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Activity patterns of Eleonora's Falcons during the pre-breeding period: the role of habitat composition on the island of Antikythira

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Abstract – Eleonora's Falcon is well known for its delayed breeding season among European breeding raptors, however its relatively prolonged pre-breeding period remains to date largely understudied. In this study we compiled information on the species' behavior based on data from systematic field surveys to investigate activity patterns of Eleonora's falcons during the pre-breeding period in an area that holds one of the largest colonies across its breeding range, namely the island of Antikythira in the southern edge of the Aegean Sea. According to our findings, large islands hosting Eleonora's falcons breeding colonies may also constitute important foraging areas during the pre-breeding period as foraging was the main activity undertaken by the falcons. Foraging was mostly performed in areas where food availability, either staging birds or insects, is expected to be highest, namely in cultivated areas. Considering the habitat composition in the study area, previous findings on the spatiotemporal activity patterns of staging migrants and our opportunistic observations of foraging falcons, our findings suggest that birds could constitute an alternative food of source during this period of the year within our study area. Therefore, the revival of agricultural practices is expected to enhance local biodiversity and constitute a conservation priority for Eleonora's falcons in the study area. Still, further studies are required to decipher the distribution pattern and habitat associations during the pre-breeding period of Eleonora's falcons and ultimately guide conservation schemes at a larger spatial scale.

Key-words: Pre-breeding period, raptor, diet, insects, staging migrant birds, habitat composition, cultivations.

INTRODUCTION

Eleonora's Falcon *Falco eleonorae* Géné, 1839 is a long-distance migratory raptor of the Palearctic, well known for its peculiar biology that has led to a high ecological specialization (Gangoso *et al*. 2013). More specifically, Eleonora's Falcon breeds colonially on rocky islets and sea-cliffs of larger islands scattered in the Mediterranean Sea and Macaronesia. Its population amounts to 29,200-29,600 individuals (Birdlife International 2018) distributed unevenly across its breeding range; hosting ca 85% of its breeding population (Dimalexis *et al*. 2008), the Aegean Sea is considered the core of the species' breeding range (Walter 1979). During its delayed breeding season, namely from late July till late October, Eleonora's falcon takes advantage of an abundant food source, i.e. migratory birds passing from its breeding colonies in autumn on their way to their wintering grounds (Walter 1968, Ristow *et al*. 1983). Yet, throughout the rest of the year Eleonora's falcon feeds mainly on flying insects (Ristow 2004) and is thus considered in principle an insectivorous species (Walter 1979, Ristow 2004).

As in many migratory birds, the amount and quality of knowledge regarding the species' ecology has traditionally been biased towards the breeding season (Marra *et al*. 2015). Despite a prolonged pre-breeding period, which extends approximately from mid-April till late July, this stage of its annual cycle remains largely unexplored, because of the species' high mobility until oviposition in late July (Wink *et al*. 1991). Therefore, information on its foraging areas and diet during this period of the year is primarily derived from sporadic field observations (Mayol 1977, Besson 1982, Ristow & Wink 1992-1994, Ristow 2004, 2010, Xirouchakis 2005, Mas 2006). However, a recent telemetry study (Mellone *et al*. 2013a) provided the first detailed information on the pre-breeding movements

(from May until the onset of the breeding period) for a handful of individuals from the species' western range in Spain that confirmed the conclusions drawn from former field observations. Following a long journey of over 7,000 km undertaken with only a few brief stops (Kassara *et al*. 2012, Mellone *et al*. 2013b), the pre-breeding period is a crucial stage during which Eleonora's Falcons replenish their depleted fat reserves, especially so breeding falcons which during this period have to feed adequately for the upcoming, also energetically-demanding, breeding period, find suitable nesting sites and mating pairs.

