



Climate determinants of breeding and wintering ranges of lesser kestrels in Italy and predicted impacts of climate change

Michelangelo Morganti, Damiano Preatoni and Maurizio Sarà

M. Morganti (<http://orcid.org/0000-0002-8047-0429>) (michelangelomorganti@gmail.com) and M. Sarà, Section of Zoology, Dept STEBICEF, Univ. of Palermo, Palermo, Italy. Current address of MM: Dept of Earth and Environmental Science, Univ. of Milan Bicocca, Milan, Italy. – D. Preatoni, Unità di Analisi e Gestione delle Risorse Ambientali, Guido Tosi Research Group, Dept of Applied and Theoretical Sciences, Univ. of Insubria, Varese, Italy.

Climate warming would theoretically create conditions for the breeding range expansion of pseudo-steppe Mediterranean and long-distance migrant species and provide the possibility for these to overwinter in the same breeding areas. However, contemporary changes in rainfall regimes might have negative effects on the climate suitability and in turn, shrink species potential range. The lesser kestrel *Falco naumanni* is highly sensitive to rainfall oscillations and has recently extended its Italian breeding range towards northern latitudes and increasing its wintering records. We modelled the effects of temperature and rainfall on current and future climate suitability for lesser kestrels in both the breeding and wintering periods by using MaxEnt. Models were based on the distribution of 298 colonies and 40 wintering records. Future climate suitability was assessed under eight different scenarios.

Spring rainfall amount resulted as the main determinant of breeding climate suitability, so its predicted reduction will determine a shrinkage in suitable areas (–42.10% in 2050; –32.07% in 2070). Specifically, the 66.05% of Italian colonies will be outside the climatically suitable area by 2050. However wide areas, suitable under current climate conditions, are still not occupied by lesser kestrel and allow the potential expansion of its Italian breeding range in the short term. Temperature seasonality mainly determined the species' winter climate suitability, which is overall predicted to boost in the next decades (+145.03% in 2050; and +123.91% in 2070). All but one future scenarios predicted a northward shift of about 40 km for both breeding and wintering climate suitability. Despite its recent expansion, we have found that climate change will pose conservation concerns for the Italian breeding population of lesser kestrels. Indeed, changes in non-climate factors will also outline the future suitability of the Italian range for lesser kestrels in both seasons with effects that might both strengthen or mitigate climate effects.

Climate change is modifying the ranges of many species of animals and plants with a general shift towards higher latitudes (Parmesan and Yohe 2003) and a concomitant expansion/reduction of the original living ranges (Thomas et al. 2006, Di Febbraro et al. 2016). Despite changes in distributions possibly indicating adaptive reactions of living organisms in a way that allows them to cope with global change (Davis and Shaw 2001), many more animal species have been suffering detrimental effects at a population level, which in turn is producing a further massive biodiversity loss at a global scale (Bellard et al. 2012). Increases in temperature is the change in climate parameters that is mainly affecting the distribution of living organisms (Chen et al. 2011), and this increase is occurring at dramatic rates since at least the second half of the 20th century (IPCC 2015). Climate warming is predicted to expand, as well as to shift northward toward the breeding ranges of bird species originally distributed in xeric Mediterranean landscapes (Huntley et al. 2007, Pearce-Higgins and Green 2014). Furthermore, climate warming has also provoked the reduction of migratory distances

(La Sorte and Thompson 2007, Visser et al. 2009, Heath et al. 2012), so the occasional overwintering at Mediterranean latitudes by long-distance migrants (Sutherland 1998, Fiedler 2003), is most likely evolving towards the establishment of new European wintering quarters, such as observations from Spain seem to confirm (Morganti and Pulido 2012). However, the climate change process is very complex and not linear as it involves changes of parameters other than temperature, especially rainfall (IPCC 2015), which may interplay with warming and have conflicting effects on species distributions. Avian species that undertake long-distance travels to and from Palaearctic latitudes and are also recently establishing new wintering populations in southern Europe represent an ideal model for studying the influence of climate on the future suitability of both breeding and wintering ranges. Predictions on the shifting of breeding latitudes due to climate change had been widely performed for both Europe and America, and – even if at a minor extent – this holds true also for wintering distribution. However, much less explored is the eventuality that climate change

would affect both distributions during the same time lapse, despite this would permit a much more complete prediction about future conservation concerns of the studied species.

Furthermore, research on range modification has often addressed passerine or wader species living at northern European latitudes (cf. Pearce-Higgins and Green 2014). Currently, poor information is available about long-distance migrant raptors breeding in the Mediterranean range, one of the areas suffering the largest impacts of climate change (IPCC 2015).

Accurate assessments of anthropogenic effects derived by global change has been now implemented with solid tools for resource management and conservation planning based on maps of species' distributions and habitat suitability (Bustamante and Seoane 2004). Species distribution models (SDMs) are numerical approaches that combine observations of species occurrence or abundance with estimates of the environmental variables of concern (Guisan and Zimmermann 2000, Phillips et al. 2004). SDMs have been currently used to predict distributions and their changes across terrestrial landscapes, freshwater habitats and marine realms (Rodríguez et al. 2007, Razgour et al. 2016), by several statistical approaches based on presence-absence or presence-only data (Guisan and Zimmermann 2000).

To study the effects of climate change on the distribution of a migratory raptor in the Mediterranean range, we used the lesser kestrel *Falco naumanni* in Italy. Several reasons make this species and its distribution range a good candidate for this type of investigation. First, the species is likely responding to climate change. This is suggested by the fact that its historical Italian breeding range was confined to two major islands (Sicily and Sardinia) and the southern part of the peninsula (mainly Apulia, Basilicata and Calabria) (Brichetti and Fracasso 2003), but it is now expanding northward along the peninsula (Gustin et al. 2014, Sarà et al. 2015). Furthermore, occasional wintering records (Brichetti and Fracasso 2003) are apparently increasing in the past few years. Secondly, the susceptibility of lesser kestrel reproductive parameters to temperature and rainfall oscillations are quite well known (Rodríguez and Bustamante 2003, Mihoub et al. 2010, Sarà 2010). All these elements offer the possibility of elaborating models representing climate suitability by a reduced and solid set of environmental variables and eventually enhancing the interpretability of results. Eventually, the shape and the geographical position of Italy offers a wide latitudinal and altitudinal range, conferring robustness to models run over this geographical range and oriented to study species-climate relationships, despite to being limited by a political border (Brambilla et al. 2016).

