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Factors influencing the occurrence of Eleonora's falcon *Falco eleonora* breeding colonies on Greek islands

Christina Kassara, Jakob Fric & Spyros Sfenthourakis

During the breeding seasons of 2004-2006, the population of Eleonora's falcon *Falco eleonora* was censused on > 900 islands in the Ionian and the Aegean Seas, Greece. However, only one third of the islands hosted breeding pairs. With our study, we aim at understanding the factors that influence the occurrence of the species' breeding colonies on Greek islands. Thus, we developed generalised linear models for all candidate explanatory variables that according to previous studies are believed to influence the occurrence of the species. We identified the best set of models based on differences in the Akaike Information Criterion, and subsequently, we applied model averaging to estimate model average coefficients for those explanatory variables included in the best set of models. According to our results based on presence-absence data from approximately 370 islands, the presence of breeding colonies is related to the coastline geomorphology, where steep cliffs with ledges are preferred. These geomorphologic characteristics are considered to offer protection from wave action and terrestrial intruders, as well as visual privacy to breeding pairs, and they have previously been associated with nest-site selection. In addition, breeding colonies are more likely to be found on islands close to freshwater bodies and to other neighbouring colonies. Freshwater bodies constitute important foraging areas and provide a means to maintain the falcons' plumage in good condition. The clustered distribution pattern of the breeding colonies is probably due to the process of first-time breeders' settlement and/or colony connectivity. Finally, in view of these preliminary results, we recommend actions to be taken in future studies in order to better understand the role of these factors during the species' breeding period.

Key words: breeding season, colony connectivity, Eleonora's falcon, *Falco eleonora*, freshwater bodies, geomorphology, Greece, model averaging

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Eleonora's falcon *Falco eleonora* is a summer visitor of the Mediterranean Sea and Macaronesia. Falcons of breeding age leave their wintering grounds in Madagascar and the surrounding islands in early spring (Gschweng et al. 2008, López-López et al. 2010, Mellone et al. 2011, Kassara et al. 2012b), and arrive a month later at their breeding grounds. However, egg laying does not occur before July (Walter 1979b). In the meantime, the falcons wander

several kilometres away from their breeding colonies in search of insects, their main food source during that period of the year (Ristow 2004, Mas 2006).

The global population of the species has been assessed very recently and has been estimated at ca 15,000 pairs, with > 80% found in the Aegean Sea, Greece (Dimalexis et al. 2008). In spite of decreasing population trends at the local level, Eleonora's falcon is listed as 'Least Concern' due both to the

size of its world population and to the large extent of its geographic range (IUCN 2011). Still, taking into account that its breeding colonies are concentrated on a few islands spread out across the species' geographic range (Walter 1979a), and that its breeding season coincides with the peak of tourist activity in these areas (Ristow 1999), the viability of Eleonora's falcon colonies can be challenged by human activities and/or negligence (Ristow 1999, Martínez-Abraín et al. 2002). In addition, the ongoing efforts for targeted conservation measures and public awareness campaigns for the species (Fric 2007) are confronted with inadequate coastal management practices in the Mediterranean Sea (De Vivero & Mateos 2005, Shipman & Stojanovic 2007). Mismanagement of biotopes, especially of wetlands, as well as uncontrolled urban expansion on Greek islands (Catsadorakis & Paragamian 2007) could pose an additional obstacle to practices aiming to sustain the population of Eleonora's falcon in Greece. Long distance migrants, such as Eleonora's falcon, are affected by events occurring both at their breeding and wintering grounds (Newton 2004). Thus, understanding the biotic and abiotic factors that play a key role during the species' life cycle is essential for efficient management practices in the long run (Ristow 1999).

In contrast to past studies, modern technological advances and geostatistical procedures have proven to be valuable tools in the study of the species' biology and ecology at broad spatial and temporal scales. For instance, in recent years, the emergence of telemetry techniques has brought new data concerning the migratory period of this long-distance migrant (e.g. Gschweng et al. 2008, López-López et al. 2009, Kassara et al. 2012b) as well as into the habitat requirements at its wintering grounds (Gschweng et al. 2012, Kassara et al. 2012b, Mellone et al. 2012). At the same time, GIS methods and environmental data available in digital format have facilitated scientists in the understanding of the role of biotic and abiotic factors during the species' breeding period, as well as on wintering grounds. In particular, one study (Urios & Martínez-Abraín 2006) in the western and another two (Kassara et al. 2012a, Xirouchakis et al. 2012) in the eastern Mediterranean islands highlighted the importance of vegetation cover, presence of neighbours, topography, micro-climate and human activity in nest-site/territory selection and reproductive performance of the species.

