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Distribution modelling of Eleonora's Falcon *Falco eleonorae* Géné, 1839 occurrence in its wintering grounds: a niche-based approach with satellite telemetry data

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Summary

Eleonora's Falcon is a long-distance migrant of the Palearctic region. In recent years, the advent of satellite telemetry has enabled a more detailed investigation of the species's migratory and wintering periods. In this study, we model the distribution pattern of four Eleonora's Falcons originating from Greece within their wintering grounds in Madagascar with the use of satellite telemetry data and a niche-based technique, Maxent. The model predicted few highly suitable areas for the occurrence of the species, restricted to elevated areas receiving large amounts of precipitation during the wintering period, containing patches of primary and degraded humid submontane forests as well as cultivation. Most of these areas occurred within the previously estimated home ranges of the four falcons, as well as of three falcons from another independent study. Taking into account the ongoing alterations in landscape structure that occur within the eastern rainforest region of Madagascar, we believe that it is imperative to better understand the ecological requirements of Eleonora's Falcon. To this end, we recommend the application of Maxent in the study of habitat selection of the species that could be further refined with the inclusion of biotic interactions and seasonal resource availability.

Introduction

Eleonora's Falcon *Falco eleonorae* is a common breeder on islands and coasts of the Mediterranean Sea and Macaronesia, while during the winter (austral summer) it is mainly found in Madagascar and adjacent islands (Walter 1979). Although the species is classified as Least Concern (IUCN 2012), with the exception of its breeding period, the rest of its annual life cycle remained poorly studied until recently. Since 2008 the migratory journey undertaken by individuals from Italy, Spain and Greece (Gschweng *et al.* 2008, López-López *et al.* 2009, López-López *et al.* 2010, Kassara *et al.* 2012, Limiñana *et al.* 2012) was revealed with the aid of satellite telemetry. This new technology has also enabled scientists to investigate the species's wintering habits on a quasi-daily basis for the first time (Gschweng *et al.* 2012, Kassara *et al.* 2012, Mellone *et al.* 2012), a task that would have been almost impossible with traditional field surveys (but see Zefania 2001).

In a previous study, we showed that four falcons originating from Greece tended to occur more often in the humid submontane forests of Madagascar during the wintering period 2009–2010, in spite of individual variability in space-use (Kassara *et al.* 2012). The findings of two recent studies have revealed a similar distribution pattern for three Spanish (Mellone *et al.* 2012) and seven Italian Eleonora's Falcons (Gschweng *et al.* 2012). According to their results, the occurrence in the north and northeastern part of the country is associated with the climate of the area (Gschweng *et al.* 2012) in addition to particular habitat types (Mellone *et al.* 2012).

In view of these findings, herein we extend our previous work by considering not only the vegetation, but also the topography and climatic conditions in Madagascar to better understand the ecological requirements of the species during the wintering period. In particular, we used a niche-based technique, Maxent (Phillips *et al.* 2006), to model the distribution pattern of four Eleonora's Falcons previously tagged with solar transmitters (see Kassara *et al.* 2012 for a detailed description) within their wintering grounds in Madagascar. Maxent is a niche-based method that has recently gained popularity since (a) it doesn't require absence data for model-building, (b) it performs well even at small sample sizes and (c) it can reconstruct non-linear, complex interactions between the response variable and a set of environmental variables (Elith *et al.* 2006). In spite of the fact that the cost of satellite transmitters remains an obstacle for large-scale projects that would otherwise allow for sound inferences at the population or even at the species level, such methodological approaches allow for the description and quantification of habitat selection even with small and unbalanced sample sizes. Maxent is well adapted to satellite telemetry data (Edrén *et al.* 2010, Friedlaender *et al.* 2011, Jiguet *et al.* 2011, Gschweng *et al.* 2012), which, coupled with proper data sub-sampling in cases where a small number of individuals have been tracked (Edrén *et al.* 2010), makes it a powerful tool for the investigation of species-habitat relationships or even for the development of effective and targeted field surveys. The landscape of Madagascar has been greatly altered since humans colonised the country and the majority of the pristine rainforests has been clear-felled (Green and Sussman 1990, Harper *et al.* 2007) for shifting cultivation and logging (Jarosz 1993). Although the rate of deforestation has slowed down in recent years (Conservation International *et al.* 2007), forest fragmentation still remains a challenge (Harper *et al.* 2007). Taking into account methodological challenges in classical habitat selection studies due to the restricted number of tracked individuals, if successful, our methodological approach will facilitate future monitoring schemes as well as conservation practices (Gschweng *et al.* 2012). Thus, to this end, we tested model transferability by contrasting model predictions with the 95% and 50% home range areas formerly estimated for the three Spanish Eleonora's Falcons in the independent study by Mellone *et al.* (2012).

