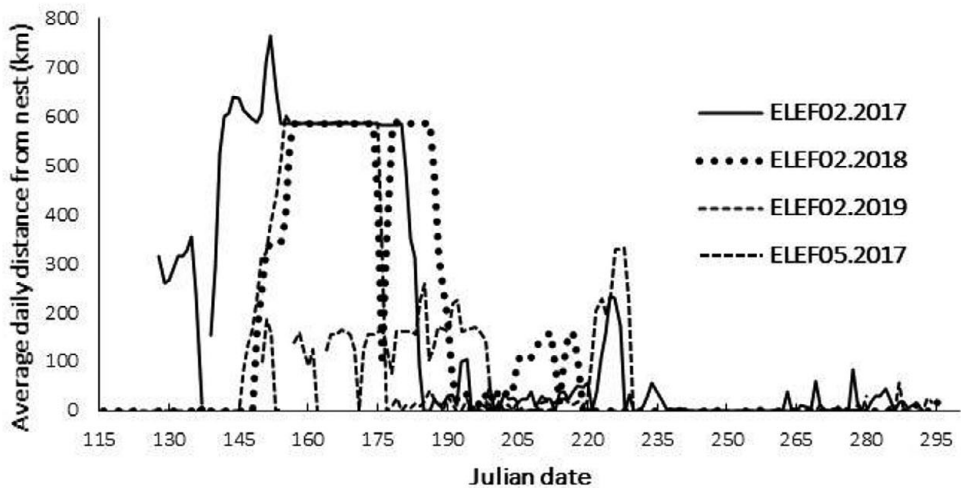
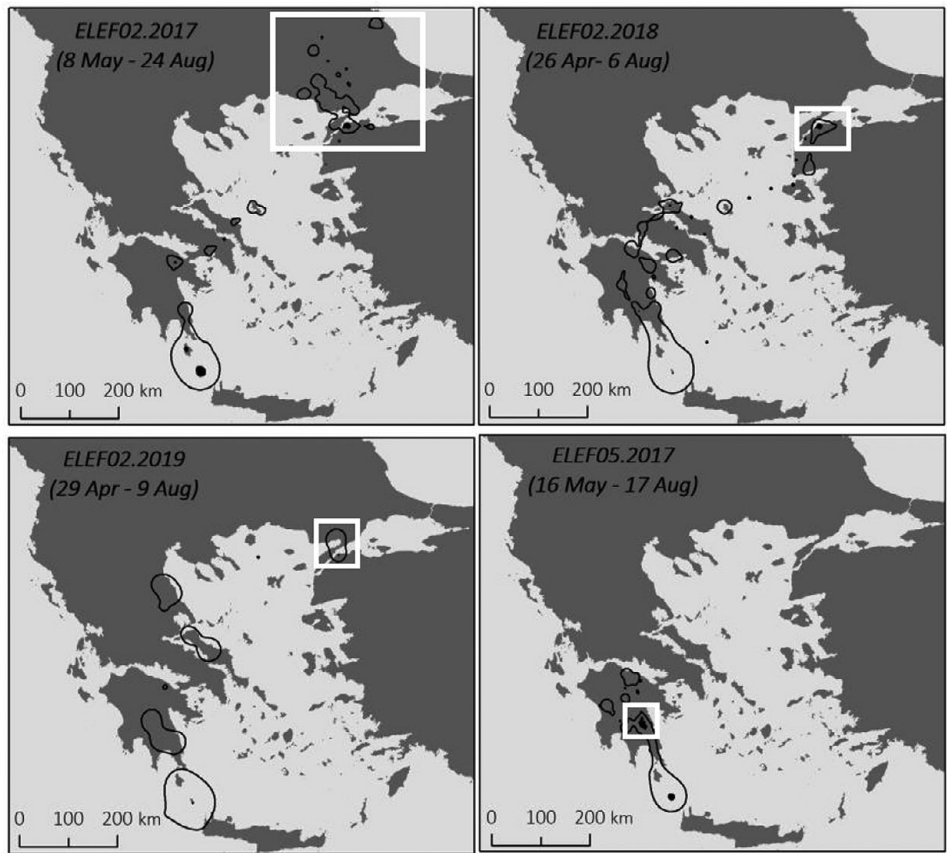


Figure 4. (a) Habitat use (95% kernels – hollow polygons and 50% kernels – filled polygons) of two falcons and (b) their relative distance to their nesting site during the pre-breeding period. White boxes highlight areas intensively used by the falcons as indicated by plateaus in Fig. 4b (Map projection: Greek Grid - epsg: 2100).

Table 3. Space use pattern results for two tagged Eleonora's Falcons during the pre-breeding period. The percent cover of land cover and the elevation (mean \pm SD) are given for the core areas (50% utilization distribution).

