Motion capacity, geography and ecological features explain the present distribution of a migratory top predator

Article *in* Ecological Research · January 2015

DOI: 10.1007/s11284-014-1226-2

Michele Panuccio
Mediterranean Raptor Migration Network

Giuseppe Lucia
Mediterranean Raptor Migration Network

Nicolantonio Agostini
Mediterranean Raptor Migration Network

Giuseppe Bogliani
University of Pavia

Motion capacity, geography and ecological features explain the present distribution of a migratory top predator

Michele Panuccio, Giuseppe Lucia, Nicolantonio Agostini, Dario Ottonello & Giuseppe Bogliani

Ecological Research

ISSN 0912-3814
Volume 30
Number 1

Ecol Res (2015) 30:181-190
DOI 10.1007/s11284-014-1226-2

Ecol Res (2015) 30: 181–190
DOI 10.1007/s11284-014-1226-2

ORIGINAL ARTICLE

Michele Panuccio · Giuseppe Lucia · Nicolantonio Agostini
Dario Ottonello · Giuseppe Bogliani

Motion capacity, geography and ecological features explain the present distribution of a migratory top predator

Received: 14 July 2014 / Accepted: 24 November 2014 / Published online: 6 December 2014

Abstract Presence and distribution of ecological barriers shapes the distribution of migratory birds as well as any other living organism. In Italy, short-toed snake eagles (*Circaetus gallicus*) breed in the northern and western areas of the peninsula but the species is rare in the south or the islands. The Italian population of this species migrates across the Mediterranean at the Strait of Gibraltar rather than crossing the large stretch of sea between Sicily and Tunisia. This suggests that, in Italy, fall migration is oriented south–north and spring migration north–south. In this paper we test the hypothesis that the accessibility of the suitable habitat area along the Italian Peninsula is in relation to the geographical migration pattern of the studied species. We integrated information from the movement ecology, the geography and the traditional ecological features in order to provide an ecological explanation of the current biogeographical pattern of our model species. We compared statistical models with and without latitude as a predictor. Each model was based on ecological and geographical variables, including land use, prey availability, spatial distribution of environmental elements (patch analysis), geomorphology, and geography. These models predict two patterns of suitability for short-toed snake eagles in Italy. Our results suggest that the abundance of this species increases with latitude despite the existence of large areas of suitable habitat in southern Italy. We suggest that the actual distribution of the short-toed snake eagle in Italy is influenced by the particular migration path used by this population, supporting the hypothesis that this species is still colonizing the Italian Peninsula through an unexpected colonization direction from north to south.

Keywords Colonization direction · Accessibility · Migratory detour · Ecological barriers · Short-toed snake eagle · *Circaetus gallicus* · Italy

Electronic supplementary material The online version of this article (doi:10.1007/s11284-014-1226-2) contains supplementary material, which is available to authorized users.

M. Panuccio (✉) · G. Bogliani
DSTA-Department of Earth and Environmental Sciences, University of Pavia, Via Ferrata 9, 27100 Pavia, Italy
E-mail: panucciomichele@gmail.com
Tel.: 0039-349-2340719

M. Panuccio · G. Lucia · N. Agostini
MEDRAPTORS (Mediterranean Raptor Migration Network), Via Mario Fioretti 18, 00152 Rome, Italy

D. Ottonello
DAIS-Department of Environmental Sciences, Informatics and Statistics, Cà Foscari University of Venice, Dorsoduro 2137, 30123 Venice, Italy

Introduction

The present distribution of an organism is the result of the interaction between ecological, movement-related and geographical features (Cumming et al. 2012). In particular the ecological niche and the probability of colonization affect the distributional limits of a species (Begon et al. 2006). Ecological niche is related to several different factors, including foraging and nesting opportunities. The probability of colonization depends on the dispersal abilities of the species and its dispersal behaviour, as well as geographic features such as natural barriers (Alerstam 1990; Tellería et al. 2009). Therefore, the current biogeographical patterns might be explained by hypotheses that are related to environmental, morphological and historical data (Cumming et al. 2012). Europe has been colonized by several species of birds since the end of the last glacial age about 10,000 years ago. Several species have colonized areas located at higher latitudes through a northern extension of their breeding ranges (Mayr and Meise 1930; Bruderer and Salewski 2008). From the end of last glaciation, Palaearctic migrants have followed a colonization path from south to north and were assisted by the process of dispersal (Alerstam 1990; Berthold 2001; Rappole and Jones 2002).

The short-toed snake eagle (*Circaetus gallicus*) is a widespread summer breeder in Europe and in the Mediterranean basin and overwinters in a wide area of Africa south of Sahara (Cramp and Simmons 1980; Ferguson-Lees and Christie 2001). It is a highly specialized raptor, preying predominantly on snakes (up to 100 %; Ferguson-Lees and Christie 2001); therefore, as a specialized predator, its distribution should coincide with the distribution of its prey (Newton 1998). A study carried out in Spain (Moreno-Rueda and Pizarro 2007) showed that short-toed snake eagles are found mainly in areas with shrub-lands, where they can easily locate and capture their prey, and in forests, which provide suitable nesting habitat. Eagle presence also correlates with snake species richness (Moreno-Rueda and Pizarro 2007). Research in Greece also showed that the presence of short-toed snake eagle is linked to forests for nest building and to open areas like pasturelands and cultivation for foraging (Bakaloudis et al. 1998, 2005). The European population of short-toed snake eagle is estimated to be less than 10,000 pairs and its status is Rare; its low reproductive rate and high diet specialization makes it vulnerable to extinction (Birdlife International 2004). The population in Italy is estimated to 350–400 breeding pairs (Birdlife International 2004), but recent counts at some migration hotspots have shown that their numbers are increasing (Baghino and Premuda 2007; Panuccio et al. 2012, 2013). Most of the breeding pairs in Italy are distributed in northern Italy and along the western slope of central Italy (Campora and Cattaneo 2006). In Southern Italy few tens of pairs do breed but it seems that the species has been expanding in recent years (Mellone et al. 2011). The short-toed snake eagle is a broad-winged raptor that uses soaring-gliding flight rather than powered flight; as a result this species tends to migrate over land and to avoid water crossing where thermal currents are absent and it would be forced to use active flight (Kerlinger 1989). Individuals belonging to the Italian population migrate both during spring and autumn across the Strait of Gibraltar (14 km of water crossing) rather than taking the Central Mediterranean flyway that is shorter, although the water crossing is longer (at least 130 km; Agostini et al. 2002a, b, 2004; Mellone et al. 2011). Similarly, individuals breeding in Greece migrate through Turkey and cross the sea at Bosphorus (Panuccio et al. 2012). Since most breeding pairs of this species in Italy are located along its migration route, Agostini and Mellone (2008) suggested that the short-toed snake eagle may still be colonizing Italy from the western part of its European breeding range and that, therefore, the population has not yet reached its carrying capacity.