The lesser kestrel has recently been downgraded from the 'vulnerable' to the 'least concern' IUCN category (Iñigo and Barov 2011); however, population trends are highly variable across the range including cases of population decline in eastern and southern Europe and the Middle East (Iñigo and Barov 2011).

In this work, we modelled changes in lesser kestrel distributions exclusively according to variation in climate, therefore assuming constant land use and other anthropogenic effects (i.e. pesticide use, colony-buildings refurbishments, etc) across future time. We also avoided considering the potential effect of biotic interactions or changes in management techniques on

reproductive success and distribution in our models (Bateman et al. 2012, Blois et al. 2013, Cartwright et al. 2014). This simplification is not unreasonable, because the lesser kestrel already occurs in human-modified pseudo-steppe habitats (Ferguson-Lee and Christie 2001) and is highly dependent on weather during reproduction (Rodríguez and Bustamante 2003). Although it generally requires high-quality and large extensions of traditional pseudo-steppe habitats (Tella et al. 1998, Franco and Sutherland 2004, Sarà 2010), land intensification could produce suitable habitats, such as alfalfa or artichoke fields (Ursua et al. 2005, Di Maggio et al. 2016). In addition, we did not include dispersal in our modelling evaluation (Rodríguez-Rey et al. 2013), because data from the recent area of expansion (Araújo et al. 2005) is limited, as well as because the lesser kestrel has complex dispersal dynamics in a close range to core-colonies (Serrano et al. 2004). We assumed here that the lesser kestrel would be able to colonize suitable habitats along Italy wherever climate conditions will permit. We thus refer our results to the potential distribution of current and future 'climate suitabilities' for the species.

The specific aims of this study are to: 1) identify climate variables among those that are known to influence lesser kestrel ecology, that determine climate suitability in both breeding and wintering periods; 2) for the first time ever, model the distribution of future climate suitabilities for both biological stages under climate change scenarios of different intensities by also checking the trends of climate parameters best predicting the range modifications of lesser kestrels; 3) compare the extension of current and future climatically suitable areas according to every scenario; 4) quantify the proportion and evidence of the location of the breeding sites that will fall outside the climatically suitable area in order to orient future conservation efforts.

Materials and Methods

Breeding sites (colonies)

We defined as a lesser kestrel breeding colony any site (typically an abandoned or destroyed rural building or a mountain cliff of variable size) where at least one active nest was directly observed (a nest containing eggs, nestlings, incubating adults) or where at least one pair of lesser kestrels performed any behaviour which is unequivocally related to reproduction (e.g., territorial behaviour, male delivering prey to female, copulation, inspection of nest chambers) during at least one breeding season (April–July) between 2000 and 2015. We gathered localizations of the Italian breeding colonies with direct field surveys in Sicily starting during 2000 (see Sarà 2010 for field methods), while researchers that locally study the breeding of lesser kestrels in the past few years have transmitted the exact locations of the colonies (Gustin et al. 2014, Muscianese 2016 and the list of contributors in Acknowledgments). With these methods, we could certify the presence of a total of 298 breeding sites of lesser kestrels in Italy between 2000 and 2015, most of which are distributed in Sicily ($n = 208$). A further 51 breeding sites are located in the Apulian–Basilicata area which includes the largest colonies of Italy, such as those in the Matera (~1000 pairs) and Montescaglioso towns (~500 pairs). Sardinia

hosted 20 colonies, while recently established colonies have been found in Calabria (6 colonies from 2013), Molise (1 colony in 2014), central Latium, (4 colonies) and northern Italy (Emilia-Romagna 7 colonies, Lombardy 1 colony). Overall, breeding populations of lesser kestrels in Italy are mainly distributed in Sicily and in south-eastern regions, to which there are some isolated nuclei in Sardinia and central and northern areas of the peninsula (Fig. 1). The spatial distribution of breeding colonies is reported at a large scale in Supplementary material Appendix 1 Fig. A1.

Wintering records

Wintering records were restricted to observations from 1st December to 31st January to avoid including late or early migrants. Part of the wintering data were gathered from <www.ornitho.it>, the Italian online citizen-based platform for collection of ornithological data (concession date: 26 February 2015, data gathering: 3 March 2015). To these records, we added personal observations from Sicily relatively to the winter 2014–2015. Finally, we included wintering observations from Sicily and Apulia recorded in Ciaccio et al. (1983), Iapichino and Massa (1989), Lo Valvo et al. (1993), Palumbo (1997) and Liuzzi et al. (2015). Possible misidentifications with the common kestrel *Falco tinnunculus* may occur in the field, especially during winter. Wintering observations stored in <www.ornitho.it> were individually checked with the observers and retained only when supported by photos or proven experience of the observer. Multiple records of wintering cases that could be referred to same individuals were excluded from the dataset. The resolution of the observations was the exact location expressed in geographical coordinates (decimal degrees).

With these methods, we gathered 40 wintering records of lesser kestrels in Italy. All of these records belong to southern regions within or very near to the breeding or post-nuptial dispersal areas, with the exception of a single record from

the town of Tolentino (Macerata) in mid-eastern Italy. Wintering cases were unevenly distributed in time between 1985 and 2015 with most of them occurring more recently than 2005 (28 records). The spatial distribution of wintering records is reported at large scale in Supplementary material Appendix 1 Fig. A2.

Climate variables selection

We used an expert-based approach (Guisan and Zimmermann 2000, Manly et al. 2002) to pre-select a reduced set of climatic variables potentially affecting both the breeding and wintering distribution of lesser kestrels in Italy from the available literature. All variables were downloaded as georeferenced images from <www.worldclim.org> (Hijmans et al. 2005). Successively, autocorrelation among variables was tested by variance inflation factor (VIF) tests (usdm package for R, Naimi 2015) and the predictor set was reduced by progressive exclusion of the variable with the highest VIF value (if this was above 3). By this process, we finally obtained a set of independent predictors, all having VIF values below 3 (Zuur et al. 2010).

