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Does habitat use and ecological niche shift over the lifespan of wild species? Patterns of the bearded vulture population in the Western Alps

Abstract We analysed bearded vulture (*Gypaetus barbatus*) occurrences collected through long-term monitoring (from 1993 to 2010) in the Western Alps (1) to test whether ecological niches shift due to individual development and (2) to verify whether these patterns could reflect their spatial distribution. Thus, we compared the distribution patterns of three age classes ('young', 'sub-adults' and 'adults') through the K-select analysis. We then computed ten species distribution models (SDMs) and their average prediction to test for differences in age class distribution. The K-select analysis showed highly significant differences in the ecological niche among all the age classes and we also found highly significant differences in all the SDMs among the three age classes considered. Our results quantitatively showed that target species exhibits age specific shifts in the ecological niche and changes in the spatial distribution of individuals. Our methods are potentially widely applicable for testing differences among age classes of other species and thus, defining the best conservation actions (such as re-introduction) by taking into account different requirements in different stages of the individuals' life.

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Introduction

Dissimilarities between the age-stage of a population, such as life-history characteristics (Swab et al. 2012), are rarely considered in habitat selection studies (Burns et al. 2013). However, age-specific characteristics are strictly related to resource selection, because individuals experience different environments and make different life-history decisions which are important for population and evolutionary dynamics (Evans et al. 2012).

Niche-based models are widely used to identify the factors affecting a species' ecological niche (Guisan et al. 2013) and could provide a useful tool for verifying changes in the ecological niche during an individual's development. Niche models typically associate the locations of a species' occurrence with multiple environmental factors (Calenge et al. 2005), and two main types of niche models can be distinguished: hindcasting and forecasting (Morrison et al. 1992). While hindcasting is the process intended to emphasize important variables which determine the current occurrence of a given species, forecasting is the process of fitting statistical models using data from the present distribution of a species and then estimating its potential distribution (Calenge et al. 2005; Pearman et al. 2008).

Species distribution models (SDMs, also commonly referred as ecological niche models ENMs, Guisan et al. 2013) show high efficiency in both hindcasting and forecasting species' distributions (Rebelo and Jones 2010; Franklin 2013). These approaches have been widely used in landscape ecology as a support tool for landscape management (Guisan et al. 2013), invasive species risk assessments (Beaumont et al. 2009), estimating the impacts of climate change on biota (Hof et al. 2012), and identifying suitable areas for species conservation (Engler et al. 2004; Johnson et al. 2004).
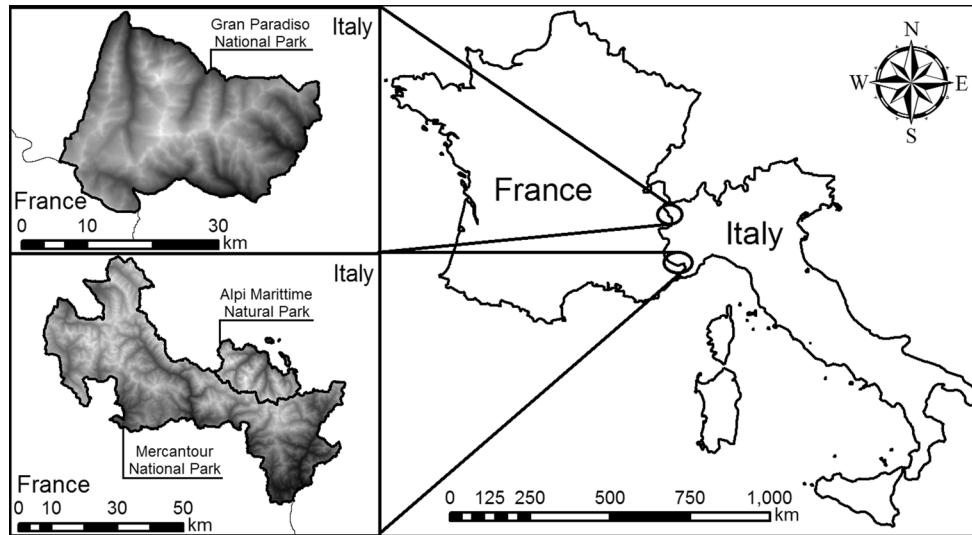
Fig. 1 Study area. At the *upper left* corners *thick black lines* indicate the border of the Gran Paradiso National Park, at the *lower left* corner *thick black lines* indicate the border of the Alpi Marittime Natural Park and the Mercantour National Park. *Fine black lines* indicate the national borders. In both the panels altitudinal ranges in *bright–dark grey* indicates *higher–lower* altitude

Nevertheless, neither hindcasting nor forecasting niche-based models have been carried out to evaluate ecological niche shift during the life history of individuals to date.