The absence of Eleonora's Falcons from their colonies during the pre-breeding period (Ristow & Wink 1992-1994) could be the rule across its breeding range, given that most colonies occur on small islets that typically offer sparse food resources during this period of the year (Wink *et al*. 1991). However, the bulk of the Greek breeding population is concentrated in a few islands (Dimalexis *et al*. 2008) that are significantly larger and probably with a higher food availability during the pre-breeding season compared to those lying at the western breeding range of the species. Herein, we explore the hypothesis that relatively large islands that host breeding colonies of the Eleonora's Falcons are important foraging areas for that species during the pre-breeding period, as implied by non-systematically collected field observations. We investigate, for the first time, the activity patterns of Eleonora's Falcons during the early pre-breeding period, i.e. April-May, based on regular field surveys on the island of Antikythira, which hosts one of the largest and densest colonies of Eleonora's Falcon worldwide (Dimalexis *et al*. 2008).

MATERIALS AND METHODS

Study area

Lying in the eastern Mediterranean Sea the island of Antikythira is a relatively hilly island located half way between the islands of Kythira and Crete with a maximum altitude of nearly 400 m a.s.l. and a surface area of ca 20 km^2. The island is mainly vegetated by phrygana and maquis, whereas cultivations currently extend over a small part of the island. Apart from some sparse cultivated trees, such as olive and almond trees, the maquis vegetation encountered on the island is rather low due to goat grazing. The island of Antikythira and its surrounding islets host a unique assemblage of biodiversity, partly own to their geographic proximity to the mainland (i.e. Peloponnese and Crete), and have thus been designated as a Site of Conservation Interest (GR3000008). In addition, given their importance as staging and breeding areas for birds they have been also designated as a Special Protection Area (GR3000012) and an Important Bird Area (GR130). Lying between the European continent and the ecological barrier formed by the Mediterranean Sea and the Sahara Desert, the island of Antikythira is a stopover site for many passerine and near-passerine species during both southward and northward migration seasons (Barboutis *et al*. 2011a, 2011b).

Field surveys

Following the arrival of the Eleonora's Falcons in the study area for a 3-year period (late April-late May 2015-2017) we conducted field surveys to record the number of falcons that are present on the island, as well as their activity patterns in 500m x 500m grid cells covering the entire surface of the island (Fig. 1). Since the nesting sites of the falcons are located on steep sea-cliffs, the surveys were conducted only in grid cells covered by less than 30% sea in order to exclude individuals whose presence was rather related to nest-site selection (i.e. 42 out of a total of 114 grid cells were excluded). The surveys took place from 8 am to 1 pm and from 5 pm to 7 pm (local time, GMT+3), i.e. during the period of the day that falcons are typically observed in the study area. More specifically, we recorded the birds' behavior in each grid cell every 5 min using the scan method (Altmann 1974) for a period of 30 min (6 scans per survey). In order to avoid double counting of the observed falcons, adjacent grids were not surveyed sequentially. To ensure that the recorded falcons were within a given grid, landmarks denoting the edge of a given grid were used. A modification of the flight categories described in Hedenstrom *et al*. (1999) was used to classify the behavior of each observed falcon in five categories: "foraging" (mixed-type flights in circuitous pattern or systematic straight-line flights in flapping mode), "soaring" (soaring flights in circular patterns), "transect flight" (straight-line flights in high altitude), "perching" and "other" (antagonistic behavior, displaying). Multiple grid cells were surveyed daily by 1 or 2 observers (mean=4.06, range=1-13 surveys per day).

The sex of the observed falcons could not be determined during the field surveys. Thus, as an index of its relative proportion during the early pre-breeding season we used the sex ratio of the falcons trapped at the study area as part of an independent study. In particular, the falcons were trapped using mist nets at a complex of small natural freshwater ponds between 1st of May and 27th of May 2016-2018.