In our study, we take advantage of these method-

ological advances, as well as of recently gathered data on the distribution of the species' breeding colonies in Greece (the LIFE-Nature Project "Conservation measures for *Falco eleonora* in Greece" LIFE 03NAT/GR/000091), in order to move a step forward in understanding the species' ecological requirements within its breeding grounds. In particular, we investigate the occurrence of breeding colonies at the island level within the centre of the species range, i.e. the Greek archipelagos. We explore factors related to the topography of the island coastline and to the landscape configuration around the islands aiming to pinpoint those that can be used as proxies of the presence of Eleonora's falcon breeding colonies on Greek islands.

Material and methods

Data preparation

During the breeding seasons of 2004-2006, 965 islands, with a total coastline of ca 6,000 km, were surveyed by boat in order to census the breeding population of Eleonora's falcons in the Ionian and Aegean Seas (Dimalexis et al. 2008). In total, 249 breeding colonies were located on 307 islands via boat surveys hosting 12,299 breeding pairs (for a detailed description of the fieldwork process, see Dimalexis et al. 2008). These breeding colonies were distributed unevenly in the Greek archipelagos, with just five in the Ionian Sea and 302 in the Aegean Sea (Dimalexis et al. 2008). Based on these data, we modelled the occurrence of breeding colonies on Greek islands as a function of the topography, presence of neighbouring colonies and the landscape configuration in adjacent areas (Table 1). In particular, we calculated the mean values of elevation, curvature and slope along the coastline of each island based on a Digital Elevation Model at a resolution of $90 \times 90 \text{ m}^2$ (Jarvis et al. 2008). In addition, we used the Corine Land Cover 2000 database (European Environment Agency 2008) to calculate the percentage of each land-cover type occurring within a buffer zone of 1, 5, 10 and 25 km around each island. Taking into account the level 1 and level 2 classification scheme, we considered the following land-cover classes for the subsequent analyses: forest (codes 311-313), artificial surfaces (codes 111-142), agriculture (codes 211-244), sparse vegetation (codes 331-335), scrubland (code 321-324), freshwater bodies (codes 411, 412) and maritime wetlands (codes 421-423). Finally, we estimated the distance between each

Table 1. Description of the explanatory variables used for modelling the occurrence of Eleonora's falcon breeding colonies on Greek islands.

Explanatory variable	Abbreviation	Description
Topography		
Elevation	ELV	Average elevation along the coastline (m)
Slope	SLP	Average terrain slope along the coastline (degrees)
Curvature	CRV	Average terrain curvature along the coastline, where negative values represent concave surfaces
Land cover		
Forest	FRT	Percentage cover of forested areas within 1, 5, 10 and 25 km radius around each island
Artificial	ART	Percentage cover of artificial areas within 1, 5, 10 and 25 km radius around each island
Agriculture	AGR	Percentage cover of cultivated areas within 1, 5, 10 and 25 km radius around each island
Sparse vegetation	SPR	Percentage cover of sparse vegetation within 1, 5, 10 and 25 km radius around each island
Scrubland	SCR	Percentage cover of scrubland within 1, 5, 10 and 25 km radius around each island
Freshwater bodies	INW	Percentage cover of freshwater bodies within 1, 5, 10 and 25 km radius around each island
Maritime wetlands	MRW	Percentage cover of maritime wetlands within 1, 5, 10 and 25 km radius around each island
Biotic factors		
Nearest neighbour	NND	Distance from nearest island hosting a breeding colony (m)

island and its nearest island hosting a breeding falcon colony. Given the resolution of the available topographical data, we excluded islands $< 0.081 \text{ km}^2$, thus feeding the subsequent analyses with 371 islands out of 965 surveyed in total during the LIFE-Nature Project "Conservation measures for *Falco eleonora* in Greece" (LIFE 03NAT/GR/000091; Dimalexis et al. 2008). Of these islands, 171 hosted breeding colonies totaling 2,145 pairs, i.e. 17% of the total Greek population estimated during the census (Dimalexis et al. 2008).