Methods

Data preparation

Out of 2,204 telemetry locations received in total via the Argos system during the wintering period 2009–2010 for four Eleonora's Falcons from Greece (Kassara *et al.* 2012), we restricted the data pool to 561 locations of high positional accuracy (i.e. LCs 1–3) for the subsequent analyses. In particular, we excluded locations received two days after/prior to arrival/departure from the wintering grounds (Gschweng *et al.* 2012). With the aim of reducing spatio-temporal autocorrelation, we considered consecutive locations that were received outside a two-hour window and located at least 1,000 m apart. In order to achieve equal representation of the four falcons in the resulting data pool, we created random subsamples of the available telemetry locations per bird that equalled the number of locations of the animal with the smallest sample size (i.e. 34 locations; Edrén *et al.* 2010). We repeated the procedure 100 times with replacement, which resulted in 100 subsamples of telemetry locations for the subsequent analyses. We also generated a random 'pseudo-absence' data set of 10,000 points across the landscape of Madagascar with the Hawth's Tools extension for ArcGIS 9.2 (Beyer 2004), subject to the constraint that they be located at least 1,000 m apart from each other as well as from the telemetry locations. In continuation, we overlaid a grid of 1 km x 1 km resolution that covered the entire country and considered every grid cell containing at least one telemetry location as 'presence cell' and every grid cell containing at least one 'pseudo-absence' point as 'background cell' for model-building for each of the 100 subsamples.

Eleonora's Falcon is an insectivorous species during most of its annual cycle (Ristow 2004). It has been repeatedly observed hawking insects near wetlands, lakes, rivers, as well as over forested, herbaceous, and cultivated areas during the breeding season (Mayol 1977, Besson 1982, Ristow and Wink 1992-94, Xirouchakis 2005, Mas 2006), the migration season (Archer 1937 in Stresemann 1954; references in Ristow and Wink 1992–94) and at its wintering quarters (Thorstrom and Rene de Roland 2000, Zefania 2001). In addition, according to two previous studies, during the wintering periods 2008–2009 and 2009–2010 the four falcons from Greece as well as three falcons from Spain were mainly distributed in high altitude areas in Madagascar (Gschweng *et al.* 2012, Kassara *et al.* 2012, Mellone *et al.* 2012). Therefore, we considered as candidate predictors of habitat suitability for the occurrence of Eleonora's Falcons across Madagascar the elevation, slope and aspect of the terrain, as well as the percentage of land cover within each grid cell (Table 1). We extracted the aforementioned topographical variables from a Digital Elevation Model of 90 m x 90 m resolution (http://srtm.csi.cgiar.org/) and calculated their corresponding mean values within each 1-km^2 grid cell. We also used a vegetation raster layer of 29 m x 29 m resolution produced by the Madagascar Vegetation Mapping Project (http://www.kew.org/gis/projects/mad_veg/datasets.html) to calculate the percentage of each land cover class within each 1-km^2 grid cell. We only considered those vegetation classes that were present within the presence cells for model building. We also considered the mean climatic conditions during the wintering period, from November to April (WorldClim database, Hijmans *et al.* 2005). As in Gschweng *et al.* (2012), we calculated the average and extreme values for the mean, maximum and minimum monthly temperature, as well as for the monthly precipitation, for each 1-km^2 grid cell (Table 1).

Model building

We first checked for the existence of multicollinearity among the candidate predictors, which could potentially overshadow the effect of a particular predictor, by calculating Spearman's correlation coefficient (r). Then we contrasted the landscape configuration within the presence and background cells using Maxent 3.3.3k (Phillips *et al.* 2006). In particular, we trained the Maxent model with 75% of each presence sub-sample (training data set) and evaluated its predictive performance with the remaining 25% (test data set). Data splitting was conducted at random once per presence subsample. We ran Maxent under default settings, except that we set the regularisation parameter (β) to 2 in order to reduce over-fitting given the restricted number of animals (Elith *et al.* 2011). We also increased the number of maximum iterations to 2,000 to achieve algorithm convergence. We chose the logistic output, which approximates the output of logistic regression, but rather than estimating directly the probability of occurrence of a target species, it quantifies habitat suitability for its occurrence across the study area in question (Phillips *et al.* 2006), i.e. Madagascar.

During model training, variable selection was based on a jackknife procedure which evaluates the explanatory information in each variable when used in isolation and the information lost when omitted from a given model. The same jackknife analysis was repeated for the test data sets in order to check whether the variables chosen when the model was fitted to the training data set were equally important when the model was fitted to the test data set. We report results as averages of the 100 Maxent models (hereafter, final model).

Model evaluation

As a measure of model predictive power, we chose the Area Under Curve (AUC score; Hanley and McNeil 1982). The AUC score ranges from 0.5, for models that predict no better than random, to 1.0, for models with perfect predictive power. Nonetheless, the AUC score has been criticised as a metric of model accuracy, because being a rank-based measure it does not account for the degree to which the predicted values have been calibrated (Lobo *et al.* 2008, Phillips and Dudík 2008), while it tends to be biased when the spatial extent to which models are carried out is large as in our case (Lobo *et al.* 2008). Thus, we also investigated the predicted values of habitat suitability

Table 1. Description of the variables regarded as potential predictors of habitat suitability for the occurrence of Eleonora's Falcon across Madagascar. Variables passing the test for multicollinearity, and thus used for model-building, are indicated with an asterisk.