Thus, our aims are (1) to test whether ecological niche shifts due to an individuals' development occur and (2) to verify if these variations could be reflected in their spatial distribution. We expect that different age groups show different selections of habitat features. Young individuals should mostly maximize the use of more profitable habitats for foraging. Instead, adults are also committed to reproduction; the same can be true for sub-adults approaching reproductive age; these last two classes must also take into account habitat suitability for nesting. Our dataset consists of the locations of wild bearded vultures (*Gypaetus barbatus*) successfully reintroduced into the Alpi Marittime Natural Park (Italy) and the Mercantour National Park (France), Western Alps (Bogliani et al. 2011).

Methods

Study area

Our study area was located in Maritime Alps, including two contiguous protected areas: the Alpi Marittime Natural Park, Piedmont, Italy, and the Mercantour National Park, France. The area covers a surface of 7784 km^2 and shows high habitat diversity as the result of a wide altitudinal range from 490 to 3297 m a.s.l. (Figure 1). Alpine habitats, pastures, and open lands (28 %), coniferous forests (22 %), and rocks and gla-ciers (10 %) occupy most of the area; uncultivated fields and shrubs (10 %), beech (12 %), and mixed woods (8 %) characterise the mountains; while human activities are concentrated in a few villages in the lower portions of the main valleys (9 %). Rivers, streams, and lakes constitute only 1 % of the total area. The environmental heterogeneity, the expansion of natural habitats, and re-introduction projects explain the high diversity of the community of wild ungulates: alpine ibex (*Capra ibex*), alpine chamois (*Rupicapra rupicapra*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*). Domestic ungulates, mostly cows (*Bos taurus*), sheep (*Ovis aries*) and goats (*Capra hircus*) are free ranging in high-altitude pastures during the summer months (Parco Alpi Marittime 2000; Parc National du Mercantour 2002).

The validation phase was carried out on data collected in the Gran Paradiso National Park, located in the north-western Italian Alps, 105 km from the Alpi Marittime and Mercantour area. It covers a surface of 720 km^2 with an altitude ranging from 700 to 4061 m a.s.l. The area is mostly covered by alpine habitats such as meadows, rocks, and glaciers; forests cover less than 20 % and human activities are concentrated only in a few villages. The availability of carrion from large ungulates is high as the park and surrounding areas host large populations of alpine ibex and alpine chamois, as well as roe deer and wild boars. Wild ungulates mostly die from winter starvation, avalanche casualties and predation by wolves (*Canis lupus*) since 2006. Domestic livestock are also present in the park and the surrounding areas during the summer months and some of them die from disease or wolf predation.

Table 1 Variables used in the development of bearded vulture hindcasting and forecasting models, average values in the whole study area and in the used cells

Feature	Variable	Unit	Available area	Used cell		
				Young	Sub-adult	Adult
Land cover	Forests	Percentage (%)	14.11 (13.85)	6.91 (2.95)	6.07 (2.04)	9.46 (4.47)
	Grasslands	Percentage (%)	18.79 (17.27)	23.99 (10.56)	29.52 (12.21)	20.41 (16.77)
	Rocky areas	Percentage (%)	9.51 (8.29)	21.04 (19.43)	14.68 (14.16)	10.87 (10.21)
	Shrub-lands	Percentage (%)	10.23 (8.64)	17.47 (16.66)	17.11 (16.62)	23.81 (11.72)
Topography	Altitude	meters a.s.l. (m)	1433 (653)	1971 (447.37)	1951 (387)	1907 (410)
	Slope	Degrees (°)	23.94 (10.58)	28.08 (9.74)	27.32 (9.48)	25.24 (9.59)
	Roughness	Ratio of isoipses' average length in the grid derived by grid side length	0.029 (0.015)	0.044 (0.032)	0.043 (0.028)	0.043 (0.033)
Anthropogenic factors	Distance to human settlements	meters (m)	6405 (4258)	8644 (4610)	9617 (5212)	12,289 (5718)

Standarddeviations (S.D.) are in parentheses

Data collection

Data collection in the Marittime Alps was carried out from October 1993 to December 2010 by trained personnel from the Alpi Marittime Natural Park and the Mercantour National Park and by volunteers external observers. In the Gran Paradiso National Park, sighting records were collected inside the park borders from 1989 to 2007. Each observation was recorded on field data sheets, marked on a detailed map, or in recent years by GPS (*Global Position System*), and the age class of the individuals was specified. The observed vultures were thus classified as young (Y; < 3 years-old), sub-adults (S; 3–5 years-old), or adults (A; > 5 years-old) on the basis of their plumage and moult, similar to the classification of Bogliani et al. (2011) and Margalida et al. (2011). Data were then georeferenced in the UTM WGS84 32 N coordinates system using ARCGIS 10.1 (ESRI, Redlands, California: http://www.esri.com/software/arcgis).