Prior to model building, we examined the level of correlation among the candidate explanatory variables. In the presence of multicollinearity (i.e. Variance Inflation Factor > 10) among the candidate explanatory variables, we ran a Principal Component Analysis and subsequently replaced any group of highly intercorrelated variables by their corresponding principal component factor (Graham 2003). In particular, only the variables 'Elevation' and 'Slope' were found to be highly intercorrelated; hence, during the model building process, we used their first principal component factor ('PES'), to which both variables were positively correlated.

Model building

We modelled the occurrence of breeding colonies using generalised linear models (GLM; McCullagh & Nelder 1989) with a binomial error distribution and a logit link function.

We explored the relationship between the occurrence of a breeding colony on a given island and all candidate explanatory variables in every possible combination using the Akaike Information Criterion

(AIC). In each case, apart from the aforementioned explanatory variables, we included a second degree polynomial of the standardised values of coordinates of the centroid of each island to address problems arising from the spatial autocorrelation observed both in the response variable, i.e. occurrence of breeding colonies, and the model residuals (Lichstein et al. 2002, Dormann et al. 2007). Since no single model was observed to dominate (i.e. $\Delta\text{AIC} \geq 6$), a model averaging procedure was used to obtain parameter estimates (Burnham & Anderson 2002). Apart from the model with the lowest AIC, only those models with $\Delta\text{AIC} < 6$ (hereafter called best set of models) were retained for model averaging using Akaike weights (Johnson & Omland 2004). First, we summed the Akaike weights for all models containing a given explanatory variable to assess the strength of evidence for that particular explanatory variable, in which case that explanatory variable with the largest weight was considered the most important one. In continuation, we weighted the parameter coefficient (β) for every variable based on the Akaike weight of the model containing that explanatory variable and then, we estimated the sum of the weighted parameters for that explanatory variable across models (model average coefficient). The higher the absolute value of the model average coefficient for a given explanatory variable, the greater its magnitude effect on the dependent variable, i.e. the probability of colony occurrence. In addition, we calculated Moran's I to check for spatial autocorrelation of residuals for each model in the best set of models (Dormann et al. 2007). We assessed the validity of the model average coefficients for each of

the best set of models using unconditional standard errors (Gibson et al. 2004). Finally, we also calculated Cook's distance to identify outliers (i.e. Cook's distance > 1).

Model evaluation

For each model comprising the best set of models, we assessed its discriminatory power and model accuracy by testing the agreement between the observed and predicted occurrence of breeding colonies by means of two different threshold-independent measures; namely the Area Under Curve score (hereafter AUC) and the biserial point correlation coefficient (hereafter COR), respectively. Being a rank-based measure, AUC does not account for the degree to which the predicted values have been calibrated. In contrast, COR considers whether big differences in predicted values correspond to big differences in probability of occurrence (Elith et al. 2006). For each model, we computed the aforementioned accuracy measures for an evaluation data set comprising 30% of the available data, while we used the rest as a training data set for model calibration (Huberty 1994 in Fielding & Bell 1997). For each model, we conducted data partitioning ten times at random, ensuring that prevalence, i.e. the percentage of occupied islands, remained constant across the resulting training and evaluation data sets.

Statistical analyses and model assessment were performed in SPSS 18.0 (SPSS Inc. 2009), while model development was conducted in R 2.12.1 (R Development Core Team 2010). All spatial analyses were implemented with the Spatial Analyst toolbox in ArcGIS 9.2 (ESRI 2006).

Results

According to the multimodel inference results and the resulting model average coefficients, the probability of occurrence of a breeding colony on a given island was associated, in descending order of importance, with 1) concave coasts, 2) increased percentage area covered by freshwater bodies within a 10-km radius, 3) elevated and steep slopes along the coastline and 4) close-by islands hosting colonies (Table 2). The presence of sparse vegetation on or within a close range to the island in question also appeared to influence the occurrence of breeding colonies; however, without a clear positive or negative effect (see Table 2).

Table 2. Multimodel inference results based on the best set of models ($\Delta AIC < 6$) for the occurrence of Eleonora's falcon breeding colonies on Greek islands. x = explanatory variable included in the model. Multimodel inference averages the three models comprising the best set of models using model weights (w_i). Values presented for the explanatory variables in multimodel inference are weighted averages of beta regression coefficients obtained in generalised linear models considering model weights w_i . AIC = Akaike Information Criterion. Σw_i = sum of Akaike weights for each explanatory variable. K = number of variables plus intercept (c). Explanatory variables: PES = principal component factor for elevation and slope. NND = distance to nearest island hosting a breeding colony. CRV = curvature. INW10 = percentage of inland freshwater bodies within a 10-km radius. SPR1 and SPR5 = percentage of sparse vegetation within a 1-km and 5-km radius, respectively. Longitude and latitude = standardised coordinates of the centroid of each island.