Tag	ELEFo2		ELEFo5	
	2017	2018	2019	2017
<i>Utilization distribution area</i>				
95% area (km ²)	18242.54	18853.50	22747.66	9671.68
50% area (km ²)	670.03	162.58	39.65	450.37
<i>Topography</i>				
Elevation (m)	210.09 \pm 136.42	128.02 \pm 85.07	134.40 \pm 77.68	1133.36 \pm 372.44
<i>Land cover</i>				
1. Artificial surfaces				
1.1 Urban fabric	1.00	2.25	0.74	0.12
1.2 Industrial, commercial and transport units	0.04	0.06	0.00	0.00
1.3 Mine, dump and construction sites	0.11	0.01	0.00	0.00
1.4 Artificial, non-agricultural vegetated areas	0.06	0.00	0.00	0.00
2. Agricultural areas				
2.1 Arable land	4.72	8.02	4.37	0.57
2.2 Permanent crops	6.07	2.15	0.04	0.00
2.3 Pastures	0.77	11.56	6.58	0.39
2.4 Heterogeneous agricultural areas	11.05	18.51	2.31	1.99
3. Forest and seminatural areas				
3.1 Forest	4.31	20.85	14.93	32.87
3.2 Shrub and/or herbaceous vegetation associations	9.54	14.36	11.03	24.35
3.3 Open spaces with little or no vegetation	2.53	3.90	24.40	3.73
4. Wetlands				
4.1 Inland wetlands	0.00	0.00	0.00	0.00
4.2 Coastal wetlands	0.07	0.00	0.00	0.00
5. Water bodies				
5.1 Inland waters	0.17	0.20	0.00	0.00
5.2 Marine waters	56.63	10.22	34.43	33.32

island but also a few over Kythira island to the north-west. Similar findings were reported by Mellone *et al.* (2012b) for two tracked female falcons from a colony in Morocco for the period between the 3rd week of September until the onset of autumn migration one month later, reporting the largest trip ever recorded of 181 km, in accordance with our findings. Previous estimates, based on the duration of hunting excursions of male Eleonora's Falcons from a colony in Sardinia (Italy), suggest that an average straight-line trip would be 24 km from the colony (Rosén *et al.* 1999), however foraging trips of up to 140 km have been recently recorded for GPS-tracked males in the Canary Islands (Gangoso *et al.* 2020). Male falcons are mainly responsible for food provision, i.e. autumn bird migrants, for their partner and their nestlings, while females attend the nestlings (Wink *et al.* 1980), thus sexual differences in hunting activity are also to be expected. However, our findings indicate that female falcons may perform equally long trips in search of food. As the nestlings become older, energy requirements increase, so the female falcons are likely to contribute to food provision for themselves and/or their nestlings, as indicated by the increasing trend of the ranging distances during the study period. Still, ranging distances are expected to be adjusted to

Table 4. Overlap (%) with protected areas for two tagged Eleonora's Falcons during the pre-breeding period, relative to total area of their respective core activity areas (50% utilization distribution).

Tag	ELEFo2		ELEFo5	
	2017	2018	2019	2017
<i>Important Bird Areas</i>				
GR003: Dadia - Dereio - Aisymi forest	0.50			
GR114: Western Skyros and islets	0.02			
GR123: East Lakonia mountains	0.09			
GR129: Kythira island	7.91			
GR130: Antikythira island and surrounding islets	2.94	2.35	29.36	4.37
<i>Key Biodiversity Areas</i>				
Canakkale Bogazi	22.05	17.01	35.68	
<i>Natura 2000 sites</i>				
GR1110010: Oreinos Evros - Koilada Dereiou (SPA)	0.50			
GR2520005: Moni Elonas kai charadra Leonidiou - spilairo Mana kai Galazia limni (SCI)				0.04
GR2520006: Oros Parnonas (kai periochi Malevis) (SCI)				62.15
GR3000008: Antikythira - Prasonisi kai Lagouvardos (SCI)	9.35	3.21	36.82	8.66
GR3000012: Nisos Antikythira kai nisides Prasonisi, Lagouvardos, Plakoulithra kai nisides Thymonies (SPA)	3.06	2.56	30.03	4.55
GR3000013: Kythira kai gyro nisides: Prasonisi, Dragonera, Antidragonera, Avgo, Kapello, Koufo kai Fidonisi (SPA)	0.05			
GR3000019: Thalassia periochi Kythiron (SPA)	1.12			

spatiotemporal differences in food abundance as has been shown for male falcons in the recent study by Gangoso *et al.* (2020).