The distribution of living organisms is a widely studied subject in ecology but, on the other hand, the interaction between distribution and migration routes is a poorly investigated topic. In this paper we test the hypothesis that the actual distribution of short-toed snake eagle in Italy reflects the colonization history and is strongly influenced by the migration route more than other ecological parameters such as prey availability and the spatial distribution of vegetation and morphology. For this purpose in the analysis we considered several ecological (land use and prey richness), topographic (altitude), and latitudinal parameters in order to determine which affect the breeding distribution of short-toed snake eagle in Italy and to determine whether some areas of Southern Italy are not suitable for short-toed snake eagles or, although if suitable, they have not been colonized or re-colonized yet.

Methods

Study area

The study was performed in Italy (301,302 km^2) including the large islands of Sicily and Sardinia. On the 01-Jan-2010 the human population was 60,340,328 (ISTAT, website: http://demo.istat.it/pop2010/index.html). The climate varies considerably with latitude. In the south it is warm, with almost no rain in summer, while in the Northern part of the Peninsula temperature is cool with rainfall more evenly distributed throughout the year. The mean altitude in Italy is 337 m above sea level. According to Corine Land Cover 2000, Italy is composed of 152,435 km^2 of cultivated lands (50.6 %), 18,835 km^2 of permanent pasture lands (6.3 %), 79,425 km^2 of woodlands (26.4 %), 22,555 km^2 of shrubs (7.5 %), 3,827 km^2 of wetlands (1.3 %) and 14,340 km^2 of urbanized areas (4.8 %). In the lowlands agriculture is very intensive and devoted mainly to monoculture, while on the hills and mountains traditional and less intensive agriculture is still practiced although land abandonment is spreading. Mainland Italy may be divided into four major geographical and vegetational areas: the Alps and the Padana plain in the north, the Apennines and the coastal slopes (7,456 km of coastlines) in the center and the south. The Alpine area is relatively unspoiled, with deciduous, mixed coniferous forests, alpine pastures above the timberline, and snowfields and glaciers on higher peaks. The Po valley is the largest lowland area in Italy, mainly covered by intensive agriculture. Large areas of the Apennine mountains are still covered by semi-natural deciduous forests, mostly oak (*Quercus* spp.), beech (*Fagus sylvatica*) and sweet chestnut (*Castanea sativa*), although large areas have been cleared for agriculture and pasture. Coastal areas in Italy are dominated by shrub and in particular by typical Mediterranean scrub. The protected areas in Italy cover a surface of 13,000 km^2 (4.3 %; Brandmayr 2002).

Sampling units

The geographical grid we used to divide the Italian peninsula in several sampling units is the same used from

Military Geographical Institute (IGM) to draw the 1:25,000 maps of Italy in UTM projections; we considered 3,541 square cells of 10 × 10 km. Because the Italian peninsula is located over three "zones" of 6 degrees in latitude, at the transition from one zone to another the grid is compressed and rotated, so some squares (less than 5 % of the total) have an area less than 100 km^2. A similar limitation of extension involves also coastal cells. To avoid effects due to the difference in size among cells, we included variables that used percent coverage instead of absolute cell surface. To determine prey availability (reptile species richness), we used the grid and data set used by Sindaco et al. (2006) for the atlas of the reptiles and amphibians of Italy made available by SHI (Societas Herpetologica Italica).

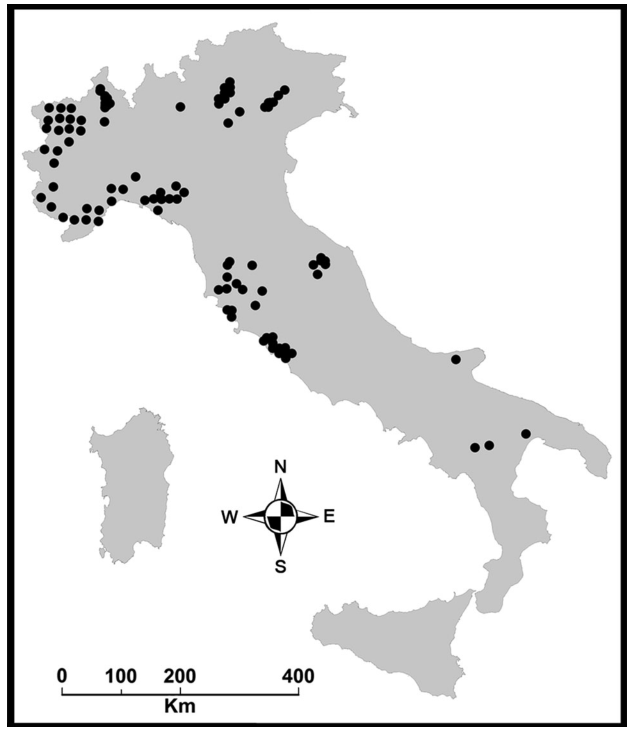

Fig. 1 Distribution map of short-toed snake eagle in Italy, according to the data compilation from different local atlases. Each *dot* denotes presence in a 10 × 10 km^2

Presence data of short-toed snake eagle

Short-toed snake eagle presence data was obtained by consulting several atlas of bird distribution in Italy; we assumed that the coverage effort for each local atlas was similar since all atlas were realized following similar guidelines (Fig. 1; Mingozzi et al. 1988; Fraissinet and Kalby 1989; Brichetti and Fasola 1990; Meschini and Frugis 1993; Gruppo Vicentino Studi Ornitologici "NISORIA" 1994; Boano et al. 1995; Ravasini 1995; Tellini Florenzano et al. 1997; Bon et al. 1999; Gellini and Ceccarelli 2000; Fracasso et al. 2003; Bordignon 2004; Pedrini et al. 2005; Bionda and Bordignon 2006; Giacchini 2007; Mezzavilla and Bettiol 2007; Ientile and Massa 2008; La Gioia 2009) and also by using personal observations of nest locations. In the atlas, the presence of species in each sample unit is listed in three ways: certain, probable and possible, following the indications of EBCC (Hagemeijer and Blair 1997). In this study, we considered only the first two categories to classify presence. In most cases we used the same grid as that used in the atlas; when the atlas grid was smaller than ours, we assigned a presence value to our cell if at least one of the atlas cells were included in our sampling units. At the end of data collecting we had 94 cells (10 × 10 km) with presence data.