The period just after arrival in Europe is critical for lesser kestrel reproductive biology, because climatic conditions during the onset of reproduction influence vegetation growth and in turn the abundance of the preferred insect prey, which ultimately determines the suitability of an area for reproduction (Rodríguez and Bustamante 2003, Serrano et al. 2001, Serrano and Tella 2003, Sarà 2010). Among the climatic factors which influence the reproductive performances of lesser kestrels, the amount of rainfall during courtship resulted as the most important factor for both Spain (Rodríguez and Bustamante 2003) and Sicily (Sarà 2010). The reproductive phenology of lesser kestrels across Italy is likely to be variable with latitude, since the southern Sicilian populations are the first ones to start breeding. Based on the observation that lesser kestrels arrive on breeding grounds between late February and early March and Sicilian kestrels

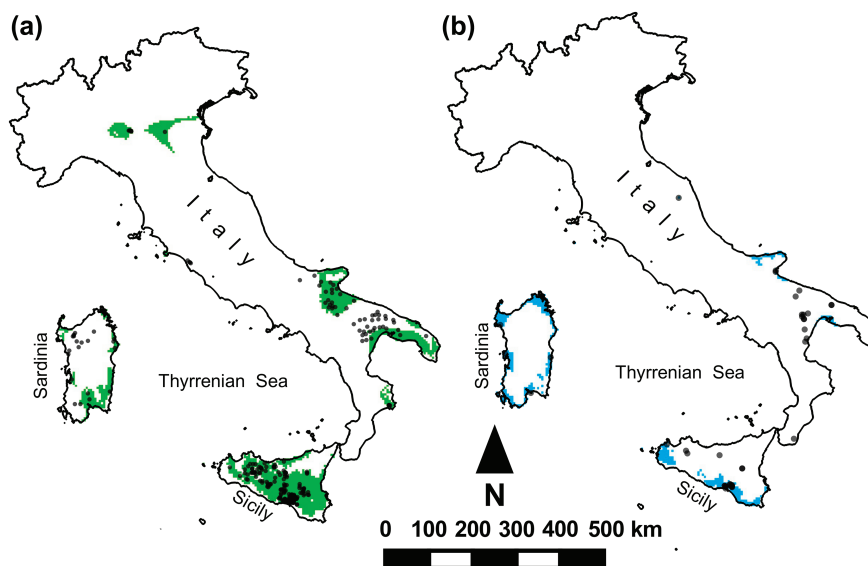


Figure 1. Distribution of climatically suitable areas for lesser kestrels in Italy under current (1950–2000) climate conditions as calculated by MaxEnt for the breeding (a) and wintering (b) biological stages. Black dots indicate current presence data, also shown in wider images in Supplementary material Appendix 1 Fig. A1, A2.

start egg-laying in mid-April whereas Italian kestrels lay until May (Brichetti and Fracasso 2003, Mascara and Sarà 2006), we summed the amount of rain in April and May to obtain a variable representing the cumulated rainfall during incubation. Additionally, we included the minimum temperature of April, because this is a critical month for reproduction (start of laying in most of Sicily, settling of colonies in the rest of Italian range) and temperatures below a certain threshold (which may vary among populations) may seriously affect the suitability of reproductive areas (Mihoub et al. 2012). We therefore outlined the initial model in order to explore climate suitability during the breeding season by these three predictors: total amount of rain in March, cumulative amount of rain during incubation (April + May) and minimum temperature in April.

Factors affecting the climate suitability for lesser kestrel during winter in Europe are virtually unexplored. In Spain, wintering cases have usually been recorded at the breeding colonies (Negro et al. 1991, Tella and Forero 2000) and seldom in non-reproductive areas (Bustamante 2012) and this situation matches our personal observations in Sicily. Cases of wintering trans-Saharan migrants in Europe have been concentrated in coastal zones with mild temperatures during winter (Morganti and Pulido 2012), thus suggesting that the minimum winter temperature would be a crucial factor also for the potential overwintering of lesser kestrels in Italian coastal plains and lowlands. The minimum temperature of the coldest month (coded in worldclim as bio6) was therefore initially included in the set of considered predictors. Lesser kestrels leave Italy towards Africa mainly in September–October (Sarà et al. 2014), so food availability (indirectly driven by rain, Rodríguez and Bustamante 2003, Serrano et al. 2001, Serrano and Tella 2003) in these two months is a likely important driver of the ‘decision’ of lesser kestrels to move or remain in Italy. Accordingly, we included monthly rainfall of both September and October in the initial models.

Broad bioclimatic variables summarizing the general conditions of an area during a specific period may be very useful in SDMs when the needs of a species are poorly known (Guisan and Zimmermann 2000, Grosbois et al. 2008). We therefore included a variable representing the variability of temperature between hot and cold seasons (i.e. temperature seasonality, coded in worldclim as bio4), along with annual rainfall (coded in worldclim as bio12), given the well-known sensibility of lesser kestrels to rainfall regimes. In conclusion, the initial set of predictors exploring winter climate suitability for lesser kestrels in Italy was composed of seven variables: monthly rainfall in September; monthly rainfall in October; minimum temperature in September; minimum temperature in October, temperature seasonality (bio4), minimum temperature of the coldest month (bio6) and annual total rainfall (bio12).

For a detailed explanation of each variable see Supplementary material Appendix 1 Table A1 and O’Donnell and Ignizio (2012).

Preliminary collinearity analysis among climatic predictors showed that the three variables selected for the breeding stage (see above) did not suffer collinearity issues ($VIF < 3$ in all cases, Supplementary material Appendix 1 Fig. A3). Therefore, they were all maintained for modelling the

climatic niche of breeding lesser kestrels in Italy (Table 1). Conversely, the set of seven variables selected for the wintering stage (see above) showed strong autocorrelation among them (Table 1, Supplementary material Appendix 1 Fig. A3). After the progressive exclusion of highly correlated variables, we obtained a final set of three independent variables ($VIF < 3$), by which the effect of climate on wintering was modelled: minimum temperature in September, rainfall in October and temperature seasonality (Supplementary material Appendix 1 Fig. A3).