Model	AIC	ΔAIC	K	w_i	c	PES	NND	CRV	INW10	SPR1	SPR5	Longitude	Latitude	Longitude*latitude	Longitude ²	Latitude ²
1	322.7	0.00	11	0.49	x	x	x	x	x	x	x	x	x	x	x	x
2	323.1	0.34	11	0.41	x	x	x	x	x	x	x	x	x	x	x	x
3	325.8	3.10	10	0.10	x	x	x	x	x	x	x	x	x	x	x	x
Multimodel inference																
Σw_i	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.486	0.410	1.000	1.000	1.000	1.000	1.000
Model average coefficient	0.230	0.701	-0.087	-7.252	5.612	2.649	2.133	-0.066	0.123	0.164	-0.694	0.164	0.123	0.164	-0.694	0.462
SE	0.350	0.139	0.013	2.293	1.468	3.303	3.066	0.248	0.177	0.312	0.256	0.312	0.177	0.312	0.256	0.137
+95% C.L.	0.916	0.973	-0.061	-2.757	8.489	9.123	8.143	0.420	0.469	0.776	-0.193	0.776	0.469	0.776	-0.193	0.731
-95% C.L.	-0.456	0.429	-0.122	-11.747	2.734	-3.824	-3.876	-0.551	-0.223	-0.447	1.195	-0.447	-0.223	-0.447	1.195	0.193

As far as the evaluation of the best set of models was concerned, in almost 90% of the cases, all three models were able to discriminate between the true presence and absence of a breeding colony on a given island, while high values of predicted probability of occurrence were associated with true presence of breeding colonies most of the time (Table 3). The residuals of all three models showed no significant spatial autocorrelation (i.e. test of global Moran's I; $P > 0.10$), while no outliers were detected (i.e. Cook's distance < 1).

Discussion

It has long been known that Eleonora's falcon breeding colonies are distributed unevenly across the species' distribution range (Walter 1979a). This pattern has remained relatively unchanged over the years and has been attributed to a high philopatry of the species (Ristow et al. 1979). So far, the absence of breeding colonies from specific island groups was related to tourist development (Dolç-Garcia & Dies 1987, BirdLife Cyprus 2004), but systematic studies are currently lacking to support this.

The first nationwide population census in Greece, which took place during the breeding periods between 2004 and 2006 enabled us to investigate this pattern based on a data pool consisting of 371 islands. Our results suggest that the topography of the coastline, the proximity of islands hosting breeding colonies as well as the extent of freshwater bodies in the surrounding area influence the probability of occurrence of breeding colonies on Greek islands of substantial size (i.e. $> 0.081 \text{ km}^2$).

Terrain geomorphology at the nest-site/territory level has previously been associated with habitat suitability for nesting (Urios & Martínez-Abraín 2006, Kassara et al. 2012a). In particular, Eleonora's falcons on one uninhabited island in the Columbretes archipelago (Urios & Martínez-Abraín 2006) and on nine uninhabited islets in the Aegean Sea (Kassara et al. 2012a) prefer to nest in elevated areas that provide shelter from wave action (Urios & Martínez-Abraín 2006, Kassara et al. 2012a), in steep and concave slopes that ensure protection from terrestrial intruders (Urios & Martínez-Abraín 2006, Kassara et al. 2012a) and in areas of such topography that ensures visual privacy from anthropic zones (Urios & Martínez-Abraín 2006). Within the same study area in the Aegean Sea, the reproductive performance of the breeding pairs on 15 uninhabited islets was

Table 3. Predictive power of the models comprising the best set of models ($\Delta\text{AIC} < 6$) for the occurrence of Eleonora's falcon breeding colonies on Greek islands, according to the Area Under Curve score (AUC) and the biserial point correlation coefficient (COR) averaged over 10 evaluation data sets for each model. Standard deviations are reported in parentheses.