Predictive variables

To model the relationship between habitat features and short-toed snake eagle presence, we first considered 30 environmental variables (Table S1) grouped into 5 categories: land use, prey availability, spatial distribution of environmental elements (patch analysis), geomorphology, and geography (latitude and longitude). Variables representing land use were obtained by Corine Land Cover 2000 to the third level. We first grouped land use categories that had similar ecological significance for the study species into seven new variables: forests, shrubs, crops and orchards, meadows and pastures, populated areas, bare rock, and wetlands. For each cell we calculated the percentage coverage of land use variables. Prey availability was measured as the number of reptile species (snakes and lizards, excluding Gekkonidae for lack of daytime activities of this family) present in each cell. Data on the presence of reptiles were derived from the atlas of Sindaco et al. (2006). Analysis of the spatial distribution of land use patches was carried out with the Esri ArcMap 9.2 Patch Analyst extension (Rempel and Carr 1999). This analysis investigates the geometry of selected patches (here, land use polygons) and perimeters (for details on these measures see Elkie et al. 1999). Data on the geomorphology were derived from digital elevation model (DEM) of Italy with a spatial resolution of 250 m. In each cell six measures of altitude were calculated: minimum, maximum, average, median, standard deviation, and the coefficient of variation. Geographical variables were represented by values of latitude and longitude of the cell centroid. In particular we used the latitude as a proxy of the distance from the main migration route of the studied species. Finally we squared the following variables to evaluate if the values of forest cover, mean altitude and mean patch fractal dimension were non-monotonically related to the suitability of the study area for the short-toed snake eagle.

Statistical models and procedure

We compared models with and without latitude as a predictor to test the hypothesis that our studied species is still colonizing Italy along north–south gradient. Here following are the details of the procedure we followed to build the different models.

We first tested for collinearity of variables within the categories inside the sampling units in order to select variables to use in the models. To do this we tested the normality of variables with Kolmogorov–Smirnov test, and if any variables were not normally distributed we transformed the data (square root, arcsine or natural logarithm depending on the variable). We used a logistic regression to test which predictive variables affect the distribution of the species in Italy. In order to verify which variables influenced the presence of short-toed snake eagles we compared variables in squares with presence data ($n = 94$) with the same number of cells without presence ($n = 94$); these cells were randomly selected among those in which the species was not present according to the distribution reported in the atlas we consulted. We also generated new variables by squaring those variables that were non-monotonically related to the presence of the species. We retained a priori the latitude as predictor since it is in our starting hypothesis, but also the three variables that have been previously considered significant in explaining short-toed snake eagles presence. These variables are: prey availability, proportion of forests, proportion of shrubs (Sánchez-Zapata and Calvo 1999; Bustamante and Seoane 2004; Bakaloudis et al. 2005; Moreno-Rueda and Pizarro 2007; López-Iborra et al. 2011). After that we tested 23 random combination of models (all containing those four retained variables) excluding those variables who were auto-correlated. The starting set of variables for the logistic regression is shown in Table 1. Model selection was made choosing the model with the smallest value of Akaike information criterion (AIC; Manly et al. 2002). As model B we run the same selected model without the latitude as predictor. In the models we forced all of the chosen variables in the same run with the Enter method in SPSS software.

Table 1 Variables used to perform logistic regression

Category	Variables
Land use	Proportion of meadows and pastures
	Proportion of crops and orchards
	Proportion of forests
	(Proportion of forests)^2
	Proportion of shrubs
Prey availability	Number of reptile species (snakes and lizards)
Spatial distribution of environmental elements (land use—patch analysis)	Mean patch edge
	Mean patch fractal dimension
	(Mean patch fractal dimension)^2
Geomorphology	Mean altitude
	(Mean altitude)^2
Geography	Latitude

We then obtained a value of probability of presence between 0 and 1 for each cell that varies depending on the model and we used this difference to compare each model including "Y_CENTR" and the corresponding model without this variable.

Moreover, to test the results of logistic regression models we generated a further model based on boosted regression trees analysis (BRT). Unlike the logistic regression, BRT fits a large number of relatively simple models which are then combined for prediction. BRT uses two algorithms: regression trees and boosting builds and combines a collection of models (De'ath and Fabricius 2000; Friedman et al. 2000; Schapire 2003; Leathwick et al. 2006; Elith et al. 2006, 2008). For the BRT model we used the same variables used in the regression model and we chose the best model selected according to lower deviance value and the area under curve (AUC) of its receiver operating characteristic (ROC).

Results

Variables used to run the analysis are shown in Table 1. The best model (Model A) with the lowest value of AIC included nine variables (Table 2). This model achieved an overall value of correct percentage of 77.7 % (84.1 % for absence and 64.9 % for presence). The AUC value of the ROC curve was 0.848. We tested the same model without the latitudinal variable; this second model (Model B) showed a higher AIC value and included eight variables (Table 2). This model achieved an overall value of correct percentage of 74.5 % (81.5 % for ab-

Table 2 Logistic regression statistics (Wald), parameter estimates (B) and significance (P) of the variables included in the short-toed snake eagle distribution Model A and B, in Italy

	Model A			Model B		
	B	Wald	P	B	Wald	P
Latitude	0.000	20.655	0.000	–	–	–
Mean altitude	−0.001	1.943	0.163	−0.002	3.453	0.063
(Mean altitude)^2	0.000	3.280	0.070	0.000	8.125	0.004
Proportion of forest	10.547	22.306	0.000	10.960	24.842	0.000
(Proportion of forest)^2	−8.895	13.975	0.000	−8.390	12.763	0.000
Number of reptile species	0.185	19.102	0.000	0.212	28.727	0.000
Proportion of shrubs	1.937	2.785	0.095	−488.816	0.061	0.805
Mean patch fractal dimension	−534.33	0.766	0.381	187.219	0.710	0.399
(Mean patch fractal dimension)^2	201.555	0.738	0.390	0.308	0.704	0.402

sence and 60.4 % for presence); the AUC value of the ROC curve was 0.824. Using the results of these two models we created two different distribution maps of probability. Model A, which includes latitude as a variable, predicts that the potential distribution of short-toed snake eagles is mainly restricted to central and northern Italy (Fig. 2a). By contrast, Model B, which does not include latitude as a variable, predicts a wider potential distribution that includes southern Italy (Fig. 2b).

Similarly, plotting the probability of occurrence of short-toed snake eagles in the sample units in relation to latitude, a clear difference between the two models appears. Model B predicted a more homogeneous probability of species distribution along the latitudinal gradient (Fig. 3b). On the other hand, according to the same model tested with latitude as predictor, the probability of occurrence of the studied species is restricted to the northern and the central part of the Italian peninsula (Fig. 3a).

The model obtained using boosted regression trees (deviance = 0.244, deviance Cross-validation estimate = 0.161; SE = 0.006) confirmed that the three most important predictive variables for the presence of short-toed snake eagle are latitude, mean altitude and the number of prey species (Fig. 4). For all these parameters, increasing values increased the fitted function of the model. Plotting the interaction between the mean altitude and the number of prey species we obtained a maximum fitted value of 0.57 (Fig. 5) in correspondence of the large number of species and a medium–high value at mean altitude. The increase of value of the forest variable was also linked to an increase in model fitting despite its low contribution in the model.