Abbreviation	Description
Topography	
ELEV *	Elevation (m)
SLOPE *	Terrain slope (degrees)
ACOS *	Cosine of terrain aspect, representing northness, where positive values correspond to north-facing slopes
ASIN *	Sine of terrain aspect, representing eastness, where positive values correspond to east-facing slopes
PRECmax *	Maximum monthly precipitation during November-April (mm)
PRECmin *	Minimum monthly precipitation during November-April (mm)
T_{mean}mean	Mean of average monthly temperature during November-April (°C)
T_{mean}max	Maximum of average monthly temperature during November-April (°C)
T_{mean}min	Min of average monthly temperature during November-April (°C)
T_{max}mean	Mean of maximum monthly temperature during November-April (°C)
T_{max}max	Maximum of maximum monthly temperature during November- April (°C)
T_{max}min	Min of maximum monthly temperature during November-April (°C)
T_{min}mean	Mean of minimum monthly temperature during November-April (°C)
T_{min}max	Maximum of minimum monthly temperature during November-April (°C)
T_{min}min	Min of minimum monthly temperature during November-April (°C)
Vegetation	
class1 *	Bare soil/Rock
class2 *	Water
class4 *	Cultivation
class5 *	Western dry forest
class6 *	Plateau grassland-wooded grassland mosaic
class7 *	Wooded grassland-bushland
class13 *	Wetlands
class14 *	Humid forest
class16 *	Degraded humid forest

within the 95% and 50% home ranges of the four Greek falcons (see Kassara *et al.* 2012 for a detailed description), as well as within the 95% and 50% home ranges of three Spanish falcons (reproduced from Figure 1 of Mellone *et al.* 2012, with permission from the British Trust for Ornithology) tracked during the wintering periods 2008–2009 and 2009–2010. Given that Mellone's *et al.* (2012) satellite telemetry project coincided partially in time with the current study, such comparisons could serve as an indication of how well the resulting final model generalises to other populations of the species.

Finally, we computed four landscape metrics with the Patch Grid Analyst for ArcGIS 9.2 (Elkie *et al.* 1999) in an attempt to understand landscape structure within all available presence grid cells of the Greek falcons better. In particular, we estimated the percent cover, patch size and number, as well as the mean proximity index for each vegetation class, which is a measure of the degree of isolation and fragmentation.

We implemented spatial analyses with ArcGIS 9.2 (ESRI 2006) and statistical analyses with SPSS 18.0 (SPSS 2009). For the latter, mean values and standard deviations are reported with statistical significance level set to $\alpha = 0.05$. All data were projected at UTM 38S zone.

Results

The initial data pool of the 561 telemetry locations received during the wintering period 2009–2010 occurred in 472 grid cells. Each of the 100 sub-samples used for the model-building

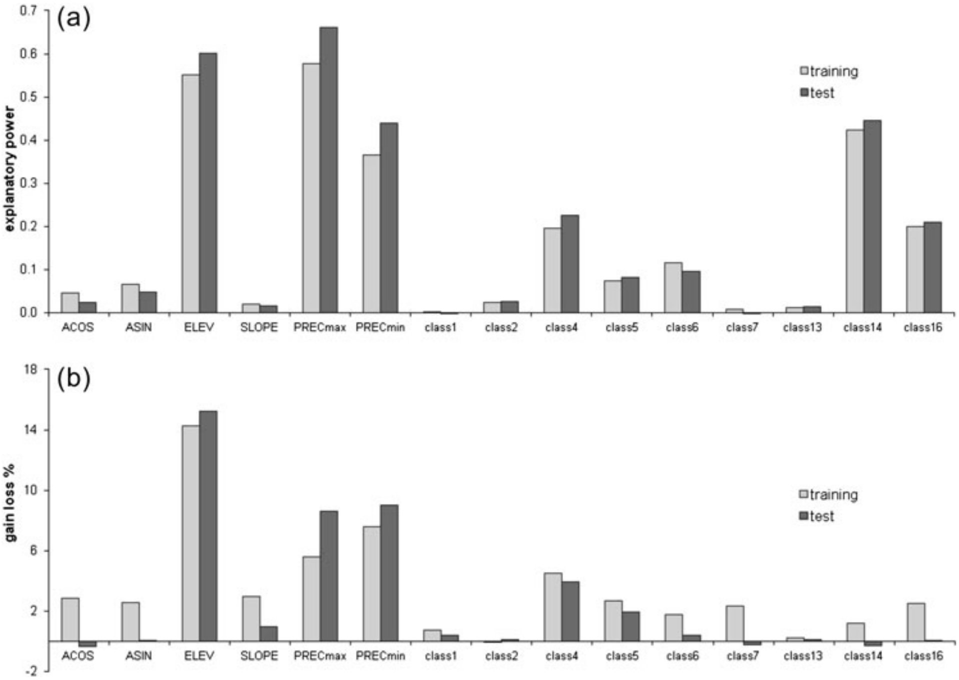

Figure 1. The relative importance of the candidate variables averaged over 100 Maxent models and quantified via (a) the explanatory power of each variable when used in isolation and (b) the loss in the gain when a particular variable is dropped from the model, judging by both the training and test data sets.