Moreover, we accounted for a spatially biased sampling effort (Stolar and Nielsen 2014) through Gaussian kernel density analysis based on all sampling locations (grouping all bearded vulture locations collected; Elith et al. 2010; Fourcade et al. 2014). We used the kernel density probability for each cell of the resulting sampling effort map to weight bias-adjusted model estimates (Stolar and Nielsen 2014; Milanesi et al. 2015; see below): ten-thousand random points within the resulting 95 % kernel density surface were thus generated to serve as background data.

Identifying which areas are available for vulture distribution is crucial due to the wide dispersal capacities and the ability to cross sub-optimal and unsuitable environments shown by the target species (Hirzel et al. 2004). Without considering habitat availability, we could potentially introduce a source of bias in the analysis (Calenge et al. 2008), and thus, we derived the minimum convex polygon (MCP) around all bearded vulture locations collected, similarly to Calenge et al. (2005).

Predictor variables

For the entire study area, we collected data on ecological, topographic, and anthropogenic features (Table 1). Land cover types were obtained from the Coordination of Information on the Environment (CORINE Land Cover 2006; http://www.eea.europa.eu/data-and-maps/data/clc-2006-vector-data-version-3), the European land cover database. We obtained topographic variables, namely altitude, slope, and landscape roughness from a Digital Elevation Model (DEM) with a spatial resolution of 15 m (ASTER GDEM; http://gdem.ersdac.jspacesystems.or.jp/). Moreover, we considered the distance from anthropogenic elements (i.e. urban areas, villages, roads, railways). Our study area included two States and three Regions, each with different availability (or deficiency) of data on both wild and domestic ungulates. Therefore, even if prey abundance has been previously used to forecast the distribution of the vulture (Hirzel et al. 2004), we did not include these predictor variables in our models to avoid biased estimates of the densities due to dissimilarities in the census techniques applied in different parts of the study area. Similarly to Hirzel et al. (2004), we re-sampled all the variables to a common resolution of 100×100 m cell size using ArcGIS 10 (ESRI, Redlands, California: http://www.esri.com/software/arcgis).

Modeling methods

Data exploration was the first step of our analyses. To avoid biases due to collinearity among predictor variables, we carried out Pearson correlation tests (Table S1), considering a threshold value of $|r| > 0.7$ (Dormann et al. 2014). Moreover, we assessed the presence of outliers in the data (Fig. S1) with multi-panel Cleveland dotplots (Zuur et al. 2010) and tested spatial autocorrelation among all bearded vulture locations collected (Fig. S2) with Moran's I correlogram (Dormann et al. 2007). In the latter analysis, which provides

useful information for discarding related observations, we considered all the bearded vulture locations (grouping locations of all age classes) to avoid the potential 'attractive' effect of adults on sub-adults and young individuals which occurred at least twice during the study period (Luca Giraudo, personal observation).

Since hindcasting should necessarily precede forecasting and, as a given statistical approach would not necessarily be as efficient for both objectives, we primarily applied the K-select analysis (Calenge et al. 2005) for hindcasting studies; while, to forecast the potential distribution of each age class, we carried out ten SDMs and their average prediction (ensemble prediction, EP; Araùjo and New 2007; Coetzee et al. 2009; Jones-Farrand et al. 2011).

Hindcasting modelling To investigate life-history changes in habitat selection for each age class of locations, we compared used and available sites through niche-based approaches. We carried out a K-select analysis widely used in hindcasting models (Calenge 2006; Hansen et al. 2009; Pellerin et al. 2010; Tolon et al. 2012; Rauset et al. 2013; Nicholson et al. 2014). This method assumes that utilisation of available resources can be defined by environmental variables in a multi-dimensional niche-space (sensu Hutchinson 1957) and is particularly suitable for use-availability data (Hansen et al. 2009). K-select is a multivariate analysis that provides a marginality value which is one measure of habitat selection. Marginality is a criterion that measures the squared Euclidean distance between the average habitat conditions used by organisms and the average habitat conditions available to them. We performed an eigenvalue-analysis of the marginality vectors to summarize the habitat selection common to all the age classes, using a randomization test with 10,000 replicates (Calenge et al. 2005). K-select analysis also provides the coefficients of all the environmental variables and thus lets us identify the effect of each predictor on the presence of each age class.