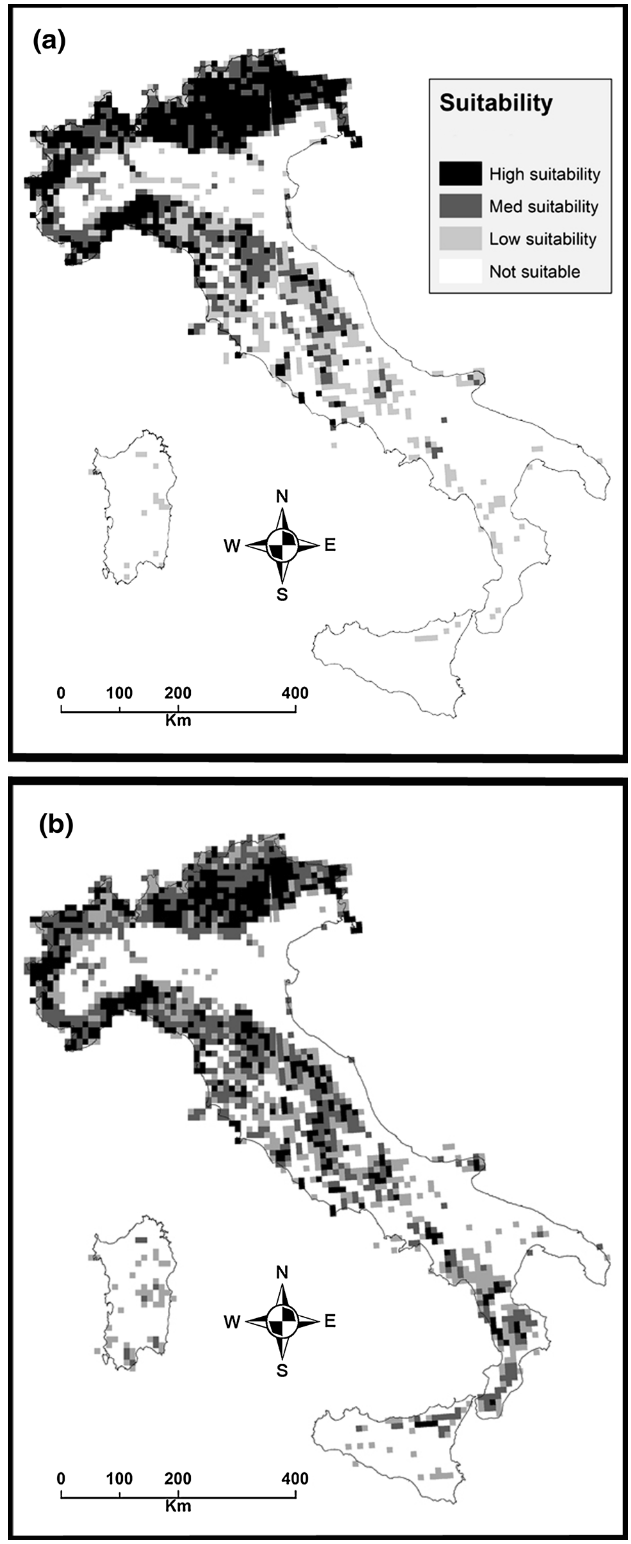

Fig. 2 Probability classes of the short-toed snake eagle distribution according to Model A (**a**) and Model B (**b**) in Italy

Discussion

Ecological parameters

This study shows that, of the variables that potentially affect the breeding distribution of the short-toed snake eagle, the strongest predictors are prey richness, forests, and the mean altitude of the territory. This result was obtained using both models A and B as well as the boosted regression tree model. Forests are important for short-toed snake eagles because the species nests in these habitats; this is in agreement with previous research (Sánchez-Zapata and Calvo 1999; Bustamante and Seoane 2004; Bakaloudis et al. 2005; López-Iborra et al. 2011). As shown by the high Wald value of the variable "square root forest" (Table 2), the increase of forested areas is important for the presence of short-toed snake eagles; however, there is a threshold value beyond which the extension of forests becomes limiting for this species, since snake eagles hunt in open areas where reptilian prey are probably abundant and most accessible (see Moreno-Rueda and Pizarro 2007; Bakaloudis 2009; López-Iborra et al. 2011). Mean altitude may be important in the BRT model because, in Italy, forests are almost absent from lowlands, such as the Po valley, and because agriculture on the Italian plains is intensive (monoculture). Therefore, lower altitudes do not

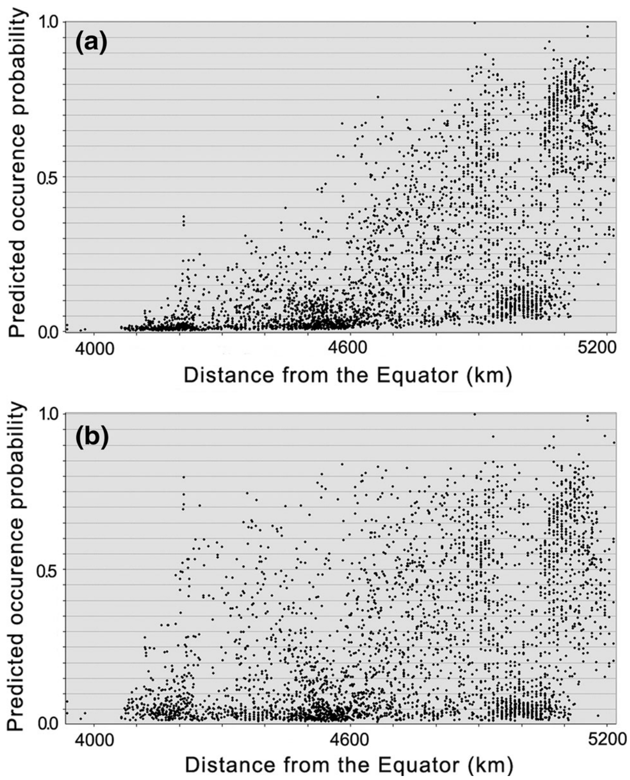

Fig. 3 The probability of occurrence of short-toed snake eagles at different latitudes in the two different models with (**a**) and without (**b**) latitude variable

provide suitable nesting habitat for short-toed snake eagles in Italy. Prey richness was the other variable that explained eagle distribution in all models. A previous study of short-toed snake eagles in southern Spain found a relationship between the presence of eagles and species richness of reptiles (Moreno-Rueda and Pizarro 2007). Despite its high trophic specialization, the short-toed snake eagle behaves as a taxonomic generalist within this prey type, and selects optimal prey sizes regardless of the species (Gil and Pleguezuelos 2001).