Wind conditions influence the flux of autumn bird migrants and undoubtedly play an important role in food availability for Eleonora's Falcons during the breeding period (Ristow *et al.* 1983a, Gangoso *et al.* 2020). It has been shown that strong N and NW winds offer better hunting opportunities as indicated by the number of pluckings found at nesting sites in a colony in northern Crete in a previous study, whereas in southern and/or weak winds, the flux of bird migrants dropped substantially and thus some falcons left their colony to hunt on insects inland to supplement their nutritional needs (Ristow *et al.* 1983a). In the Canary Islands easterly winds seem to provide the most favourable hunting opportunities judging by the number of stored prey found near their nesting sites, but when unfavourable wind conditions prevail for a prolonged period of time, male falcons visit the opposite mainland in Africa, staying up to 10 days away from their breeding colony (Gangoso *et al.* 2020). During the breeding period (from 15 July until 31 October 2015–2018) the prevailing winds in our study area were from the north-northeast, while southerly and western winds were significantly weaker (Table S4). Thus, in accordance with the above, we found that the nest attendance pattern of the six female Eleonora's Falcons was influenced by the wind conditions, as the falcons were more likely to be at their nesting sites in wind conditions unfavourable for hunting, i.e. when southerly and/or weaker winds blew. On the other hand, our findings did not provide evidence for directionality during ranging events, as shown in six out of eight cases, contrary to a previous study in the aforementioned Italian colony (Rosén *et al.* 1999). However, this comes as no surprise, since the Italian colony is shadowed by the huge land mass of Sardinia in the east, thus hunting opportunities are higher over the open sea in the north and west. On the contrary, in our study area the incoming flow of autumn migrants from the north is not obstructed by prominent land masses nor by the topography of the island of Antikythira, but rather occurs in a broad front; therefore the entire airspace around and above the island should be regarded as hunting grounds for the falcons that breed in the area.

Our data also indicated that night-time ranging activity was rather limited, as has been shown during the wintering period (Hadjikyriakou *et al.* 2020a), and occurred close to the nesting sites and on average in nights with half-moon; yet there was large variability among and within individuals.

Another recent study indicated that night-time hunting by Eleonora's Falcons might be more widespread than previously thought, in particular close to artificially lit areas during the breeding period (Buij and Gschweng 2017). Our study area, though, is a sparsely populated island with few artificial lights inland, that are located several kilometres away from the places where night-time activity was recorded. Therefore, night-time ranging activity as a result of attraction to artificial lights is highly unlikely. It still remains to be clarified whether or not night-time ranging activity was facilitated by better visual conditions, i.e. moonlight, given that our findings were not conclusive and that our sample size was rather small.

In the case of the Moroccan colony, inland movements were attributed to insect hunting and drinking/bathing, considering the landcover composition of the visited areas (Mellone *et al.* 2012b). In our study area in 2017 insect hunting was recorded at 18h00 (local hour, UTC+3) almost on a daily basis from 7 September until 24 September (A. Evangelidis pers. obs.), while bird hunting was recorded after sunset from 9 to 16 October in the interior of Antikythira island (N. Tsiopelas pers. obs.) the time when most migrants are expected to resume their migration after staging over at the island (e.g. Åkesson *et al.* 1996). Therefore, inland movements related to bird hunting cannot be ruled out in our study area. Anecdotal data from our study area also suggest a peak in the attendance of falcons at freshwater ponds at midday-early afternoon (K. Bairaktaridou unpubl. data), which fits well the time-budget of the inland movements of the tracked falcons. Last but not least, social interactions among breeders deserve further investigation considering the visits of one falcon to nesting cliffs in the opposite side of the island on three occasions.

Pre-breeding period

During the pre-breeding period two female Eleonora's Falcons from Antikythira island dispersed in the eastern Mediterranean region (from S Greece to SE Bulgaria and NW Turkey), occurring in diverse lowland and mountainous areas and making irregular visits to their colony in the meantime. In particular, the tracked falcons were observed in the Peloponnese, Evia island, Skyros island, Evros region and Çanakkale region, as well as at their colony. Field observations from the eBird database also confirm a fairly regular presence of the species in the transboundary area between Greece and Turkey, including the Çanakkale region, but also in Evia, Skyros and Antikythira islands (Figure. S3). Additionally, our own observations indicate that the south-eastern part of Peloponnese is used for insect hunting by groups of Eleonora's Falcons (20–100 individuals) in June and July (N. Tsiopelas pers. obs.). Therefore, our findings complement these field observations by highlighting the importance of Peloponnese during the pre-breeding period, as well as the airspace between south-east Peloponnese and Antikythira, which should be considered as the main flyway corridor the falcons use to reach these areas.