process contained half of the available presence grid cells (221.03 ± 4.30). The preliminary check for multicollinearity revealed no strong correlations among the candidate variables (Spearman $r < 0.6$), but for the temperature variables which were highly intercorrelated among each other ($0.75 < r < 0.98$), as well as with the topographical variable "elevation" ($-0.97 < r < -0.77$). Thus, we only included the variable "elevation" in the model-building process, which was thereafter also considered as a proxy for any possible effect of the temperature variables on Eleonora's Falcon occurrence.

When used on its own, the variable maximum monthly precipitation (PRECmax) had the greatest explanatory power both for the training and test data sets, followed by elevation (ELEV), the percent cover of humid forest (class14), minimum monthly precipitation (PRECmin), the percent cover of degraded humid forest (class16) and of cultivation (class4) (Figure 1a). The final model lost the most explanatory power when the variable elevation (ELEV) was dropped from the model, followed by the minimum monthly precipitation (PRECmin), maximum monthly precipitation (PRECmax) and the percentage cover of cultivation (class4), degraded humid forest (class16) and of humid forest (class14) (Figure 1b).

Judging by the corresponding response curves, habitat suitability increased sharply in areas above 800 m altitude (ELEV), which receive at least 28 mm of rainfall during the driest month (PRECmin) and at least 250 mm of rainfall during the wettest month (PRECmax) of the period November–April. In addition, habitat suitability varied proportionally with the percentage cover of degraded humid forest (class16). The same applies for the percent cover of intact humid forest (class14) and cultivation (class4), but in these cases the increase in habitat suitability was more subtle (Figure 2). Actually, all these vegetation classes did not occur over extended areas within the presence grid cells, but were distributed in relatively fragmented and isolated patches (Table 2).