What factors, then, explain the correlation between prey species richness and eagle distribution? Different hypotheses have been proposed to explain this correlation. One possibility is that the abundance of reptile individuals correlates with reptile species richness and the abundance of individuals determines the presence of raptors (Evans et al. 2005; Moreno-Rueda and Pizarro 2007). Intra- and inter-species interactions have also been proposed. It has also been hypothesized that the presence of short-toed snake eagles increases reptile species richness by controlling the most abundant species and reducing the intensity of competition in the reptile community through a top-down process (Moreno-Rueda and Pizarro 2007).

Differently from previous research, our model did not reveal shrubland to be an important variable. This may be because other variables have a higher importance in explaining the probability of the occurrence of the studied species in the study area (i.e. number of reptile species and proportion of forests).

The role of the latitude

In our first Model (A) latitude also had a significant effect on the breeding distribution of short-toed snake eagles in Italy. Its effect is the opposite of that documented in Spain (López-Iborra et al. 2011), where latitudinal increase was shown to have a negative effect on the distribution of the species. By contrast, we found that eagle presence seems to increase with latitude. However, the distribution of the short-toed snake eagle in Europe does not lead to the conclusion that latitude could have, at a continental scale, the effect showed in the model A. In fact, this eagle is widely distributed in southern Europe at the same latitude of southern Italy in Spain, Greece and Turkey (Handrinos and Akriotis 1997; Mañosa 2003; Kirwan et al. 2008). In addition, our model B clearly showed that large areas, especially in the southernmost part of the peninsula, are suitable for this species although the known distribution, showed by data available for Italy, is well represented by the map obtained with the Model A. The discrepancy between model B and the actual distribution of the short-toed snake eagle in Italy (well reflected by Model A) could result from the interaction between the motion capacity of the species and the geography of the Italian Peninsula. The Central Mediterranean is a dispersal barrier for this species, since short-toed snake eagles avoid crossing large bodies of water during migration by using soaring-gliding flight over land (Agostini et al. 2002a, b; Mellone et al. 2011; Panuccio et al. 2012). The majority of birds breeding in Italy migrate to and from Africa through the Strait of Gibraltar; in spring they arrive in Italy about 1,000 km NW of southern regions of the Peninsula via southern France. As suggested by previous research (Agostini and Mellone 2008), the actual distribution in Italy may reflect the particular migration path used by this population. Considering the increasing number of breeding pairs and of the occupied territories in central and southern Italy (Baghino and Premuda 2007; Mellone et al. 2011), our results support the hypothesis that short-toed snake eagles are still colonizing the country moving from north to south of the peninsula primarily along its western slope. However, we cannot exclude that the increasing number of the short-toed snake eagle in Italy reflects a recovery from a previous reduction of the population (i.e. conservationist effort, urbanization) but also in this case our results indicate that the latitudinal gradient could explain the actual distribution of the species.

Does the distribution reflect the colonization process?

All the above considerations lead us to further questions: from where is the short-toed snake eagle

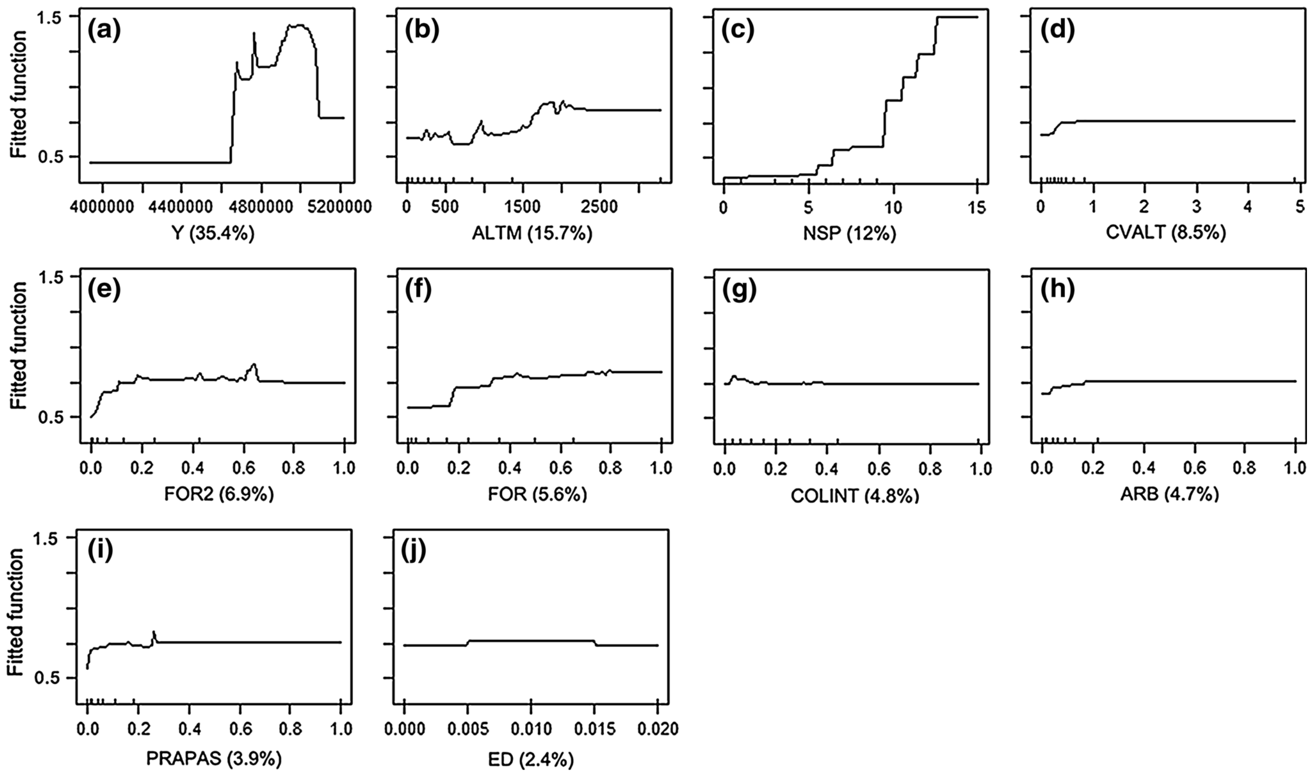

Fig. 4 Variation in probability occurrence of short-toed snake eagle predicted by BRT model (*Y* latitude, *ALTM* mean altitude, *NSP* number of reptile species, *CVALT* standard deviation of altitude, *FOR2* square root forests, *FOR* forests, *COLINT* crops and orchards, *ARB* shrubs, *PRAPAS* meadows and pastures, *ED* urbanized areas)