Depending on the resolution of the sampling grid, topographic factors may be crucial for the accuracy of species distribution models, so they should be considered along with climatic factors (Virkkala et al. 2010, Gillingham et al. 2012). We therefore performed exploratory tests to prospect the inclusion of altitude in the predictor set, in which we found, as expected (Baum 1949), extremely high collinearity between altitude and climate. Other topographic variables potentially relevant at small spatial scale in determining occurrence probability (i.e. slope, aspect, solar radiation) were not considered because the cell size of our grid ($\sim 25 \text{ km}^2$) was too coarse to reliably represent their variability.

Bioclimatic envelope modelling

We fitted bioclimatic envelopes to model the ideal climatic conditions for breeding and wintering of lesser kestrels both

Table 1. Summary of variables predicting climatic suitability for the breeding and wintering distribution of lesser kestrels in Italy as obtained by MaxEnt modelling and based on current climate conditions (1950–2000, worldclim.org). AUC = Area Under (ROC) Curve, measures the accuracy of the model in a 0–1 scale (1 = maximum accuracy) and has been calculated over five repetitions of the model based on different randomly selected subsets of presence data; Effect: + and – indicate, respectively, positive and negative relationships between the climate variable and climate suitability while +/- indicate a quadratic relation; C% = percentage contribution to the model, measures the contribution of each predictor to explain the model variance; PI = variable permutation importance, measures the importance of a predictor by randomly permuting its values among the training points. § = variable effect excluded by preliminary collinearity analysis (see text).

	Variable	Effect	C%	PI
Breeding AUC ± SD: 0.838 ± 0.024	Cumulated rainfall incubation (April + May)	+/-	49.5	41.6
	Rainfall March	+/-	37.3	19.2
	Minimum temperature April	+/-	13.2	39.2
Wintering AUC ± SD: 0.735 ± 0.065	Temperature Seasonality (bio4)	–	84.9	59.4
	Minimum temperature September	+	9.5	23.8
	Rainfall October	–	5.6	16.8
	Minimum temperature of the coldest month (bio6)	§		
	Annual rainfall (bio12)	§		
	Rainfall September	§		
	Minimum temperature October	§		

for current and future climatic conditions by using maximum entropy modelling (MaxEnt) implemented in the package *dismo* (Hijmans et al. 2011) in R 3.1.2 (R Core Team). MaxEnt is one of the most efficient statistical softwares for species distribution modelling based on presence-only data (Elith et al. 2006, 2011) as it can significantly predict species distribution even with low sample size (Pearson et al. 2007, Wisz et al. 2008, Baldwin 2009). The cell size for climatic variables was set to 2.5 degree minutes (~4.8 km at 45° latitude), a spatial scale that includes most foraging movements of lesser kestrel from their colonies (Tella et al. 1998, Calabuig et al. 2010) and, thus, significantly represents local climatic conditions that the species comes across during breeding. We have maintained the same cell size when modelling wintering climate suitability to facilitate comparisons with breeding models.

Bioclimatic data for both current and future conditions were downloaded from the <www.worldclim.org/dataset> (Hijmans et al. 2005) at the same resolution of 2.5 minutes. Current conditions are a mean value calculated through interpolation of real data from 1950 to 2000. To represent future conditions, we chose two different values of Representative Concentration Pathways (RCPs). RCPs are the greenhouse gas concentration trajectories adopted by the IPCC (2014) and are used to describe future climates according to a possible range of radiative forcing values in the year 2100 (Dif-ferbaugh and Field 2013). We selected two RCPs of + 4.5 and + 8.5 W/m² to represent intermediate and intense climate change, respectively (Stewart et al. 2015, Mi et al. 2016). For each RCP, we downloaded predictions on bioclimatic variables for both 2050 and 2070 and according to two different global climate models (GCMs): BCC-CSM1-1 ('BC' thereafter) and GISS-E2-R ('GS' thereafter) to obtain 8 projection scenarios (2 RCPs × 2 periods × 2 GCMs).

With the aim of accounting for the unevenly distributed sampling effort (Kramer-Schadt et al. 2013), which was higher in Sicily and in the historic Italian range for lesser kestrels, we opted to create an ad-hoc background layer (Syfert et al. 2013, Fourcade et al. 2014). Specifically, we first calculated a bias map derived from the geographic density of presence points; successively, we generated 10-fold background points with the same density of presence points, thus reproducing the same behaviour that MaxEnt uses when supplied with a raster bias map. This approach allowed us to use the same background points during the cross-validation procedure. MaxEnt was run using its default configuration (Merow et al. 2013).

With the aim of obtaining a cross-validation of the models, we randomly partitioned the original presence data in five groups of equal size (i.e. each containing the 20% of the data) and used each one as a test-set against a MaxEnt model built using the rest of the data as a training set (random partitioning sensu Radosavljevic and Anderson 2014). Model performance statistics (receiver operating characteristics – ROC, area under curve – AUC) were then obtained by averaging the five models. Final models were eventually created using the whole dataset.

Eventually, in order to obtain a spatially-explicit evaluation of the reliability of the models, we produced MESS maps (Elith et al. 2010), which identify the areas in which extrapolation occurs. After having obtained a MaxEnt output

layers, representing on a continuous scale (ranging from 0 to 1) the climate suitability for lesser kestrels during a given period and scenario, we transformed them into binomial presence/absence distribution maps to improve the interpretability for potential applications in concrete conservation actions. To convert current continuous suitability maps into binary maps, we assigned 'presence' to all values above the threshold of 'maximum training sensitivity plus specificity' (Liu et al. 2013) which is routinely calculated by MaxEnt. The outputs of the prediction models were converted into binary presence/absence maps by using the threshold values of the breeding and wintering current distribution models respectively. Furthermore, we corrected the binary presence/absence maps using the MESS maps and eliminating the cells in which MESS maps indicated extrapolation (values below zero).

Eventually, we inspected the response curves generated by MaxEnt to assess whether the relationships between each climate variable and suitability were restricted to a precise range of values (quadratic relation), or if otherwise linked (positively or negatively) with a given climatic variable.