To gain a better understanding on the contribution of birds on Eleonora's Falcon diet, during the spring season of 2016-2017 all confirmed indications of foraging or foraging attempts of the Eleonora's Falcons on other bird spe-

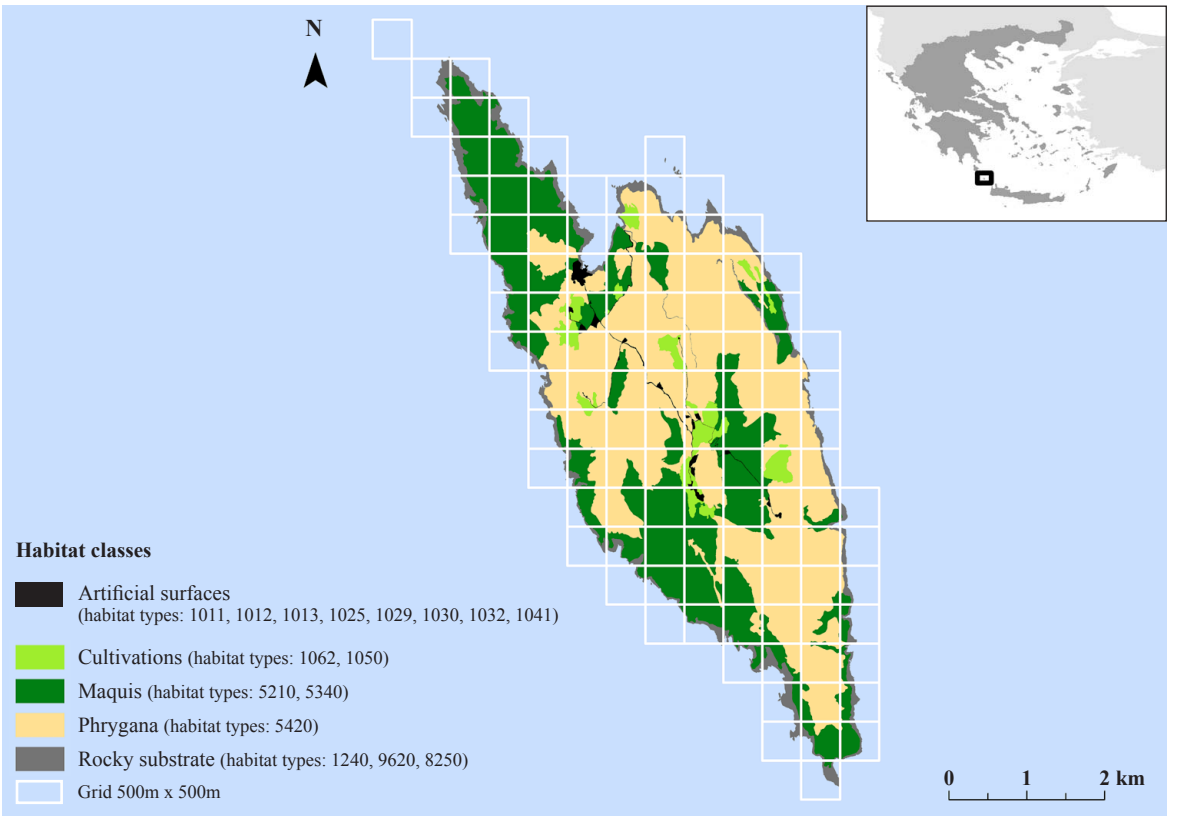

Figure 1. Habitat composition and location of the study area.

cies were recorded opportunistically. Only observations where it was clear that the falcons were either attacking a bird or seen preying on birds were recorded.

Statistical analyses

For each 30min survey we estimated the maximum number of falcons displaying a certain behavior type during the six snapshot scans. In continuation, we assigned each survey to the period of the day it was conducted, namely "morning" (8 am - 11 am), "midday" (11 am - 1 pm) and "afternoon" (5 pm - 7 pm), and we tested for statistically significant differences in the timing of each behavior type via χ^2 tests.