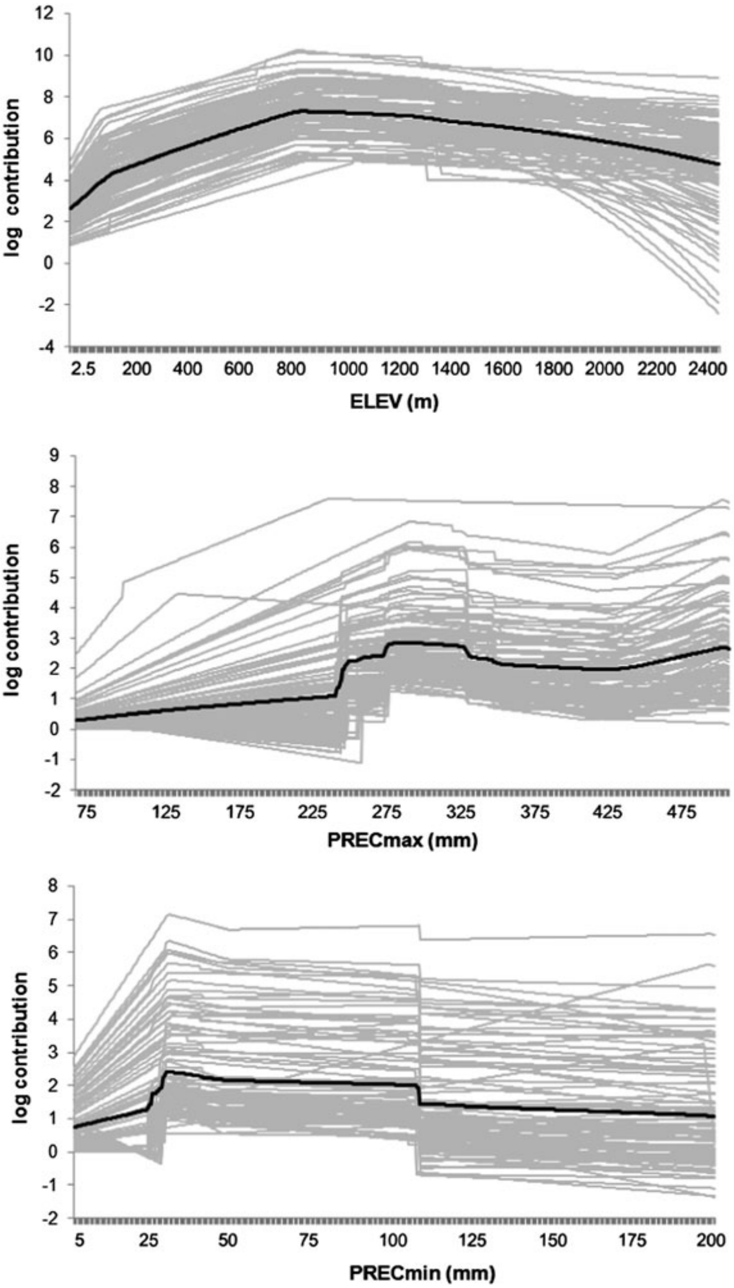

Figure 2. Response curves of the predicted habitat suitability across the range of values for the six most important predictors: elevation (ELEV), maximum (PRECmax) and minimum (PRECmin) monthly precipitation for the period November–April, percent cover cultivation (class4), percent cover humid forest (class14) and percent cover degraded humid forest (class16). Each graph illustrates how the response variable (i.e. habitat suitability) varies with each predictor while all other predictors are held at their mean sample value. Grey lines represent response curves for all 100 bootstrapped Maxent models, while the bold black lines represent the resulting mean curve.

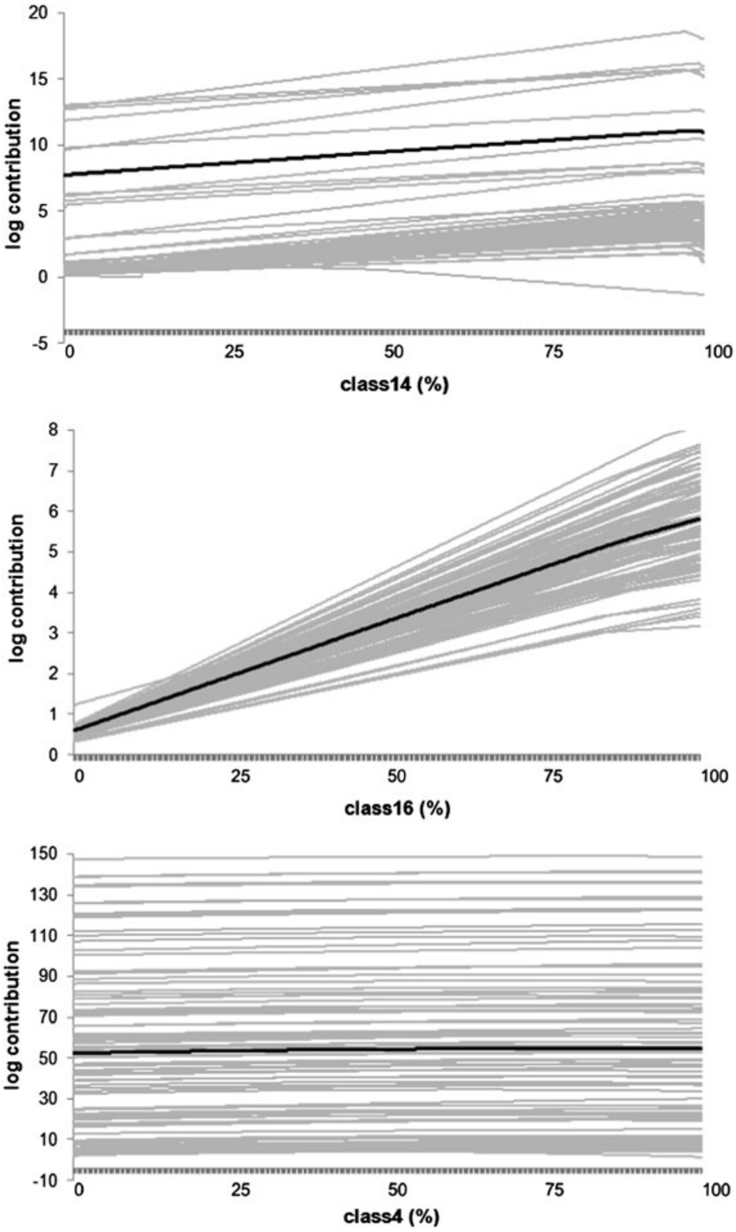

Figure 2. Continued.

The Maxent models fitted the training data sets very well (training AUC = 0.942 ± 0.005), while their predictive power was quite high (test AUC = 0.906 ± 0.018). If we consider as areas of high likelihood of Eleonora's Falcon occurrence grid cells with average predicted suitability values greater than 0.75, then it is very likely that Eleonora's Falcons will be observed in only 0.53 % of Madagascar. These areas are distributed along a north-south axis (Figure 3a) in what is known as the humid submontane forest ecoregion. Although most of them occur within the 95% Greek

Table 2. Landscape structure within 472 presence grid cells, summarised by the average proportion of each vegetation class (Class proportion), mean number of patches (MPN), mean size of patches (MPS) and the mean proximity index (MPI). Smaller values of MPI are indicative of more fragmented and isolated patches. Standard deviations are reported in parentheses. Vegetation class abbreviations as in Table 1.