Forecasting modelling To verify differences in the spatial distribution among age classes, we developed ten SDMs: (1) maximum entropy algorithms (MAXENT; Phillips et al. 2006), a density-based model that calculates several functions to identify the best approximation between the distributions of predictors at occurrences of each age class and those of the rest of the study area, (2) factorial decomposition of Mahalanobis distances (MADIFA; Calenge et al. 2008), based on a decomposition of Mahalanobis distances into uncorrelated axes of which the first axes are then selected to compute scores of habitat suitability, (3) generalised linear models (GLM; McCullagh and Nelder 1989), a logistic regression model that relates occurrences of each age class and pseudo-absences with predictors, (4) boosted regression trees (BRT; Friedman 2001), a regression model that combines regression trees and boosts methods resulting in an additive regression model in which individual terms are simple trees, (5) generalized additive models (GAM; Hastie and Tibshirani 1990), a regression model which involves smoothing functions derived by predictor variables to estimate parametric components of linear predictors, (6) classification tree analyses (CTA; Breiman et al. 1984), a recursive partitioning algorithm that applies splitting rules to develop decision trees and partition the data to reduce the conditional variation in the response variable, (7) artificial neural networks (ANN; Ripley 2007), a non-linear regression model based on hidden variables (derived by linear combinations of the predictors), (8) flexible discriminant analyses (FDA; Hastie et al. 1994), a discriminant analysis based on mixture models, (9) multivariate adaptive regression splines (MARS; Friedman 1991), a non-linear regression that automatically models non-linearity interactions between variables, (10) random forests (RF; Breiman 2001), an ensemble classifier that consists of many decision trees which constitute "the forest".

We also calculated the average of the predictions of the ten single methods (ensemble prediction, EP). The values of the cells of the resulting distribution maps ranged from 0 to 1, and we considered a threshold of 0.5 to distinguish areas suitable for bearded vultures (Bailey et al. 2002; Fukuda et al. 2013). The values of the sampling effort map (see above) were used as weights in K-select and MADIFA as a bias grid in MAXENT and as case weights in all other methods (Elith et al. 2010; Stolar and Nielsen 2014; Milanesi et al. 2015). Finally, we tested for residual spatial autocorrelation with Moran's I correlogram (1—predicted SDMs values for each location; De Marco et al. 2008).

Model validations and comparisons

To assess model efficiencies, we compared the predicted values with originals through the use of (1) Area under the ROC (*Receiver Operator Characteristics*) Curve (AUC; Fawcett 2004; Ko et al. 2011) and (2) the Boyce Index (BI; Boyce et al. 2002). AUC varies from 0 (worse than a random model with the value 0.5) to 1 (perfect model), while BI varies from −1 to 1 (positive values indicate predictions consistent with the evaluation data set, 0 indicates that the model is similar to a random model. To classify the accuracy of validation, we followed Swets (1988): 0.90–1.00 = excellent; 0.80–0.90 = good; 0.70–0.80 = fair; 0.60–0.70 = poor; 0.50–0.60 = fail. For each age class, we carried out ten *k-fold cross-validations* using a random sub-sample of 50 % of locations alternatively to calibrate the models and the remaining 50 % to validate them (Boyce et al. 2002). We also used new field data (N = 577) collected from January 2011 to December 2012) in the Marittime Alps and an external data set provided by the Gran Paradiso National Park (N = 1,787) collected from July 1989 to June 2007 in the north-western Alps (Italy) to validate the models after the projection of SDM predictions in this area. Finally to test for differences in the distribution of age classes, we compared the resulting distribution maps and the ratio between the predicted distribution areas of three age-classes

Table 2 Results of the randomisation tests of marginality on bearded vulture age classes (a) and relative coordinates of marginality vectors on habitat variables (b)

	Young	Sub-adult	Adult
(a) Tests of the marginality (Bonferroni_level = 0.05/3 = 0.0166)			
Marginality	0.052	1.055	7.177
Randomisation test (*P value*)	< 0.0001	< 0.0001	< 0.0001
(b) Selection of habitat variables by each age class (Bonferroni_level = 0.05/18 = 0.0027, two-tailed test)			
Altitude	0.01	−0.12*	−0.64*
Distance to human settlements	1.25*	1.53*	1.68*
Forests	0.23*	−0.61*	−0.44*
Grasslands	0.39*	0.43*	0.53*
Shrub-lands	1.59*	2.14*	2.41*
Slope	−0.83*	−0.91*	−0.91*
Rocky areas	−0.53*	−0.59*	−0.58*
Roughness	−0.19*	0.35*	0.29*