Moreover, we explored whether the abundance of foraging falcons varied as a function of the habitat types present on the island, the period of day the survey was conducted (as above) and the mean minimum air temperature during each period of the day, following the modelling procedure described hereupon. Considering that (a) Eleonora's Falcon depends mainly on insects during the study period and (b) insect phenology depends on diurnal variation of ambient temperature (Chen *et al*. 2015), we considered the period of the day and the minimum air temperature as important factors affecting insect activity. Temperature data were recorded on an hourly basis at a local meteorological station operated by the National Observatory of Athens. In addition, given that landscape composition affects the demographics of insects (Neokosmidis *et al*. 2018) we also included the effect of habitat type in our modelling procedure. Habitat types were provided by the latest monitoring Natura 2000 project (NCMA 2017). For the purpose of this analysis we reclassified the original habitat types (NATURA 2000 coding scheme) into five classes, namely "artificial areas" (habitat types 1011-1041), "cultivations" (habitat types 1050, 1062), "maquis" (habitat types 5210, 5340), "phrygana" (habitat type 5420) and "rocks" (habitat types 1240, 8250, 9620) (Fig. 1). Then, we estimated the percent cover of each habitat class in each grid cell and classified it into three cover classes; low (percent cover >20%), medium (percent cover 20%-70%) and high (percent cover >70%).

During the 3-year study period all grid cells were surveyed at least once (mean=1.69, range=1-3 years), while more than one surveys were conducted in each grid cell

on an annual basis (N=1-4 surveys per year). In a few cases (N=13) where there were multiple surveys in the same grid cell within the same year and in the same period of the day, we retained the one with the highest count and discarded the remaining ones(s). In order to account for the high number of zero observations (i.e. absence of foraging falcons during the field surveys), we built mixed zero-inflated models (Zuur *et al*. 2009) with random intercepts, a negative binomial distribution and a log link function. For each habitat class (but for "artificial areas", whose percent cover was classified as "low" in all surveyed grid cells), we built separate models (hereafter, habitat models). We considered as fixed terms the main effects of period of the day, mean minimum temperature and percent cover of the corresponding habitat, as well as the interaction of the latter with the period of the day. We also added Julian day and the grid cell code as random factors. We followed a backward stepwise elimination procedure, according to which the exclusion of a term from each model was assessed via likelihood-ratio tests, to decide on the final structure of the model (Zuur *et al*. 2009).

All statistical analyses were performed in R v3.4.4 (R Core Team 2018) using the 'glmmTmB' package (Brooks *et al*. 2017). Statistical significance level was set at α=0.05. Mean values and standard deviations (SD) are given.

RESULTS

After data filtering, we analyzed data from a total of 251 surveys, corresponding to 2,475 field observations. During the 3year study period a total of 767 Eleonora's Falcons were observed, most of which were foraging (55.28% of observations, χ^2=720.960, df=4, p<0.05), followed by soaring (24.77%). Concerning the timing of each behavior type, foraging was most common in the morning and soaring at midday, while the frequency of the remaining behavior types did not present statistically significant variability during the day.

Based on our classification scheme the island is mainly covered by phrygana (52%) and maquis (35%), while rocks, cultivations and artificial areas are very limited, namely covering 8%, 4% and 1% of the island, respectively. According to the results of the model building process, only the habitat model for the habitat class "cultivations" contained the corresponding percent cover in its final structure. The remaining habitat models contained only the period of day and the mean minimum temperature, suggesting that their corresponding percent cover did not influence the abundance of foraging Eleonora's Falcons. Thus, hereafter we present and discuss only the results of the habitat model for "cultivations". More specifically, during the study period the abundance of foraging falcons was positively affected by the increase in the mean minimum air temperature and was significantly higher in grids with a medium percent cover of cultivations compared to those with a low percent cover, yet less so during midday and afternoon (Table 1).

Sixteen cases of Eleonora's Falcons attacking or preying on migrant birds were recorded in spring 2016 and 2017 (Table 2). Based on the results of a simultaneous independent ringing study in the study area (ABO unpubl.) the timing of the bird hunting events in 2016 coincided with the peak of migrant birds captured in the mist nets, while in 2017 the spread of these events was more uniform and did not seem to be associated with the shifts in the abundance of migrant birds.

Sex-ratio data derived from trapping surveys in the study area (14 days during May 2016-2018) suggest that males outweigh females during the early pre-breeding period (67.3% males vs 32.7% females, N=52).