Vegetation class	Class proportion (%)	MPN	MPS (ha)	MPI
class1	12.92 (10.81)	1.31 (0.63)	10.75 (9.62)	2.76 (9.01)
class2	1.65 (1.47)	1.00 (0.00)	1.60 (1.43)	n.a.
class4	15.77 (19.53)	2.33 (1.44)	8.52 (15.91)	11.22 (39.26)
class5	32.28 (29.04)	2.29 (1.15)	21.71 (28.20)	25.02 (80.41)
class6	47.50 (37.18)	2.02 (1.31)	35.57 (37.55)	28.74 (79.30)
class7	30.18 (27.54)	2.49 (1.50)	17.14 (23.67)	25.44 (62.52)
class13	2.85 (1.88)	1.11 (0.33)	2.50 (1.67)	0.19 (0.58)
class14	48.78 (36.34)	2.01 (1.37)	38.03 (37.36)	20.48 (59.72)
class16	29.68 (27.15)	2.54 (1.50)	16.65 (23.85)	36.07 (86.80)

home range areas (90.81 %), the 95% Spanish home range areas also contain a considerable amount (58.58 %, pooled years) (Figure 3b).

During the wintering periods 2008–2009 and 2009–2010, the formerly estimated home range areas of the four Greek and the three Spanish Eleonora's Falcons overlapped to a great extent (Figures 3b, 3c; Tables S1, S2 in the online supplementary material) for spatial overlap of individual home ranges). The average predicted habitat suitability within the 95% home range areas was estimated at 0.297 (SD = 0.219) for the Greek falcons and at 0.268 (SD = 0.231) for the Spanish falcons (Table 3). Within the core areas of their home range areas (i.e. 50% contours), the average predicted habitat suitability was estimated at 0.450 (SD = 0.223) for the Greek falcons and at 0.485 (SD = 0.231) for the Spanish ones (Table 3).

Discussion

Eleonora's Falcon is one of two non-resident representatives of the Falconidae family in Madagascar (Fergusson-Lees and Christie 2001). Previous field surveys linked its presence to the eastern highlands, although there have also been sporadic occurrence reports from the rest of the country (Zefania 2001). While habitat selection patterns are hard to investigate through field surveys in such large study areas, quite recently three satellite telemetry projects (Gschweng *et al.* 2012, Kassara *et al.* 2012, Mellone *et al.* 2012) have contributed a more detailed description of the location of the species across its wintering grounds.

In a previous study based on the Global Land Cover Project 2000 classification, we showed that four Eleonora's Falcons originating from Greece were located more frequently than by chance in humid submontane forests (Kassara *et al.* 2012). Here, thanks to the availability of a more recent and detailed vegetation classification scheme (Madagascar Vegetation Mapping Project), the consideration of topographic and climatic variables, as well as the application of a newly introduced methodology (Maxent), we investigated their distribution pattern more thoroughly. In addition, having applied a proper data sub-sampling we were able to generalise our results in spite of the low number of individuals.

In particular, we showed that the Greek falcons prefer elevated areas receiving high amounts of rainfall during the wintering period and consisting of a mosaic of pristine or degraded humid forest and cultivation. A closer look at the landscape structure within the areas where the four Greek falcons were detected revealed that they occurred in rather fragmented and isolated patches of the aforementioned vegetation classes. Thus, our results verify the hypothesis put forward by Mellone *et al.* (2012) in their recent study, in which they attributed habitat selection of three Spanish falcons within the core of their home range areas to a "spill-over effect" of insect prey from primary forests to nearby degraded humid forests and cultivation. Even if habitat fragmentation