* $P < 0.0001$
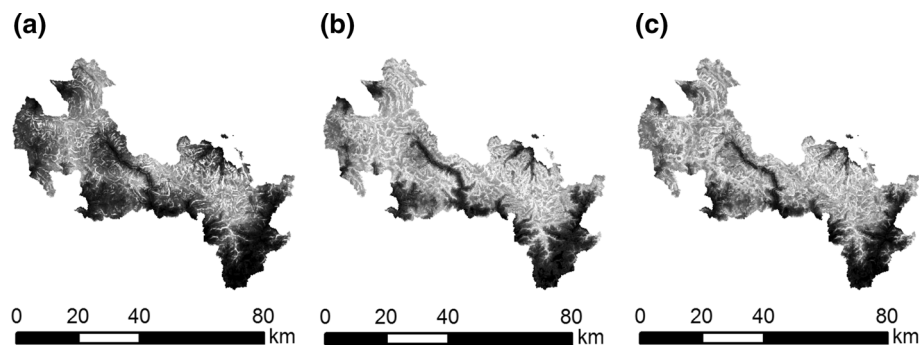
Fig. 2 Species distribution maps of the age classes **a** young, **b** sub-adult and **c** adult obtained with ensemble species distribution models (*bright–dark grey* indicates *higher–lower* species occurrence probability) in the Alpi Marittime Natural Park (ITA) and in the Mercantour National Park (FR)

by paired *t* tests. All the statistical analyses carried out in this paper were computed in the open-source software R (v. 3.1.2 http://www.R-project.org/).

Results

A total of 5068 observations of bearded vultures were collected from January 1993 to December 2010 in the Maritime Alps. Identified individuals, and (consequently) age-assignment, represented 87.39 % (N = 4,429) of the total observations. Of the total observations, 51.59 % were Y (n = 2285), 34.84 % (n = 1543) were A and 13.57 % (n = 601) were S.

Pearson correlation tests showed low collinearity among predictor variables (Table S1), and thus, we considered all the predictors for further analyses. We also removed outliers (Fig. S1) and autocorrelated locations (between a distance of 150 m; Fig. S2), and thus we developed hindcasting and forecasting models with a total of 1564 bearded vulture locations. The proportion of locations for each age class was similar to those of the initial dataset: 54.02 % were Y (n = 845), 31.21 % (n = 488) were A and 14.77 % (n = 231) were S.

K-select analysis showed how habitat use differed significantly for all the age classes (P < 0.0001), as indicated by the randomisation tests carried out on the marginality vectors (Table 2), and eigenvalues indicated that the first axis explains most of the marginality present in the dataset (λ_1 = 7.177, P < 0.0001; Table 2). Specifically, altitude, landscape roughness and forest cover showed significant opposite patterns in Y compared to S and A (Table 2). Moreover, shrub-lands were more highly selected by S and A than by Y (Table 2). Grasslands were positively selected among the three age classes while slope and rocky areas were negatively selected (Table 2).

SDMs showed that both the size and the number of suitable areas for bearded vultures in our study area were different for the three age classes considered (Fig. 2). The minimum surface area suitable for the vulture was predicted by MAXENT in all the three age classes considered. Actually, 419 km² (5.39 % of the study area) resulted suitable for young individuals, 1013 km² (13.02 % of the study area) were suitable for sub-adults and 1194 km² (15.35 % of the study area) for adults (Fig. 2). On the other side, MADIFA showed the widest suitable areas for all three age classes considered.

Table 3 Values of the t-statistic derived by pairwise *t* tests of ten distribution models (*MAXENT* maximum entropy algorithms, *MADIFA* factorial decomposition of Mahalanobis distances, *GLM* generalised linear models, *BRT* boosted regression trees, *GAM* generalized additive models, *CTA* classification tree analyses, *ANN* artificial neural networks, *FDA* flexible discriminant analyses, *MARS* multivariate adaptive regression splines, *RF* random forests) and their ensemble prediction (EP) among three age classes considered (*A* adults, *S* sub-adults, *Y* young)

Model	A vs. S	S vs. Y	A vs. Y
MADIFA	0.98	1.06	1.21
MAXENT	61.83*	−172.58***	−233.82***
GAM	53.31*	−138.88***	−197.17***
FDA	47.41*	−165.81***	−216.37***
ANN	79.18*	−157.49***	−237.06***
MARS	52.05*	−155.05***	−210.77***
GLM	25.51*	−186.41***	−217.01***
CTA	−117.91***	−303.04***	−178.72***
BRT	104.79***	−179.73***	−281.44***
RF	−51.64*	−229.27***	−176.37***
EP	28.67*	−190.31***	215.287***

For abbreviations of species distribution models see materials and methods section

*** $P < 0.0001$; * $P < 0.05$

A total of 3115 km^2 (40.03 % of the study area) was classified as suitable for young individuals while 3821 km^2 (49.09 % of the study area) for sub-adults and finally adults reached the maximum suitable surfaces, 3895 km^2 (50.05 % of the study area), among the three age classes considered (Fig. 2). GLM classified the minimum number of continuous areas suitable for the Y vulture (N = 762), while ANN those of S (N = 378) and A (N = 1,017). RF showed the maximum number of suitable continuous areas for Y (N = 5472), while MAXENT and CTA showed those of S and A (N = 6799 and N = 6205, respectively).