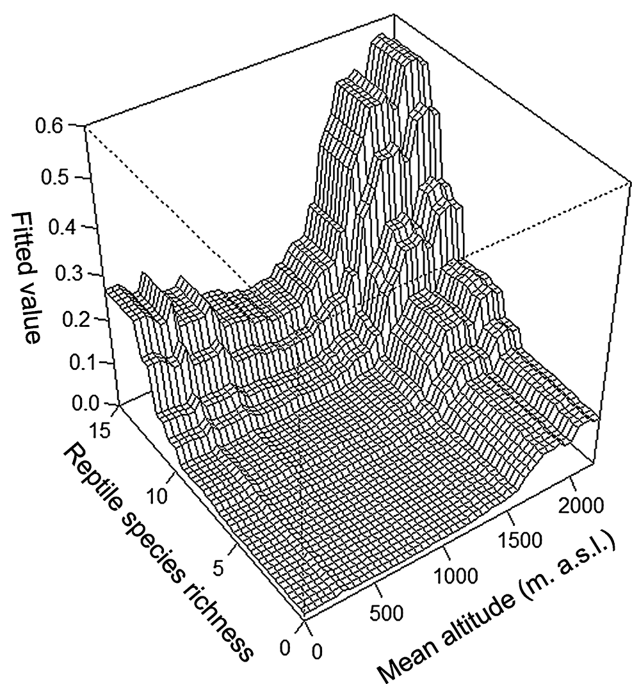

Fig. 5 Prediction surface of the decision tree realized combining the two main predictor variables of the model: mean altitude (ALTM) and the prey species richness (NSP)

colonizing the Italian peninsula? What is the original range distribution of short-toed snake eagle? These are topics linked to the origin of the Palearctic-African migration system and of migration itself. Most authors agree that birds started to migrate from tropical to temperate areas (Alerstam 1990; Rappole 1995; Safriel 1995; Berthold 2001; Rappole and Jones 2002; Böhning-Gaese and Oberrath 2003; Jahn et al. 2004). According to this hypothesis, migration is an adaptation of tropical birds to use seasonally abundant resources in temperate regions in order to optimize breeding success or to avoid seasonal resource depression (Alerstam 1990; Rappole 1995; Rappole and Jones 2002; Alerstam et al. 2003).

Alerstam and Enckell (1979) indicate that competition in Africa savannas during the breeding season was a prerequisite for the evolution of the Palearctic-African migration system. Glaciations were also events of paramount importance in the evolution of migrations. During cold glacial phases, the earth surface available for many bird species drastically decreased (Moreau 1972). Since the northern polar front shifted south, temperate forests and bush vegetation were reduced; furthermore the range extension of tundra, deserts and steppes reduced the Mediterranean and the tropical vegetation to a minimum (Hooghiemstra et al. 2006; Bruderer and Salewski 2008). During interglacial periods, including the current one, ancestral species diverged into what are known as ''twin'' species, distinctly sedentary, partially migrants and completely migrants (Berthold 2001; Rappole, 2005). Rappole and Jones (2002) provide evidence that most species that currently migrate descended from tropical residents. For the Palearctic-African migration system, 42 of 185 species of migrants (23 %) have conspecific populations that breed in the Tropics while 139 (75 %) have Tropical-breeding congeners (Rappole and Jones 2002). Of the snake eagles (*Circaetus* spp.), only the short-toed snake eagle is a complete migrant while the other five species (Beaudouin's snake eagle, *C. beaudouini*, black-chested snake eagle, *C. pectoralis*, brown snake eagle, *C. cinereus*, east African snake eagle, *C. fasciolatus*, banded snake eagle, *C. cinerascens*) live in tropical Africa and are mainly resident (Ferguson-Lees and Christie 2001). However, it is hard to generalize a model like the southern-home theory since birds continuously adapt their migratory behavior according to changes in resource availability (Bruderer and Salewski 2008). In fact, the current migratory system began evolving about 15,000 years ago at the end of the last glaciation and is still evolving; the consequence of this process is not fully predictable (Berthold 2001). Rappole and Jones (2002) proposed a mechanism for the evolution of long distance migration, via gradual colonization at the edge of the breeding range furthest from the wintering area, with populations on the edges more exposed to extinction risk. Consistently with this hypothesis, we suggest that the Italian population of the short-toed snake eagles should be considered as part of a metapopulation comprising those of Western Europe (France, Spain). Small and isolated populations of southern Italy, despite the increasing number, could be considered as small patches of this metapopulation system cut off from the bulk of the population of Western Europe. As a matter of fact, distribution and abundance of migrants could be influenced by the cost of reaching areas located far away from the main migratory pathways (Henningsson and Alerstam 2005a, b; Tellería et al. 2009) and several studies show that isolation could lead small and periphery patches to local extinction (Lomolino et al. 1989; Peltonen and Hanski 1991; Hanski et al. 1995; Whitcomb et al. 1996; Smith and Gilpin 1997; Thomas and Hanski 1997; Hanski 1998; Dunham and Rieman 1999; Clinchy et al. 2002; Wahlberg et al. 2002). In support of this hypothesis, historical data confirm that the short-toed snake eagle was breeding in areas of southern continental Italy and Sicily at least until the end of the 19th century (Salvadori 1872; Lucifero 1898; Arrigoni degli Oddi 1929) while current data show that it is no longer found in those areas. Its failure to re-colonize the southernmost areas of Italy may, therefore, be due to the distance from the center of its current metapopulation range. In this scenario, we predict that this trend will lead to increasing occupancy in the future in southern Italy but, being at the edge of population distribution, it is likely that density remains lower than in Northwestern Italy, despite the availability of suitable areas for this species.

Conclusions

The direction of migration is the result of natural selection; for this reason it is likely that only migration routes leading to survival areas and avoiding ecological barriers are favored by natural selection through an increasing of survival rates and fitness. Therefore, it is expected that migratory populations may follow their historical expansion route (Salewski and Bruderer 2007), and the main migration flyways of short-toed snake eagles breeding in Europe may restrict accessibility to and colonization of other potential breeding regions (Henningsson and Alerstam 2005a, b). The southerly direction of colonization of Italy performed by short-toed snake eagle suggests that birds facing a natural barrier show behavioural plasticity leading to unexpected migratory and colonization directions.

Acknowledgments We wish to thank Massimo Campora, Guido Cattaneo, Ugo Mellone and Paolo Forconi for their help in providing data of short-toed snake eagles presence and the *Societas Herpetologica Italica* (SHI) for allowing to use the data of prey species richness. We are grateful to Simona Tarantino for her assistance in setting out the figures. We appreciate the improvements in English usage made by Christina Riehl through the Association of Field Ornithologists' program of editorial assistance. MEDRAPTORS (www.raptormigration.org) is a network of ornithologists that works to improve research and conservation of migrating birds of prey.