DISCUSSION

Based on the findings of the present study, the island of Antikythira, apart from its significance as a breeding site, should also be considered an important foraging area for Eleonora's Falcons during the early pre-breeding period. Eleonora's Falcons are particularly abundant over areas hosting cultivations, especially so in the morning compared to midday and afternoon. Their abundance seems to be also modulated by weather conditions; more falcons are likely to be observed in the study area during days with higher minimum temperatures. This spatio-temporal activity pattern reflects well the species' insectivorous diet during this period of the year. A few extended cultivated areas (i.e. of medium percent cover in the 500m x 500m grid cells) are concentrated in the central part of the island. This part of the island is the most heterogeneous in terms of habitat composition, consisting of grid cells occupied by three habitat classes, namely phrygana, maquis and cultivations, but for one grid cell covered only by cultivations and phrygana). Hence, this spatially localized mosaic could indeed host a relatively higher number of insects compared to the rest of the island (Solé-Senan *et al*. 2018). Nonetheless, Eleonora's Falcons could also be attracted to cultivated areas not only to hunt on insects but also on staging migrant birds. The latter could indeed complement the species' diet, given their (a) high abundance in the morning and in cultivated areas, as revealed from ringing and point count surveys conducted as part of an independent study during the same study period (LIFE El-

ClimA 2017a), and (b) the timing of recorded bird hunting events by Eleonora's Falcons that coincided with the peak of migrant birds ringed in the study area, especially so in 2016. We should point out here that ca 97% of the bird species that stopover in the study area in spring are insectivorous, thus are expected to have similar habitat preferences with Eleonora´s Falcons during this time of the year. If insects were the exclusive food source of Eleonora's Falcons, this would have been supported by an increase of foraging falcons during midday. On the contrary, our findings suggest a drop in their numbers in midday compared to morning.

As revealed by previously published tracking data, three Eleonora's Falcons originating from western Mediterranean colonies were mainly attracted to forests during the pre-breeding period located several hundred kilometers away from their colonies (Mellone *et al*. 2013a). Their movement patterns confirmed that the falcons spend a considerable amount of time away from their colonies, visiting insect-abundant areas, mainly coniferous and broad-leaved forests. In addition, they provided for the first time evidence on the connectivity of these foraging areas with the falcons' breeding/natal colonies, their site fidelity to these areas and the range of their pre-breeding movements. A similar pattern seems to hold true for two female Eleonora's Falcons originating from our study area (LIFE ElClimA 2017b). Yet, the tracking data that are available to date pertain to a limited number of falcons, almost exclusively from females (4 female breeders and one immature falcon), and as a consequence the ecology of male breeders during the pre-breeding period remains largely unknown. Despite the fact that we could not determine the sex, breeding status or the breeding origin of the observed falcons, the data presented in this study provide evidence of regular foraging activity in the study area during the pre-breeding period. The higher frequency of males compared to females in the study area during the pre-breeding period, as revealed by independent trapping surveys, agrees with the expected labor division between the two sexes during this time of the year. If male falcons are mainly responsible for nest-site selection and subsequent defense, their pre-breeding movement range could indeed be more restricted to the

Table 1. Mixed zero-inflated model results describing the relationship between the abundance of foraging Eleonora's Falcons and the mean minimum air temperature (Tmin) during three periods of the day (pMorning = morning (reference level), pMidday, pAfternoon) and the percent cover of cultivations (lowCultiv = low (reference level), mediumCultiv = medium). The model terms that comprised the final GLMM were chosen following a backward stepwise elimination procedure.

Model terms	Estimate	Standard error	p-value
Intercept	-2.515	1.345	0.061
Tmin	0.152	0.070	0.030
pMidday	-0.103	0.264	0.696
pAfternoon	-0.296	0.267	0.268
mediumCultiv	1.688	0.512	0.001
pMidday x mediumCultiv	-1.872	0.632	0.003
pAfternoon x mediumCultiv	-2.691	1.037	0.009

Table 2. Opportunistic observations of Eleonora's Falcons foraging on bird species in spring 2016 and 2017.