Paired *t* tests showed significant differences in all SDMs per cell among the three age classes considered except for MADIFA (Table 3). By excluding MADIFA, highly significant differences were recorded between S and Y and between A and Y in all the SDMs (Table 3), while between A and S only CTA and BRT showed highly significant differences (Table 3). Similarly, paired t-tests showed significant differences ($P < 0.0001$) considering the ratio between the predicted distribution areas of three age-classes between S and Y and between A and Y in all the SDMs.

K-fold cross-validations, carried out with sub-samples of the original data, showed significant values for all the evaluation methods of all distribution models in the three age classes considered (Table 4; Fig. S3), highlighting the high predictive accuracy of our models. Similarly to the original data, model validation carried out with new field data collected in the Maritime Alps showed significant values for both AUC and BI statistics of all the distribution models among the three age classes of bearded vulture (Table 4; Fig. S3). This suggests that our models were accurate also in predicting the occur-

rences of our target species in a different temporal range. Moreover, we recorded a high predictive accuracy of all the distribution models when also projecting their predicted values in the Gran Paradiso National Park (Fig. 3). In fact, the validation with external dataset showed significant values for both the validation statistic for all the three age classes (Table 4; Fig. S3), meaning that our models were accurate also in predicting occurrences of bearded vulture derived by an independent dataset.

Considering the residuals of all the SDMs in the three age classes, Moran's I values were < 0.05 and statistically non-significant at each distance indicating no autocorrelation.

Discussion

Even if niche models and SDMs were widely used in landscape ecology to achieve a variety of objectives (Guisan et al. 2013), this study represents their first application for verifying different patterns in the ecological niche of different age classes. In fact, we showed significant differences both when hindcasting the ecological niche and when forecasting the potential distribution of the three age classes considered, and thus, we encourage researchers to further investigate ecological niche shift between age classes to promote the best conservation and management actions.

Different patterns in ecological niche and spatial distribution of age classes

Since we considered the same set of predictor variables for developing both hindcasting and forecasting models, as well as the same available area for the three different age classes of bearded vultures, we verified that differences among ecological niches were due to differences in the distribution patterns of individuals of different age classes.

As suggested by several authors (e.g. Dormann et al. 2007; Zuur et al. 2010) to reduce biased estimations, we discarded autocorrelated and outlier species locations to reduce biased estimation and only used unrelated predictors to develop our models. In fact, when modelling the ecological niche of species, deep data exploration, as undertaken in this study, is fundamental in avoiding biased estimations resulting from various factors (e.g. spatial autocorrelation among species occurrences, incidence of outliers and collinearity among predictor variables; Dormann et al. 2007; Zuur et al. 2010). Moreover, we used a sampling effort map to equally weight pseudo-absences to presences in the development of reliable hindcasting and forecasting models, because pseudo-absences equally weighted to presences yield the most reliable distribution models (Barbet-Massin et al. 2012).

Table 4 Model validation of ten species distribution models (*MAXENT* maximum entropy algorithms, *MADIFA* factorial decomposition of Mahalanobis distances, *GLM* generalised linear models, *BRT* boosted regression trees, *GAM* generalized additive models, *CTA* classification tree analyses, *ANN* artificial neural networks, *FDA* flexible discriminant analyses, *MARS* multivariate adaptive regression splines, *RF* random forests) and their ensemble prediction (EP) developed for the three age classes considered (*A* adults, *S* sub-adults, *Y* young)