Assessment of change between current and future climatic suitable areas

We quantified the change between current and future climatic suitability for lesser kestrels in Italy by comparing the number of grid cells with suitable climate conditions between current and future scenarios for both breeding and wintering distributions. Then, we plotted each colony site within the borders of the climatically suitable area obtained for breeding under each of the eight projection scenarios in order to assess permanence within the suitable area. This informed us about the relative importance of change in any scenario by estimating the percentage of colony sites confined outside the climatically suitable area in the future. Eventually, we quantified shifting of the barycentre between the current and the future climatically suitable areas by calculating the linear vectors among these points in terms of kilometres and direction (Parmesan and Yohe 2003, Domisch et al. 2013).

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.jq87d>> (Morganti et al. 2017).

Results

MaxEnt models evaluation

Cross-validated MaxEnt models performed fairly well for both breeding and wintering distributions, as fairly small standard deviation of AUC suggests in both cases (breeding: AUC ± SD = 0.838 ± 0.024; wintering: AUC ± SD = 0.735 ± 0.065). However, averaged ROC curves (Supplementary material Appendix 1 Fig. A4) suggest a lower performance of the wintering model with respect to the breeding one, possibly due to the smaller sample size (40 presence data with respect to the 298 for breeding

distribution). MESS maps revealed that performance of the models was high in coastal and southern areas, while the extrapolated the most at northern latitudes and at higher altitudes (Supplementary material Appendix 1 Fig. A5). Successive results and conclusions are exclusively based on the cells where models performed well according to MESS maps (i.e. non-negative MESS scores).

Meaningful climatic predictors

MaxEnt modelling of the breeding distribution under current climatic conditions showed that the cumulated rainfall during incubation was the most important factor predicting lesser kestrel occurrence (Table 1). All the factors included in the breeding model had a quadratic effect (Table 1). Likewise, MaxEnt modelling of the wintering distribution under current climatic conditions showed that temperature seasonality had the largest explanatory power for determining the wintering presence of the species, followed by the minimum temperature of September (Table 1). More specifically, their effects were almost linear since the wintering presence of lesser kestrels was overall negatively related with temperature seasonality and positively to the minimum temperature in September. Distributions of climatic suitability for breeding and wintering lesser kestrel across Italy under current climatic conditions are shown in Fig. 1.

Climate change effects on future potential distribution

For each of the climate variables included in the MaxEnt models, we have drawn the distribution of values under current and future conditions for both the breeding and wintering distributions (Supplementary material Appendix 1 Fig. A6–A11). Tukey post-hoc tests exploring the direction of climate change variables between current conditions and future scenarios showed that overall, rainfall will drop while temperature will raise (Table 2). In particular, the most important variable affecting breeding climate suitability, i.e. the cumulated rainfall during incubation will drop in all but one scenario, while temperature seasonality and the minimum temperature in September which mainly determine wintering climate suitability will raise in all scenarios (Table 2).

Change between current and future climatically suitable areas

The future projection of climate suitability for lesser kestrels in Italy predicted a remarkable reduction in the areas which actually have suitable climate conditions for breeding (Fig. 2, Table 3), contrasting with the large increase in areas climatically suitable for overwintering (Fig. 3, Table 3).

The breeding climate suitability is predicted to decline both for intermediate and intense climate change scenarios in 2050 and 2070 and this would occur independently from the global climate model considered. On average, climatically suitable areas will be reduced until 2050 by $42.10\% \pm 12.08$ SD; corresponding to a $-15\,481$ km² shrinkage of the current extension. A slightly minor reduction of suitable areas should occur between 2050 and 2070 (mean loss for 2070 with respect to current conditions: $-32.07\% \pm 18.41$; $-11\,794$ km²). However, some specific scenarios like the BCC-CSM1-1 with intense climate change (Table 3) would predict even higher losses than average, i.e. -56.08% of the current breeding suitable climate distribution in Italy.

Conversely, wintering climate suitability has been predicted to boost across Italy from the current conditions to 2050 ($+145.03\% \pm 68.94$ SD on average) and to 2070 ($+123.91\% \pm 74.59$ SD; see Table 2 for detailed data). This range expansion occurs regardless of the intensities of climate change and global climate models considered. The maxima predicted increases are $+218.34\%$ in 2050 and $+204.80\%$ in 2070 (Table 3).

In addition to range shrinkage (breeding) and expansion (overwintering), the future climate suitability for lesser kestrels in Italy has been predicted to shift both for breeding (mean shift length \pm SD = 47.68 ± 40.81 km) and wintering cases (43.79 ± 21.60 km, Fig. 4). All scenarios but one, (i.e. the 33.33 km southward shift in 2050 predicted for breeding climate suitability under the GISS-E2-R -rcp8.5) predict that the breeding and wintering climate suitability will be moving toward the north of the Italian peninsula (Fig. 4). Overall, the mean direction of the shift is northward for both the breeding and wintering climate suitability. The mean shift direction (having 0° as north) is $2.00^\circ \pm 58.08^\circ$ (degrees \pm SD) and $349.75^\circ \pm 22.47^\circ$ for breeding and wintering respectively.

Table 2. Change of climate variables predicting the distribution of lesser kestrels, as resulting from Tukey tests of the difference between current climate conditions and eight future scenarios. All differences are significant at $p < 0.01$ and the direction of change is positive (+) or negative (–), with one exception (ns = no significant difference). RCP = Representative concentration pathways indicating intermediate (4.5 W/m²) or high (8.5 W/m²) degree of climate change.