Date of observation	Foraging output	Foraged species
6/5/2016	Successful	Unknown
7/5/2016	Unsuccessful	*Riparia riparia*
8/5/2016	Unsuccessful	*Hirundo rustica*
11/5/2016	Unsuccessful	Unknown
14/5/2016	Successful	Unknown
16/5/2016	Unsuccessful	Unknown
3/5/2017	Successful	Unknown
7/5/2017	Successful	Unknown
11/5/2017	Unsuccessful	*Hirundo rustica*
14/5/2017	Unsuccessful	Unknown
19/5/2017	Unsuccessful	*Delichon urbicum*
19/5/2017	Unsuccessful	*Delichon urbicum*
19/5/2017	Unsuccessful	*Oriolus oriolus*
20/5/2017	Successful	Unknown
25/5/2017	Successful	Unknown
28/5/2017	Successful	*Delichon urbicum*

vicinity of the colonies, hence their more regular occurrence on the island of Antikythira.

As mentioned the majority of the Greek breeding population is concentrated in a few islands, featuring the islands of Antikythira (our study area), Psara, Skyros, Tilos, Astypalea and Alonisos that are at least 2000 ha and host more than 300 pairs each during the breeding period (LIFE ElClimA 2016, HOS unpubl.). Judging by the regular presence of Eleonora's Falcons during the pre-breeding period not only in our study area but also at least in some of these islands (e.g. Skyros) we postulate that such large islands do not only constitute important nesting grounds but also foraging areas, given local food availability, before the onset of the breeding period (Scetaric Legan & Piasevoli 2005). Even though systematic insect surveys are currently lacking, judging by the habitat composition of adjacent areas (e.g. Peloponnese, Crete; https://land.copernicus.eu/pan-european/corine-land-cover/clc2018) that include among others forested areas and water bodies that typically attract flying insects (Vimal *et al*. 2017), overall our study area is expected to host a significantly less abundant insect fauna. Therefore, the phenological match between the occurrence of Eleonora's Falcons and numerous staging migratory birds on the island of Antikythira could suggest a more influential role of the latter in Eleonora's Falcon feeding ecology during the early pre-breeding period.

In fact, the relative contribution of vertebrates and invertebrates in Eleonora's Falcon feeding habits has not been studied in detail to date and could vary within seasons in finer temporal scales according to food availability. For example, it has been shown that insects may complement or even substitute the species' diet during the breeding season, especially so in windless days when the abundance of migratory birds drops significantly (Ristow *et al*. 1983). Similar fine-scale variability in food preferences is likely to persist beyond the species' breeding season depending on the seasonality of food sources locally, as also reported in a colony on islets located in NE Crete (Ristow & Wink 1992-1994). Compared to the Cretan islets, our study area is substantially larger and represents one of the most important staging areas for migrant birds in the country during the spring season. Thus, hunting on migrant birds could be more frequent for being locally more abundant.
Still, agricultural abandonment, which in our study site has led to loss of habitat heterogeneity and overgrazing, could exert pressure to both food sources during the early pre-breeding period. The island of Antikythira represents a typical example of ongoing depopulation and population ageing that occurs on various Mediterranean islands with profound effects on land management (Petanidou *et al*. 2008). The once diverse crops cultivated in the study area, covering nearly 50% of its surface during the first half of the 19th century (Bevan *et al*. 2013), have been since progressively abandoned and recolonized by wild vegetation (Palmer *et al*. 2010), i.e. phrygana and maquis.

Based on our findings we recommend a detailed investigation of insect abundance patterns in the future in order to shed more light into the relative contribution of the bird and insect fauna to the feeding habits of the species during the pre-breeding period in the study area. Furthermore, we encourage the investigation of activity patterns of Eleonora's Falcons on other islands where the species is regularly observed during the pre-breeding period to contribute to the understanding of its habitat requirements year-round and any sex-related variability in its distribution pattern. To this end, extensive telemetry studies should be prioritized for providing detailed spatiotemporal data. Last but not least, considering the preference of both Eleonora's Falcons and staging birds over cultivated areas and the fact that the study area hosts one of the largest colonies of the former worldwide, we emphasize on the importance of the preservation of the remaining patches of cultivations on the island of Antikythira for a successful, long-term management of its bird fauna.

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