References

Agostini N, Baghino L, Coleiro C, Corbi F, Premuda G (2002a) Circuitous autumn migration in the short-toed eagle (*Circaetus gallicus*). J Raptor Res 36:111–114

Agostini N, Baghino L, Panuccio M, Premuda G (2002b) A conservative strategy in migrating short-toed eagles (*Circaetus gallicus*). Ardeola 49:287–291

Agostini N, Baghino L, Panuccio M, Premuda G, Provenza N (2004) The autumn migration strategies of juvenile and adult short-toed eagles (*Circaetus gallicus*) in the Central Mediterranean. Avocetta 28:37–40

Agostini N, Mellone U (2008) Does migration flyway of short-toed snake-eagles breeding in central Italy reflect the colonization history? J Raptor Res 42:158–159

Alerstam T (1990) Bird migration. Cambridge University Press, Cambridge

Alerstam T, Enckell PH (1979) Unpredictable habitats and evolution of bird migration. Oikos 33:228–232

Alerstam T, Hedenström A, Åkesson S (2003) Long-distance migration: evolution and determinants. Oikos 103:247–260

Arrigoni degli Oddi E (1929) Ornitologia italiana. Hoepli, Milano

Baghino L, Premuda G (2007) Nuovi dati sulla migrazione primaverile ''a circuito'' del biancone, *Circaetus gallicus*, in Italia. Avocetta 31:70–72

Bakaloudis DE (2009) Implications for conservation of foraging sites selected by short-toed eagles (*Circaetus gallicus*) in Greece. Ornis Fennica 86:89–96

Bakaloudis DE, Vlachos CG, Holloway GJ (1998) Habitat use by short-toed eagle *Circaetus gallicus* and reptilian prey during the breeding season in Dadia Forest (north-eastern Greece). J Appl Ecol 35:821–828

Bakaloudis DE, Vlachos CG, Holloway GJ (2005) Nest spacing and breeding performance in short-toed eagle *Circaetus gallicus* in northeast Greece. Bird Study 52:330–338

Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystem, 4th edn. Blackwell publishing, Oxford

Berthold P (2001) Bird migration. A general survey. Oxford University Press, Oxford

Bionda R, Bordignon L (2006) Atlante degli uccelli nidificanti del Verbano Cusio Ossola. Quaderni Natura e Paesaggio del VCO

Birdlife International (2004) Birds in Europe: population estimates, trends and conservation status. Birdlife Conservation series No. 12, Cambridge

Boano A, Brunelli M, Bulgarini A, Montemaggiori A, Sarrocco S, Visentin M (1995) Atlante degli Uccelli nidificanti nel Lazio. Alula 1–2: volume speciale

Böhning-Gaese K, Oberrath R (2003) Macroecology of habitat choice in long-distance migratory birds. Oecologia 137:296–303

Bon M, Cherubini G, Semenzato M, Stival E (1999) Atlante Degli uccelli nidificanti in Provincia di Venezia. SGE, Padova

Bordignon L (2004) Gli Uccelli della Provincia di Novara. Provincia di Novara

Brandmayr P (2002) Ambienti e fauna nel paesaggio italiano. In: Minelli A et al (eds) La fauna in Italia. Touring editions, Torino, pp 30–45

Brichetti P, Fasola M (1990) Atlante degli uccelli nidificanti in Lombardia 1983–1987. Editoriale Ramperto, Brescia

Bruderer B, Salewski V (2008) Evolution of bird migration in a biogeographical context. J Biogeogr 35:1951–1959

Bustamante J, Seoane J (2004) Predicting the distribution of four species of raptors (Aves: Accipitridae) in southern Spain: statistical models work better than existing maps. J Biogeogr 31:295–306

Campora M, Cattaneo G (2006) II Biancone *Circaetus gallicus* in Italia. Riv Ital Orn 76:1–46

Clinchy M, Haydon DT, Smith AT (2002) Pattern does not equal process: what does patch occupancy really tell us about metapopulation dynamics? Am Nature 159:351–362

Cramp S, Simmons KEL (1980) The birds of the Western Palearctic, vol II. Oxford University Press, Oxford

Cumming GS, Gaidet N, Ndlovu M (2012) Towards a unification of movement ecology and biogeography: conceptual framework and a case study on Afrotropical ducks. J Biogeogr 39:1401–1411

De'ath G, Fabricius KE (2000) Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81:3178–3192

Dunham JB, Rieman BE (1999) Metapopulation structure of bull trout: influence of physical, biotic, and geometrical landscape characteristics. Ecol Appl 9:642–655

Elith J, Graham CH, Anderson RP, NCEAS Modeling Group (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151

Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. J Anim Ecol 77:802–813

Elkie PC, Rempel RS, Car AP (1999) Patch Analyst User's Manual. NWST Technical Manual. Ont Min Nat Resour Northwest Sci Technol. Thunder Bay, Ontario TM–002

Evans KL, Warren PH, Gaston KJ (2005) Species energy relationships at the macroecological scale: a review of the mechanisms. Biol Rev 80:1–25

Ferguson-Lees J, Christie DA (2001) Raptors of the World. Helm, London

Fracasso G, Verza E, Boschetti E (2003) Atlante degli Uccelli nidificanti in provincia di Rovigo. Provincia di Rovigo

Fraissinet M, Kalby M (1989) Atlante degli uccelli nidificanti in Campania (1983–1987), Monografia n. 1. ASOIM, Salerno

Friedman JH, Hastie T, Tibshirani R (2000) Additive logistic regression: a statistical view of boosting. Ann Stat 28:337–407

Gellini S, Ceccarelli PP (2000) Atlante degli uccelli nidificanti nelle province di Forlì-Cesena e Ravenna (1995–1997). S.T.E.R.N.A., Amministrazioni Provinciali di Forlì-Cesena e Ravenna

Giacchini P (2007) Atlante degli uccelli nidificanti nella provincia di Ancona. Provincia di Ancona

Gil JM, Pleguezuelos JM (2001) Prey and prey-size selection by the short-toed eagle (*Circaetus gallicus*) during the breeding season in Granada (south-eastern Spain). J Zool 255:131–137

Gruppo Vicentino Studi Ornitologici "NISORIA" (1994) Atlante degli uccelli nidificanti nella Provincia di Vicenza. Gilberto Padovan Editore, Vicenza

Hagemeijer WJM, Blair MJ (1997) The EBCC atlas of European breeding birds: their distribution and abundance. T. and A.D. Poyser, London

Handrinos G, Akriotis T (1997) The birds of Greece. Helm, London

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hanski I, Pakkala T, Kuussaari M, Lei G (1995) Metapopulation persistence of an endangered butterfly in a fragmented landscape. Oikos 72:21–28

Henningsson SS, Alerstam T (2005a) Barriers and distances as determinants for the evolution of bird migration links: the arctic shorebird system. Proc R Soc B 272:2251–2258

Henningsson SS, Alerstam T (2005b) Patterns and determinants of shorebird species richness in the circumpolar Arctic. J Biogeogr 32:383–396

Hooghiemstra H, Lézine AM, Leroy SAG, Dupont L, Marret F (2006) Late Quaternary palynology in marine sediments: a synthesis of the understanding of pollen distribution patterns in the NW African setting. Quat Int 148:29–44