Model	AUC			BI		
	A	S	Y	A	S	Y
Original data (average of ten subsamples)						
RF	0.987***	0.964***	0.975***	0.988***	0.979***	0.988***
BRT	0.922***	0.874***	0.856***	0.998***	0.998***	0.998***
MAXENT	0.913***	0.859***	0.843***	0.998***	0.998***	0.988***
CTA	0.911***	0.793***	0.854***	0.983***	0.998***	0.998***
MARS	0.903***	0.871***	0.828***	0.952***	0.964***	0.998***
GAM	0.898***	0.889***	0.851***	0.988***	0.998***	0.998***
FDA	0.898***	0.852***	0.861***	0.976***	0.976***	0.988***
GLM	0.887***	0.924***	0.863***	0.998***	0.976***	0.988***
ANN	0.870***	0.895***	0.864***	0.964***	0.931***	0.988***
MADIFA	0.745***	0.740***	0.777***	0.956***	0.904***	0.952***
EP	0.936***	0.885***	0.866***	0.988***	0.997***	0.988***
New field data						
RF	0.859***	0.799***	0.844***	0.964***	0.966***	0.964***
BRT	0.844***	0.811***	0.816***	0.831***	0.964***	0.976***
MAXENT	0.836***	0.792***	0.789***	0.952***	0.852***	0.976***
CTA	0.796***	0.789***	0.794***	0.717***	0.943***	0.762***
MARS	0.849***	0.801***	0.806***	0.794***	0.758***	0.976***
GAM	0.817***	0.779***	0.802***	0.806***	0.879***	0.964***
FDA	0.839***	0.804***	0.801***	0.915***	0.952***	0.927***
GLM	0.816***	0.771***	0.781***	0.831***	0.806***	0.927***
ANN	0.816***	0.751***	0.768***	0.903***	0.855***	0.964***
MADIFA	0.725***	0.731***	0.761***	0.883***	0.842***	0.942***
EP	0.851***	0.786***	0.812***	0.855***	0.916***	0.915***
External data						
RF	0.758***	0.835***	0.827***	0.828***	0.837***	0.836***
BRT	0.758***	0.869***	0.831***	0.811***	0.855***	0.773***
MAXENT	0.78***	0.857***	0.824***	0.897***	0.815***	0.858***
CTA	0.712***	0.771***	0.781***	0.817***	0.824***	0.845***
MARS	0.752***	0.818***	0.814***	0.855***	0.945***	0.918***
GAM	0.785***	0.824***	0.819***	0.873***	0.727***	0.982***
FDA	0.762***	0.818***	0.806***	0.819***	0.818***	0.855***
GLM	0.742***	0.787***	0.787***	0.818***	0.827***	0.801***
ANN	0.819***	0.763***	0.772***	0.814***	0.773***	0.864***
MADIFA	0.713***	0.732***	0.699*	0.864***	0.824***	0.733***
EP	0.929***	0.878***	0.846***	0.835***	0.816***	0.818***

Area Under the Curve (AUC) varies from 0 (worse than random model, 0.5) and 1 (best discriminating model). Boyce' Index (BI) varies from −1 to 1 and higher values indicate good agreement between predictions and data with 0 corresponding to random agreement
*** $P < 0.0001$; * $P < 0.05$

Considering hindcasting models, the K-select analysis led us to identify the main features of the habitat selected by the different bearded vulture age classes. Thus, we detected a functional response in habitat selection, i.e. a variation of the habitat selection according to the age classes considered. This analysis is therefore suitable for defining several groups of animals that select the same habitat characteristics (Calenge et al. 2005). Actually, we showed that all three age classes have significantly different ($P < 0.0001$) patterns of distribution compared to random ones. Moreover, we found that sub-adults and adults, while significantly different ($P < 0.0001$), shared similar patterns, especially when considering altitude, distance to human settlements, forest cover, and shrub-lands.

Forecasting models also showed differences among the age classes considered. In fact, SDMs showed different patterns in the potential distribution of the three bearded vulture age classes. Similarly to the K-select analysis, we found that sub-adults and adults were more similar, while significantly different ($P < 0.05$), potential distribution patterns than the young individuals did, except for CTA and BRT. Thus, in agreement with the hindcasting model, forecasting models showed that young individuals had different patterns of distribution compared to the other two age classes. These differences can be explained by the behaviour of young individuals. In fact, large vultures often do not secure territories until they are several years old due to their exploratory behaviour (Phipps et al. 2013), and thus they can show different patterns in their distribution (Krüger et al. 2014). Immature birds are mainly concerned with finding and tracking food resources, whereas sub-adults and adults have additional ecological requirements that are
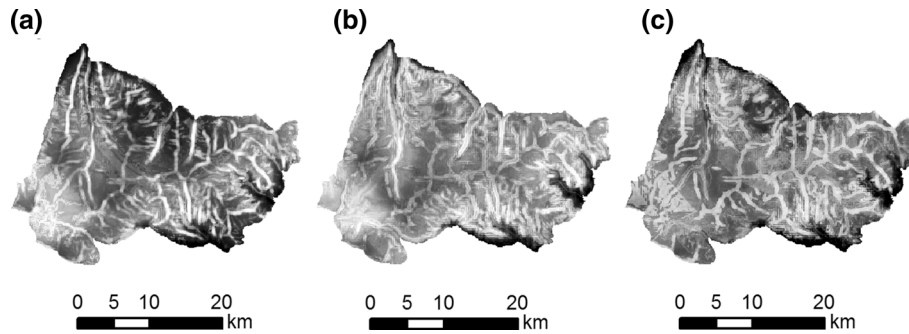
Fig. 3 Projection of the results of the ensemble species distribution models (*bright–dark grey* indicates *higher–lower* species occurrence probability) for the age classes **a** young, **b** sub-adult and **c** adult in the Gran Paradiso National Park (IT)