Parnonas Mt (Peloponnese) and Çanakkale region represented the largest core activity areas of two falcons, the latter being repeatedly visited in subsequent years by the same falcon (ELEFo2) in June. Even if we exclude 2019 due to the large sampling interval of the GPS data (3x times higher than in previous years), the size of the core activity area located in Çanakkale region was substantially reduced in 2018 compared to 2017 (and even more in 2019). Even though we could not estimate the exact age of the falcon, this pattern could be the result of increasing experience, being better acquainted with the region and making better use of available resources before settling to its colony. Reduced experience in early years is also supported by the rather delayed onset of the egg-laying period in 2017, relative to later years (2018 and 2019) but also the species' breeding biology (Walter 1979, Ristow 1999). June was the period of highest ranging activity for both falcons, while in May and in July the falcons tended to perform shorter trips to Peloponnese, Kythira and Crete, of also shorter duration. July represents the month of courtship for Eleonora's falcons and the onset of the egg-laying period (Ristow 1999), thus their ranging activity is expected to be reduced.

A similar activity pattern was shown for two adult female and one juvenile Eleonora's Falcons originating from the Balearic and Columbretes islands (Spain), respectively (Mellone *et al.* 2013a) and one female adult Eleonora's Falcon originating from San Pietro island (Italy; Gschweng *et al.*

2008). During the pre-breeding period and especially in June the Spanish falcons roamed in France, Spain and Italy occurring in areas more than 500 km from their colonies until the onset of the breeding period. One of the two Spanish falcons was tracked for two years and its movement pattern highlighted an intensively used area lying c.400 km away from its colony in southern France that it visited in both years. Another intensively used area was indicated in western Spain for the Spanish juvenile falcon, c.180 km away from its natal colony. Similarly, the Italian adult falcon spent two months in the Italian mainland before visiting its colony in mid-August (Gschweng *et al.* 2008), but no information on space use was provided by the authors. Although not directly comparable with our findings since we implemented a more focused land cover composition analysis only considering the core activity areas of the two tracked falcons, Mellone *et al.* (2013a) also concluded that the Spanish falcons occurred in a variety of habitats, including forests, shrublands and cultivated areas, as in our study.

Despite the small sample size of the tracked falcons, the site-fidelity pattern indicated by both our study and that of Mellone *et al.* (2013a) suggests that specific areas could play an important role in the species' conservation at its breeding grounds and this certainly deserves further investigation. Our findings also pinpoint the need for transnational cooperation in that direction. In addition, we showed that islands typically known as breeding sites (Skyros, Kythira, and Antikythira) are also part of the core activity areas during the pre-breeding period, while similar evidence was provided for protected sites where the species' presence was not recorded at all (Natura sites GR2520006 and GR2520007; IBA sites GR003 and GR123). A recent study has pinpointed the importance of the island of Antikythira as a foraging ground for the species during the first half of the pre-breeding period, with a large number of falcons observed hunting, mainly over cultivated areas, from the end of April until the end of May (Kassara *et al.* 2019). This time-window fits well with the movement pattern of the two tracked falcons in May. Moreover, even though detailed data on the insect abundance in Çanakkale region and Parnonas Mt are currently lacking, there is evidence that they host high biodiversity, owing to low level of human activities and increased landscape diversity Özgül and Koç 2016; <http://natura2000.eea.europa.eu/Natura2000/SDF.aspx?site=GR2520006>). If we consider the anticipated climatic changes in the eastern Mediterranean region (Giannakopoulos *et al.* 2011), future resource availability is expected to be reduced mainly due to a shortened vegetation growth period as a result of water shortage and habitat loss due to increased fire severity. In fact, according to future predictions, both core activity areas, Parnonas Mt and Çanakkale region, fall into the subregions that will be mostly affected by climate change in the eastern Mediterranean region (Giannakopoulos *et al.* 2011).

To sum up, based on our findings and considering the high mobility of Eleonora's Falcon while at its breeding grounds, tracking technology is undoubtedly an asset for the study of the species' movement ecology and consequently, its conservation. We therefore highly recommend the continuation of tracking studies to collect high precision relocation and environmental data from animal-borne sensors, of even finer sampling frequency, from other colonies as well as from male Eleonora's Falcons to account for inter-individual, sex- and site-related variability, as recently implemented in the Canary Islands (Gangoso *et al.* 2020). Taking into account the increasing demand for renewable energy investments, especially in wind energy, information on the 3D space use regarding both the breeding and pre-breeding period could guide decisions on the installation of wind farms in continental and insular environments, as well as in offshore areas in Greece. Regarding the pre-breeding period, an increase in telemetry studies would facilitate the implementation of targeted field surveys in intensively used areas to unveil habitat preferences, as well as to identify current pressures and future threats, as has been also suggested for the wintering period of the species (Hadjikyriakou *et al.* 2020a).

Supplementary Material

To view supplementary material for this article, please visit <http://dx.doi.org/10.1017/S0959270920000714>.

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