Ientile R, Massa B (2008) Atlante della biodiversità della Sicilia. Vertebrati Terrestri. Cap. 2 Uccelli (Aves). Collana Studi e Ricerche dell'ARPA Sicilia, Palermo

Jahn AE, Levey DJ, Smith KG (2004) Reflections across hemispheres: a system-wide approach to new world bird migration. Auk 121:1005–1013

Kerlinger P (1989) Flight strategies of migrating hawks. Chicago University Press, Chicago

Kirwan GM, Boyla KA, Castell P, Demirci B, Özen M, Welch H, Marlow T (2008) The birds of Turkey. Helm, London

La Gioia G (2009) Atlante degli uccelli nidificanti in provincia di Lecce (2000–2007). Edizioni del Grifo, Lecce

Leathwick JR, Elith J, Francis MP, Hastie T, Taylor P (2006) Variation in demersal fish species richness in the oceans surrounding New Zealand: an analysis using boosted regression trees. Mar Ecol Prog Ser 321:267–281

Lomolino MV, Brown JH, Davis R (1989) Island biogeography of montane forest mammals in the American southwest. Ecology 70:180–194

López-Iborra G, Limiñana R, Pavon D, Martinez-Perez J (2011) Modelling the distribution of short-toed eagle (*Circaetus gallicus*) in semi-arid Mediterranean landscapes: identifying important explanatory variables and their implications for its conservation. Eur J Wildlife Res 57:83–93

Lucifero A (1898) Avifauna Calabra. Elenco delle specie di uccelli sedentari o di passaggio in Calabria. Avicula, Siena

Manly BFJ, McDonald LL, Thomas DL, McDonald TL, Erickson WP (2002) Resource selection by animals: statistical design and analysis for field studies, 2nd edn. Kluwer Academic Publisher, Dordrecht

Mañosa S (2003) Aguila culebrera, *Circaetus gallicus*. In: Martí R, Del Moral JC (eds) Atlas de las Aves Reproductoras de España. Dirección General de Conservación de la Naturaleza, Sociedad Española de Ornitología, pp 172–173

Mayr E, Meise W (1930) Theoretisches zur Geschichte des Vogelzuges. Vogelzug 1:149–172

Mellone U, Limiñana R, Mallìa E, Urios V (2011) Extremely detoured migration in an inexperienced bird: interplay of transport costs and social interactions. J Avian Biol 42:468–472

Meschini E, Frugis S (1993) Atlante degli uccelli nidificanti in Italia. Suppl. Ricerche Biologia Selvaggina, INFS

Mezzavilla F, Bettiol K (2007) Nuovo Atlante degli Uccelli nidificanti in provincia di Treviso (2003–2006). Associazione Faunisti Veneti, Treviso

Mingozzi T, Boano G, Pulcher C (1988) Atlante degli uccelli nidificanti in Piemonte e Val d'Aosta 1980–1984. Monografie VIII. Museo Regionale di Scienze Naturali di Torino, Torino

Moreau R (1972) The Palaearctic-African bird migration system. Academic Press, London

Moreno-Rueda G, Pizarro M (2007) Snake species richness and shrubland correlate with the short-toed eagle (*Circaetus gallicus*) distribution in south-eastern Spain. Ann Zool Fennici 44:314–320

Newton I (1998) Population limitation in birds. Academic Press, London

Panuccio M, Agostini N, Premuda G (2012) Ecological barriers promote risk minimization and social learning in migrating short-toed snake eagles. Ethol Ecol Evol 24:74–80

Panuccio M, Agostini N, Baghino L, Bogliani G (2013) Visible migration of short-toed snake-eagles: interplay of weather and topographical features. J Raptor Res 47:60–68

Pedrini P, Caldonazzi M, Zanghellini S (2005) Atlante degli Uccelli nidificanti e svernanti in provincia di Trento. Museo Tridentino di Scienze Naturali, Trento. Studi Trentini di Scienze Naturali, Acta Biologica, vol 80, p 2

Peltonen A, Hanski I (1991) Patterns of island occupancy explained by colonization and extinction rates in shrews. Ecology 72:1698–1708

Rappole JH (1995) The ecology of migrant birds: a Neotropical perspective. Smithsonian Institution Press

Rappole JH (2005) Evolution of old and new world migration systems: a response to Bell. Ardea 93:125–131

Rappole JH, Jones P (2002) Evolution of old and new world migration systems. Ardea 90:525–537

Ravasini M (1995) L'Avifauna nidificante nella provincia di Parma. Tipolitotecnica, Parma

Rempel EPR, Carr A (1999) Patch Analyst User's Manual. Ontario Ministry of Natural Resources. Northwest Science and Technologies, Thunder Bay TM-002, Ontario

Safriel UN (1995) The evolution of Palaearctic migration—the case for southern ancestry. Isr J Zool 41:417–431

Salewski V, Bruderer B (2007) The evolution of bird migration—a synthesis. Naturwissenschaften 94:268–279

Salvadori T (1872) Fauna d'Italia. Uccelli. Vallardi editore, Milano

Sánchez-Zapata JA, Calvo JF (1999) Raptor distribution in relation to landscape composition in semiarid Mediterranean habitats. J Appl Ecol 36:254–262

Schapire R (2003) The boosting approach to machine learning, an overview. In: Denison DD et al. (eds) MSRI Workshop on Nonlinear Estimation and Classification, Springer

Sindaco R, Doria G, Razzetti E, Bernini F (2006) Atlante degli Anfibi e dei Rettili d'Italia. Societas Herpetologica Italica. Edizioni Polistampa, Firenze

Smith AT, Gilpin ME (1997) Spatially correlated dynamics in a pika metapopulation. In: Hanski IA, Gilpin ME (eds) Metapopulation biology: ecology, genetics, and evolution. Academic Press, London, pp 401–428

Tellería JL, Ramírez A, Galarza A, Carbonell R, Pérez-Tris J, Santos T (2009) Do migratory pathways affect the regional abundance of wintering birds? A test in northern Spain. J Biogeogr 36:220–229

Tellini Florenzano G, Baccetti N, Arcamone E, Meschini E, Sposimo P (1997) Atlante degli uccelli nidificanti e svernanti in Toscana (1982–1992). Quaderni Museo Provinciale di Storia Naturale, Monografie n.1, Livorno

Thomas CD, Hanski I (1997) Butterfly populations. In: Hanski IA, Gilpin ME (eds) Metapopulation biology: ecology, genetics, and evolution. Academic Press, London, pp 359–386

Wahlberg N, Klemetti T, Hanski I (2002) Dynamic populations in a dynamic landscape: the metapopulation structure of the marsh fritillary butterfly. Ecography 25:224–232

Whitcomb SD, Servello FA, O'Connell AF Jr (1996) Patch occupancy and dispersal of spruce grouse on the edge of its range in Maine. Can J Zool 74:1951–1955