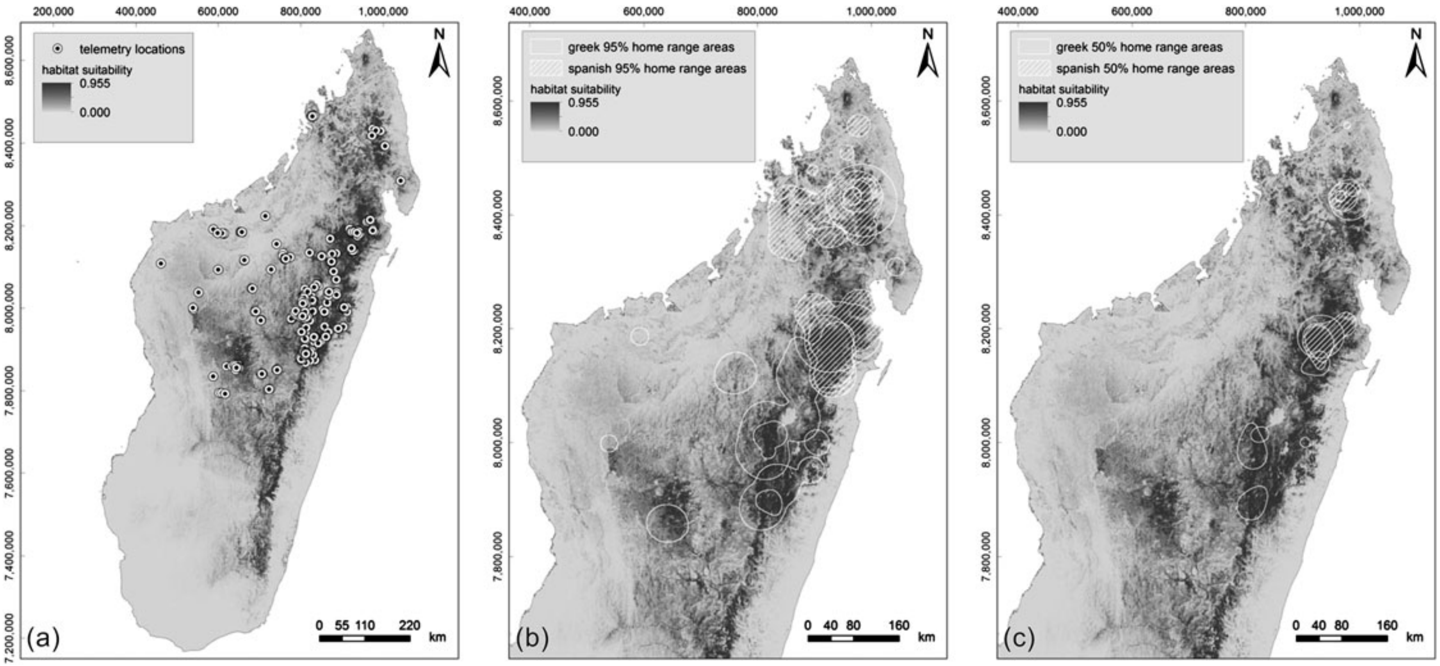

Figure 3. (a) Predicted habitat suitability for Eleonora's Falcon occurrence across Madagascar based on the telemetry locations received from four satellite-tracked individuals originating from Greece during the 2009–2010 wintering period. (b) The 95% home range areas and (c) 50% home range areas of the four Greek falcons (adapted from Kassara *et al.* 2012) as well as of three Spanish falcons that overwintered in Madagascar during 2008–2009 and 2009–2010 are overlaid (reproduced from Figure 1 of Mellone *et al*. 2012, with permission from the British Trust for Ornithology).

Table 3. Predicted habitat suitability for Eleonora's Falcon occurrence within the 95% and 50% home ranges of four Greek and three Spanish falcons during the wintering periods 2008–2009 and 2009–2010.

Predicted habitat suitability								
	95% home range areas				50% home range areas			
PTT	mean	SD	min	max	mean	SD.	min	max
	Wintering period 2009–2010							
94118	0.207	0.205	0.001	0.939	0.349	0.241	0.003	0.955
94119	0.330	0.185	0.003	0.880	0.433	0.183	0.089	0.857
94120	0.325	0.192	0.003	0.945	0.469	0.166	0.038	0.941
94121	0.291	0.210	0.003	0.952	0.468	0.195	0.031	0.935
80399	0.405	0.239	0.001	0.955	0.611	0.185	0.055	0.955
80402	0.228	0.180	0.004	0.917	0.302	0.167	0.024	0.746
	Wintering period 2008–2009							
80399	0.219	0.207	0.000	0.952	0.444	0.233	0.010	0.937
80400	0.199	0.218	0.006	0.937	0.343	0.246	0.010	0.866
80402	0.099	0.120	0.004	0.732	0.408	0.213	0.055	0.816
	Pooled data							
Greek kernels	0.297	0.219	0.001	0.955	0.450	0.223	0.003	0.955
Spanish kernels	0.268	0.231	0.000	0.955	0.485	0.237	0.010	0.955

proves profitable for Eleonora's Falcons in the short-term by providing better hunting opportunities in open habitats (like degraded forests and cultivation) located close to insect-rich habitats (primary forests) (Mellone *et al.* 2012), further shrinkage of pristine humid forests and subsequent land-use changes could ultimately lead to reduced species richness (Edwards *et al.* 2011, Gibson *et al.* 2011). Habitat destruction, followed frequently by habitat fragmentation, has been repeatedly linked with biodiversity loss (Mittermeier *et al.* 2004). This also holds true for forest insect species (Holloway *et al.* 1992) upon which Eleonora's Falcon feeds (Thorstrom and Rene de Roland 2000, Ristow 2004 and references therein), such as winged termites, ants (Watt *et al.* 1997) and beetles (Didham *et al.* 1998). Eleonora's Falcon is also commonly found foraging near watercourses (Mayol 1977, Besson 1982, Ristow and Wink 1992–94, Mas 2006) that attract insects such as dragonflies that are also included in the species' diet (Walter 1979, Zefania 2001, Ristow 2004). Although the vegetation classes "water" and "wetlands" were not among those most informative of the species' occurrence, the predicted habitat suitability around areas such as Lake Aloatra within the Central Plateau, was relatively high. Thus, we cannot exclude the possibility that Eleonora's Falcons also exploit such foraging areas during the wintering period, although less consistently than the humid submontane forests and cultivation of the eastern highlands (Zefania 2001).