Year of predictions	RCP	GCM	Breeding			Wintering		
			Rainfall March	Rainfall April + May	Min T April	BIO4 (Temperature seasonality)	Rainfall October	Min T September
2050	4.5	BCC-CSM1-1	+	–	+	+	–	+
		GISS-E2-R	+	–	+	+	–	+
	8.5	BCC-CSM1-1	–	–	+	+	–	+
		GISS-E2-R	–	–	+	+	+	+
2070	4.5	BCC-CSM1-1	–	+	+	+	+	+
		GISS-E2-R	–	–	+	+	–	+
	8.5	BCC-CSM1-1	ns	–	+	+	–	+
		GISS-E2-R	+	–	+	+	–	+

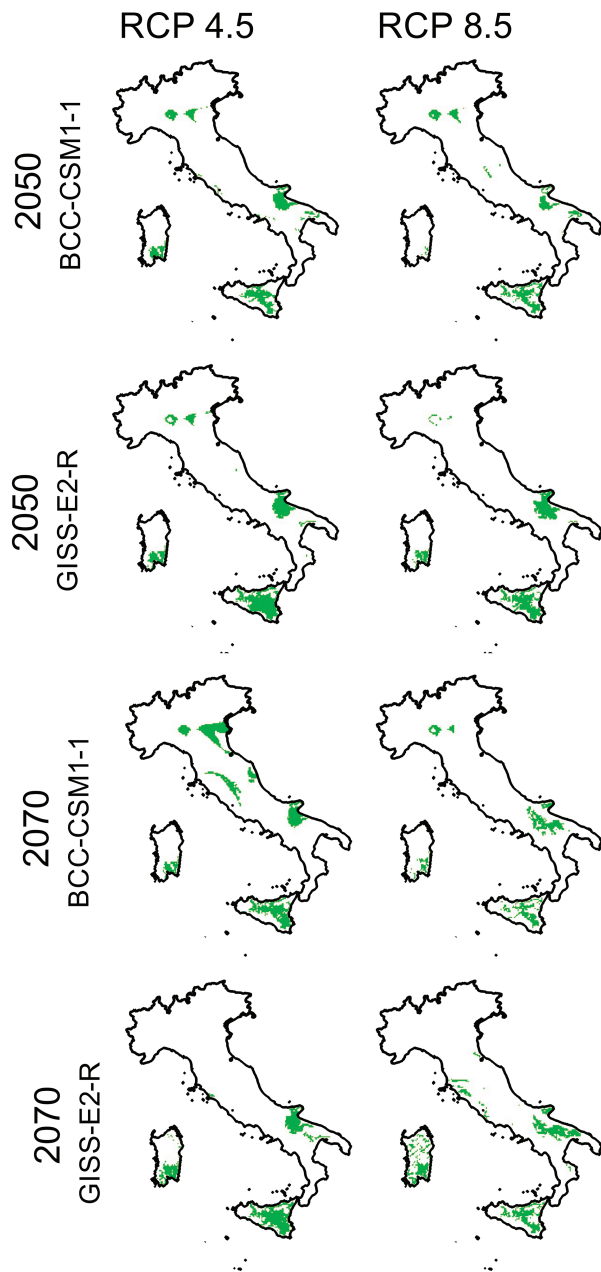


Figure 2. Projections of future climate suitability in 2050 and 2070 for the breeding of lesser kestrels in Italy, depending on two intensities of climate change (RCPs pathways 4.5 and 8.5, intermediate and intense respectively) and two global climate models (BCC-CSM1-1 and GISS-E2-R).

Geographic placement of current breeding sites with respect to future climatic suitability

105 (35.23%) of the 298 currently known Italian breeding colonies of lesser kestrels will remain outside the borders of the climatic suitable areas under all the eight predicted future distributions. 70 of these colonies are the bulk of the Sicilian population in south-eastern Sicily (known as the Gela Plain breeding area). 12 colonies from the Apulia-Basilicata breeding population will encounter the same fate, including three colonies of more than 50 breeding pairs.

On the contrary, only 22 colonies (7.38%) will remain within the borders of the climatically suitable area in all the scenarios. These 22 colonies are all small in size (estimated as less than 10 breeding pairs each) and stay in north-western Sicily ($n = 18$) and in Apulia-Basilicata ($n = 4$).

The remaining 171 breeding sites are predicted to remain or not remain in climatically suitable areas depending on the considered scenario. On average, most of the current breeding sites will stay outside the climatically suitable areas in the future (66.05% in 2050, 74.00% in 2070, Table 3). The worst negative prediction is that 83.22% of breeding sites will be located in a climatically unsuitable condition in 2070 (BCC-CSM1-1, rcp8.5, see Table 4).

Discussion

We used a climate-only approach to model the effect of eight scenarios of climate change on the potential distribution of wintering and breeding lesser kestrels in Italy. Our work represents one of the rare case in which range modification due to climate change are estimated for both breeding and wintering range in a single work and the first time that this is due for lesser kestrel, a widely-studied species. All the considered future scenarios consistently predicted a reduction of the areas suitable for potential breeding and a concurrent expansion of those suitable for overwintering. In addition, we obtained a spatial response equivalent to a northern range shift in both future distributions. Adjustment of geographical distributions to the changing climate is one of the general responses that birds, as other terrestrial organisms, are expected to exhibit (Huntley et al. 2006, Pearce-Higgins and Green 2014), usually moving towards higher latitudes (Virkkala et al. 2010).

Some authors argued about the relative merits of SDMs in predicting climate change-induced range shifts, listing a number of potential pitfalls associated with the exclusion of species interactions, dispersal constraints and the role of adaptation capacity in determining how species will respond to climate change (Guisan and Thuiller 2005, Sinclair et al. 2010). Nonetheless, we agree with Araújo et al. (2005) and consider these models as a useful tool in advancing the general understanding of climate-change impacts, also when model predictions might be questioned. Our findings posited a baseline for framing a discussion about the fate of a colonial raptor distributed in a large country of the western Palearctic area and is supposed to increase over time.

Our models forecast a contraction of the suitable breeding range with the side-effect that three-quarters of the current breeding sites will be confined outside the climatically suitable areas in the next decades. These sites include some of the largest colonies at global level (e.g. ~1000 pairs in the town of Matera in the Basilicata region) and most of Sicilian population located in the south-east of the island (400–500 pairs in 2010–2015, Sarà et al. 2015). These latter sites fall within the areas mapped as the most vulnerable to desertification in Sicily (Carnemolla et al. 2015). Noteworthy, southern Sicilian colonies stay near the southern edge of both the Italian and European breeding distribution of the species (Iñigo and Barov 2011, Orta and Kirwan 2016), so

Table 3. Extension of climatically suitable areas for the breeding and wintering distributions of lesser kestrels in Italy under current (1950–2000) and future climatic conditions. Future climate has been calculated for two different periods centred around 2050 and 2070 respectively and provide two different projections of the intensity of climate change and two global climate models (GCM).