Model	AUC	COR
1	0.897 (± 0.016)	0.682 (± 0.027)
2	0.897 (± 0.017)	0.683 (± 0.028)
3	0.895 (± 0.021)	0.679 (± 0.036)

highest in well-sheltered nests, such as those under boulders, in rock cavities and in islet complexes that were located close to greener areas that presumably are richer in insects (Xirouchakis et al. 2012). In continuation of the aforementioned studies, here we showed that even at the island level the presence of breeding colonies is related to steep and elevated coasts with ledges and caves (i.e. concave coasts), which in turn provide good nesting sites at a smaller scale (Urios & Martínez-Abraín 2006, Kassara et al. 2012a).

We also demonstrated the effect of landscape configuration in the vicinity of the islands hosting breeding colonies. From the end of the spring migration until the first weeks of the breeding season, Eleonora's falcons are regularly observed hunting in areas with freshwater, either on the island where they breed or on nearby islands (Scetarić Legan & Piasevoli 2005). Freshwater bodies attract significant numbers of flying insects, such as dragonflies, upon which the species feeds at this time of the year (Ristow 2004, Mas 2006). Freshwater bodies such as wetlands, lakes and rivers, along with forested, herbaceous and cultivated areas, are typical foraging areas for Eleonora's falcons (Mayol 1977, Besson 1982, Ristow & Wink 1992-94, Xirouchakis 2005, Mas 2006). Moreover, freshwater bodies are also important for the required daily water intake by the falcons during the insect-feeding period given the lower water content of insects compared to birds. In addition, Wink et al. (1979) suggested that bathing in open water can help Eleonora's falcons dispose of ectoparasites that are commonly found on their plumage, while at the same time, it helps maintain the elasticity of their feathers (Ristow et al. 1980). In periods when water resources become scarce or the energetic cost of flight in search of water is prohibitive, bathing in open water could be replaced or complemented with sunbathing and dust bathing (Ristow et al. 1980).

To our knowledge, the effect of the proximity of

other occupied islands on the occurrence of breeding colonies has not been highlighted nor investigated before. It could reflect the choice of first-time breeders to settle on islands close to their natal colony taking advantage of familiarity with local environmental conditions (Ortego et al. 2008). Older, thus more experienced pairs settle early during the breeding season (Ristow & Wink 2004) taking over the most suitable nesting territories (Kassara et al. 2012a). In such cases, first-time breeders would have to either occupy inferior nesting sites or settle on nearby islands in order to avoid competition (Negro et al. 1997, Forero et al. 2002). Eleonora's falcons become sexually mature at the age of 2-4 years, while up to that age they tend to stay away from their natal colony (Ristow et al. 1983). Therefore, this hypothesis would imply that the first-time breeders have already been acquainted with areas around their natal colony either as fledglings (but see Olea 2001) or as prospectors before reaching sexual maturity (Boulinier et al. 1996, 2002, Sergio & Penteriani 2005) or during the pre-breeding period of their first breeding attempt (Danchin et al. 1998).

The fluctuation of the population size of certain Eleonora's falcon colonies over the years has been attributed to a variety of causes, such as the application of different census techniques, implementation (or not) of protection measures, human disturbance and predation (see Ristow 1999, López-Darias & Rumeu 2010). However, it is not possible to exclude the possibility of a dynamic exchange of individuals among neighbouring colonies in the framework of population regulation. The species is characterised as site tenacious (Ristow et al. 1979); yet in extreme cases, such as the deterioration of its breeding habitat, disturbance by human presence (Martínez-Abraín et al. 2002) or bad breeding experience in the previous year (Calabuig et al. 2008), some members of a colony might be forced to settle on nearby islands, a behaviour indicative of the presence of metapopulations. Colony connectivity has already been demonstrated for a relative of Eleonora's falcon, the lesser kestrel *Falco naumanni*, a raptor exhibiting both philopatric and dispersal behaviours within a population (Calabuig et al. 2008). The smaller the distance between breeding colonies, the higher the immigration rate, in spite of the lesser kestrel's dispersal ability (Ortego et al. 2008).

Our preliminary results stress the need to clarify the relation between the biology of Eleonora's falcon and the landscape in the surrounding areas,

as well as to investigate the process of colony connectivity and recruitment of first-time breeders. Hence, in view of our findings, we encourage future studies to monitor the movements of individuals, originating preferably from neighbouring colonies, with the use of modern telemetry technology, capture-recapture field processes (Ponchon et al. 2012) coupled with molecular analysis in order to investigate resource use during the species' pre-breeding and breeding season, as well as studying the mechanism of natal and breeding dispersal.

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