In previous studies, both the Spanish and the Greek Eleonora's Falcons used multiple centres of activity (Kassara *et al.* 2012; Mellone *et al.* 2012), which could be the result of seasonal differences in food availability (Gschweng *et al.* 2012). For instance, swarms of winged termites provide an abundant yet ephemeral food source (Olson and Alvarenga 2006) for Eleonora's Falcons, which tend to emerge after rainfall (Eggleton and Davies 2001). Precipitation proved to be an important predictor for the four Greek falcons' presence in the current study, as well as for seven Italian falcons in the study by Gschweng *et al.* (2012). Actually, due to a greater number of tracked individuals, which allowed for a multi-temporal approach, the latter study revealed that the seasonal movements of the Italian falcons were determined, among other things, by the rainfall pattern across the country which in turn affected vegetation phenology and food availability during the wintering period (Gschweng *et al.* 2012). Thus, our results provide further evidence for the effect of seasonality in food availability.

In addition, although considering also the underlying probability distribution of the falcons' occurrence would have been more informative of the actual space use (Fieberg and Kochanny 2005), the percentage of between-group spatial overlap of the estimated 95% home range areas of the four Greek Eleonora's Falcons and the three Spanish falcons was at the same level as the percentage of within-group spatial overlap (Tables S1, S2). Eleonora's Falcon global population numbers approximately 15,000 breeding pairs (Dimalexis *et al.* 2008), of which approximately 70% are believed to overwinter in Madagascar (Walter 1979). Given that the final Maxent model predicted only a few highly suitable areas for the species' occurrence, it comes as no surprise that the home ranges of falcons originating from different breeding regions overlapped to such a great extent. Thus, even at such a low sample sizes as the one used in the current study, Maxent can produce reliable predictions, transferable in time as well as to other populations of the species (Gschweng *et al.* 2012). Satellite telemetry data are by default dependent, correlated in space and time, and available in many cases for only a few individuals (but see Jiguet *et al.* 2011). Hence, a proper sub-sampling of the data ensuring equal representation of all individuals in the data pool used for subsequent analyses, as well as a careful interpretation of the results is essential even with such efficient modelling techniques.

The importance for species-ecosystem interactions to be better explored and understood is even more crucial in landscapes such as those of Madagascar that have been extensively altered ever since humans colonised the country (Jarosz 1993). Deforestation within the eastern rainforest, which originally extended over an area of 11.2 million hectares prior to human colonisation was estimated at 32% in the 1950s and 66% in the mid-1980s (Green and Sussman 1990). A more recent study showed that almost half of the humid, dry and spiny forests of Madagascar occur in patches less than 500 km^2, while most of these patches were found close to non-forest edges in the 2000s (Harper *et al.* 2007). The same authors argue that humid forests are less severely affected by deforestation and fragmentation in comparison to dry and spiny forests (Harper *et al.* 2007). Still, these figures would have been promising given that the political, social, and environmental interests are in line, which, as history has shown, is not the case for the eastern highlands of Madagascar (Jarosz 1993, Vågen 2006).

Besides, the impact of forest management policies on the insect fauna of Madagascar, non-targeted pest control practices are known to have adverse food chain effects that could affect Eleonora's Falcon in the long term. Locust outbreaks in the country have been mitigated by spraying with fipronil (among other insecticides) that was considered responsible for the decline of termites and consequently of insectivorous vertebrates, in a case study in south-western Madagascar (Peveling *et al.* 2003). An estimation of the risk of indirect poisoning of Eleonora's Falcon from insecticides in its wintering grounds would be premature at this stage since hard data are currently lacking. Still, carry-over effects related to habitat deterioration or decreased quality of sexually mature individuals while still at their wintering quarters are expected to have severe consequences in species showing strong migratory connectivity (Webster *et al.* 2002) such as Eleonora's Falcon. Thus, understanding the ecological requirements of Eleonora's Falcon during the wintering period via satellite tracking projects coupled with species distribution models such as Maxent can be regarded as an essential first step to a holistic approach of the species' conservation, as well as a guide for fieldwork in target areas. The inclusion of factors related to age or sex-depended idiosyncrasies (van Toor *et al.* 2011) and temporal variability in available resources (Gschweng *et al.* 2012) could allow for refined predictions that are closer to the realised niche of the species in the future.

Supplementary Material

The supplementary materials for this article can be found at journals.cambridge.org/bci

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