	Current suitable area	Year of prediction	Climate change intensity	GCM	Future suitable km ²	% of change	Mean prediction change ± SD
Breeding climate suitability	36 775 km ²	2050	Intermediate (rcp 4.5)	BCC-CSM1-1	21 050	-42.76	-42.10 ± 12.08
				GISS-E2-R	27 000	-26.58	
			High (rcp 8.5)	BCC-CSM1-1	16 150	-56.08	
				GISS-E2-R	20 975	-42.96	
		2070	Intermediate (rcp 4.5)	BCC-CSM1-1	33 425	-9.11	-32.07 ± 18.41
				GISS-E2-R	24 725	-32.77	
Wintering climate suitability	11 450 km ²	2050	Intermediate (rcp 4.5)	BCC-CSM1-1	31 450	174.67	145.03 ± 68.94
				GISS-E2-R	26 375	130.35	
			High (rcp 8.5)	BCC-CSM1-1	36 450	218.34	
				GISS-E2-R	17 950	57.76	
		2070	Intermediate (rcp 4.5)	BCC-CSM1-1	14 225	24.24	123.91 ± 74.59
				GISS-E2-R	34 900	204.80	
			High (rcp 8.5)	BCC-CSM1-1	26 225	129.04	
				GISS-E2-R	27 200	137.56	

we argue that the Maghreb breeding population will come across a similar fate.

In agreement with Rodríguez and Bustamante (2003), we found that breeding distribution is mostly predicted by an optimal quantity of rainfall during spring. The quadratic relationship we have found between occurrence and the amount of rainfall during the incubation stage highlights the strict requirements of lesser kestrels and warns about its vulnerability. As has been observed for other European breeding bird species, any change away from the species' optimum would result in adverse effects on distribution (Jiguet et al. 2006). Unfortunately, seven out of the eight future scenarios that we have considered forecast a significant reduction in rainfall quantities in the next decades.

However, it must be stressed that the expansion (and not a contraction) of the western European breeding range of lesser kestrels has been recorded since the year 2000 and onwards. Indeed, new lesser kestrel colonies have been found in central and northern Italy in the last ten years (Gustin et al. 2014, Sarà et al. 2015) and a similar expansion of the breeding range is occurring in other western Palearctic countries (France: Mihoub et al. 2012, Spain: Ortego 2010). Assuming the accuracy of our predictions, this contradiction suggests that lesser kestrel populations in Italy, and probably in the whole western Palearctic, are currently slowing their response to climate change. Evidence (reviewed by La Sorte and Jetz 2012) suggests that communities in the past have responded to rapid climate change with lag effects estimated at < 100 years (Williams et al. 2002), limited at the temporal-scale of glaciation events, but still not perceptible at a human scale. During the initial phases of climate change, the limited pressure exerted on species' climatic niches generates lag effects in species' distributional responses. When climate change progresses and populations more consistently occur outside their climatic norms, population dynamics and evolutionary processes accelerate and responses become more evident (La Sorte and Jetz 2012 and references therein).

In conclusion, the northward expansion of lesser kestrels in the western Palearctic would be a first small signal of this species' tracking climate change and further monitoring

would be necessary to assess the extent and speed of the reaction, which can be scored from a no- to full-response according to La Sorte and Jetz (2012). Current breeding climate suitability largely overlaps with the known distribution of lesser kestrels in Italy, but it leaves some areas virtually suitable for the species where reproduction has recently been initiated (i.e. north-eastern Po plain: provinces of Mantua, Modena, Ferrara). This suggests that Italian lesser kestrel populations may still potentially expand northward, while the opposite is observed in the Apulia-Basilicata reproductive area, where many colonies already stay outside the climatically suitable area. In addition, there is the possibility that species preferences regarding breeding ecological niche adapt in relatively short periods ('short' in evolutionary terms) paralleling the changes in climatic condition (Martínez-Meyer et al. 2004). The lesser kestrel has specific habitat requirements corresponding to grasslands and traditional arid croplands (Donazar et al. 1993, García et al. 2006, Sarà 2010, Di Maggio et al. 2016). In the next decades, agricultural intensification has been predicted to greatly reduce both the quality (Sirami et al. 2013, Sokos et al. 2013) and extension (Lehsten et al. 2015) of these land-uses. The distributional response of lesser kestrels to climate change, regardless of its speed, would thus interact with another array of environmental factors which in turn produce complex outcomes that are difficult to predict in detail.

Conversely, our modelling is concordant with the documented increase of wintering records, which actually occurs in southern regions of Italy. The area of winter climate suitability resulted in restricted to definite coastal areas of southern Italy under current climatic conditions and was mostly determined by temperature seasonality, another climate parameter that will increase at a global scale (IPCC 2015). For this reason, our findings forecast an extraordinary expansion of the winter climatic niche for lesser kestrels in Italy. This would encompass both Italian kestrels that might become partial-migrant or resident (Morganti 2015) and individuals from other nearby northern populations that might find favourable conditions for overwintering in the peninsula. Theoretical models on adaptability of migratory