not uniquely trophic (Hirzel et al. 2004). The forests of our study area, which are more used by young bearded vultures, are not very dense and can be explored by individuals which roam far from potential nesting areas in search of prey remains. Several large mammals, including red deer, roe deer, alpine chamois, alpine ibex and wild boar, locally reach high density inside open forests, where they are preyed upon by the wolf (*Canis lupus*), which recolonized the Western Alps and reach fairly high density as well. All birds include predictable sources of food into their home range. This is particularly important in the case of young, inexperienced birds, which stay in the exploration phase for long periods (Gil et al. 2014).

In fact, even if all ten SDMs and their EP showed differences among models in the prediction of suitable areas (e.g. extent, distribution, and number), we found overall different patterns of distribution among age classes confirming that they all had a high efficiency in describing age class occurrences. Differences among SDMs were due to different assumptions, complexities of algorithms, methods to relate the response, and the predictor variables (Tsoar et al. 2007; Warren and Seifert 2011). Since there is no consensus regarding the best method to forecast species' distribution (Qiao et al. 2015), we strongly suggest to test for multiple SDMs and, in order to avoid single model uncertainty, their ensemble prediction (Araùjo and New 2007; Coetzee et al. 2009; Jones-Farrand et al. 2011).

However, like with all biological models, we strongly encourage carefulness in interpreting our results due to variability in natural ecosystems and bias in data used to develop the models, as well as uncertainty in model predictions, which could increase the uncertainty of the results (Pauly and Christensen, 2006; D'Elia et al. 2015). Moreover, while available, additional factors such as distribution and density of food resources, the degree to which threats have been eliminated or reduced, density of competitors, and nest predators should be included and tested in the analyses. Contrary to what expected by Hirzel et al. (2004), we have not noticed an effect of mineral composition of the substrate. We did not observe a scarcity of the species in landscapes dominated by silicate substrates. Additionally, the collection of new field data will increase our ability to identify remaining areas of unoccupied but suitable habitat across both neighbouring and distant regions. However, we showed that SDMs had high predictive accuracy, suggesting that our models might be useful for forecasting the presence of individuals of different age classes. Indeed, our models retained strong predictive performance also across geographic space and time, as highlighted by the high values of the validation statistics derived by the two external datasets. Therefore, even if the bearded vulture is recolonising part of its historical range, both hindcasting and forecasting models produced useful results despite the violation of the species-environment equilibrium assumption (Cianfrani et al. 2010).

Thus, in agreement with several authors (González et al. 2006; Morrison and Wood 2009; Krüger et al. 2014), we found that the spatial distribution differed according to an individual's age. The majority of niche and distribution models for vultures thus far so not disentangle age specific characteristics at occurrence points (e.g. Donázar et al. 1993; Hirzel and Arlettaz 2003; Margalida et al. 2008; Bogliani et al. 2011). Indeed for the first time, our research increased model precision in identifying age specific threat areas to prioritise threat reduction measures. In fact, the ecological niche and requirements of the bearded vulture differed significantly among the three age classes considered in the Western Alps. Therefore, our age specific models offer a more detailed description of the vulture's ecological niche in contrast to models with grouped occurrence data and showed a better interpretation of the comparison of different vulture habitats in geographic space. This information is also essential identifying the most suitable sites for conservation and reintroduction of a species that requires different, but proximal, ecosystems to survive and reproduce. Moreover, our findings are particularly important for species that take a long time to mature (Penteriani and Delgado 2009), and knowledge of these differences may further contribute to ensuring that management actions are targeted appropriately (Krüger et al. 2014).

Indeed, the exploratory behaviour of young vultures may expose them to multiple threats, therefore, young individuals can be exposed to different threats or different levels of threat than those found for sub-adults and adults (Penteriani et al. 2005; Penteriani and Delgado 2009; Krüger et al. 2014). In large vultures, non-adults form a large proportion of the population (Kenward et al. 2000), thus conservation measures designed to protect breeding birds only may not be sufficient for safeguarding the population as a whole (Penteriani et al. 2005; González et al. 2006; Krüger et al. 2014) and vice versa.

Age-specific niche modeling may also be useful for species that use different environments in different stages of their life history which is essential for species' survival and reproduction. We concluded by strongly encouraging the separate testing and modelling of ecological niche age specific patterns because it is assumed (often incorrectly) that individuals achieve their needs during the life without variations of requirements.

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