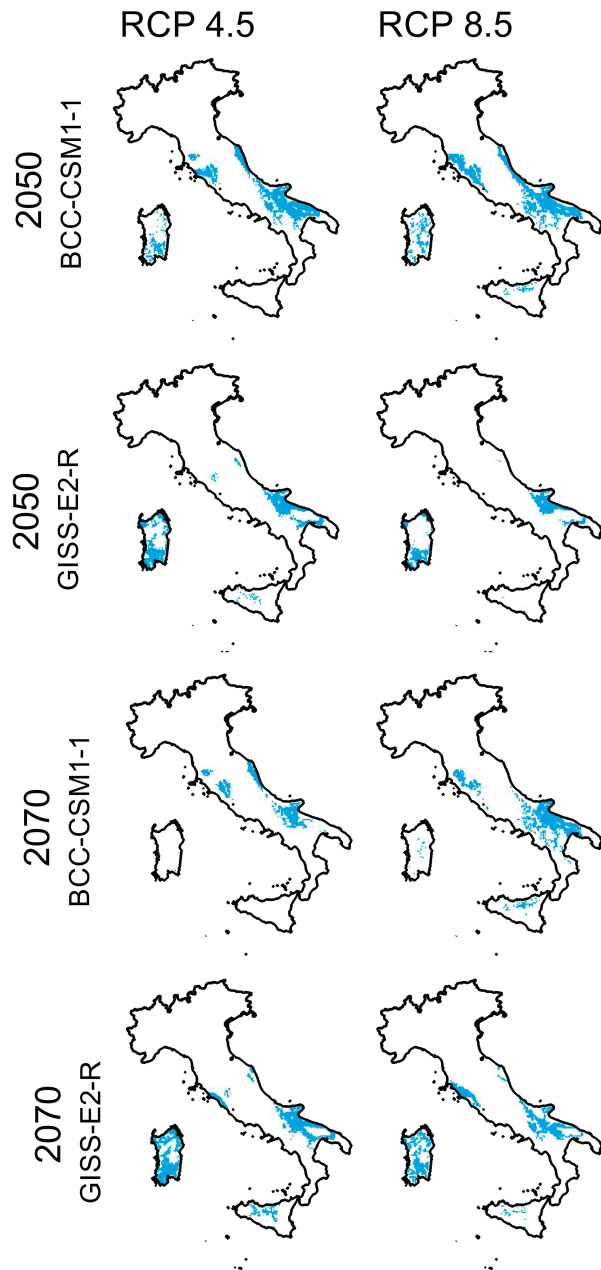


Figure 3. Projections of future climate suitability in 2050 and 2070 for the overwintering of lesser kestrels in Italy, depending on two intensities of climate change (RCPs pathways 4.5 and 8.5, intermediate and intense respectively) and two global climate models (BCC-CSM1-1 and GISS-E2-R).

Table 4. Number and proportion of Italian breeding sites of lesser kestrels that will be distributed inside or outside the borders of the predicted future climatically suitable area for breeding (n = 298 breeding sites).

Year of prediction	Climate change intensity	GCM	Colonies still in climatically suitable areas	% of colonies excluded from suitable areas	Mean % of colonies excluded from suitable areas \pm SD
2050	Intermediate (rcp4.5)	BCC-CSM1-1	79	73.49	66.05 \pm 14.48
		GISS-E2-R	164	44.97	
	Intense (rcp8.5)	BCC-CSM1-1	68	77.18	
		GISS-E2-R	94	68.46	
2070	Intermediate (rcp4.5)	BCC-CSM1-1	81	72.82	74.00 \pm 8.81
		GISS-E2-R	112	62.42	
	Intense (rcp8.5)	BCC-CSM1-1	50	83.22	
		GISS-E2-R	67	77.52	

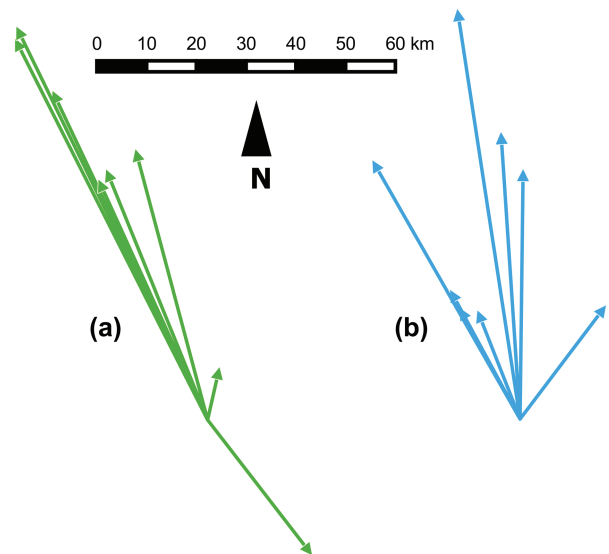


Figure 4. Vectors showing the shift of the barycentre of future climate suitability for lesser kestrels in Italy with respect to current ones for both breeding (a) and wintering (b) periods.

strategies propose that once a wintering population is established at a given European latitude due to climate warming, the strategy for suppressing or shortening migration should spread in the interested population due to several advantages that new-resident birds may have with respect to migratory conspecifics (Coppack et al. 2003, Coppack and Pulido 2004, Morganti 2015). Additionally, as selective pressures for early arrivals and occupancy of the best nesting sites (Kokko et al. 2006) are very strong in cavity nesters (Rubolini et al. 2005, Saino et al. 2010), they promote the occurrence of resident behaviour especially among males. We should therefore expect males to be most commonly observed in winter than females, which would be confirmed by our database, where 57% of winter observations recorded the sex of the bird as males (even assuming the possible field underrepresentation of female kestrels, which are very similar to the common kestrel).

However, we suggest some caution in interpreting the results about the prediction of a fast spread of species in the next few winters given the strong conservatism of both wintering niches (Martínez-Meyer et al. 2004) and the use of specific habitats during winter (Tella and Forero 2000). Other biogeographical factors may also occur to limit the real future distribution of birds, despite the occurrence of

potentially available niches (Engler et al. 2014). In conclusion, a suitable climate is a necessary but not sufficient condition for the presence of stable wintering populations, since the latter would be the product of interaction between environmental conditions and climate suitability.

Although planetary climate change mitigation seems to be the only challenge to halt the ongoing biodiversity crisis (Edenhofer et al. 2014), there is an urgent need to incorporate climate change into conservation research by focusing most on potential policy and management changes (Godfrey et al. 2009). At regional level, compensative measures to climate change should necessarily be integrated into conservation planning (Hannah et al. 2002). Our modelling estimated the distributional response of lesser kestrels in Italy based on spatially explicit data and the findings we have obtained may help focus the geographic core of the species' range and prioritize the areas under high risk of losing breeding populations due to climate change.

Lesser kestrels could become a very useful flagship species to attract public attention to the problems climate change is causing with migratory birds (Robinson et al. 2009) and help promote conservation of pseudo-steppe habitats and their wildlife. Specifically, our findings suggest active protection of both the main breeding sites in southern Italy and the recently established populations at northern latitudes to conservation managers and stakeholders, which probably represent the forefront of future northward expansion of the species at the European scale.

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Supplementary material (Appendix JAV-01179 at <www.avianbiology.org/appendix/jav-01179>). Appendix 1.