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Different trends of neighboring populations of Lesser Kestrel: Effects of climate and other environmental conditions

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Abstract

The sensitivity of population trends to the climate and environment is generally considered a species-specific trait. However, evidence that populations may show different responses to the climate and environmental conditions is growing. Whether this differential sensitivity may arise even among neighboring populations remains elusive. We compared the trends of two neighboring populations of the Lesser Kestrel *Falco naumanni*, using data from a 12-year survey of 158 colonies in Sicily, Italy; the two populations inhabiting a lowland and an highland area, respectively. Population trends were modeled through the TRIM algorithms implemented in R (package *rtrim*). A reversed U-shaped population trend was observed in the lowland, while the highland population showed oscillations around a stable trend. Sahel rainfall 2 years before each annual survey significantly affected population variation in the lowland, while rainfall in March and an index of primary productivity in the breeding areas affected population variation in the highland. This suggests that the population in the lowland may be limited mainly by winter survival in Sahel, because the lowland may be an optimal breeding area for this species. In contrast, the highland population, which occupies a different part of the climatic niche of the species, may be limited mainly by reproductive output, because rainfall in March and the primary productivity in May could represent prey availability immediately before and during the breeding months. Overall, our findings suggest that population-specific environmental sensitivity might occur even over small (<100 km) geographical scales, highlighting the need for population-specific conservation strategies.

KEYWORDS

global change, migratory birds, NAO, NDVI, population trend, Sahel precipitation index

1 | INTRODUCTION

Fluctuations in the size of wild animal populations are largely associated with oscillations in the climate and/or environment (Aars & Ims, 2002; Sæther, Sutherland, & Engen, 2004; White, 2008). Recently, human-induced climate variations (IPCC, 2014) have affected population fluctuations of several species (Burrows et al., 2014; Garcia, Cabeza, Rahbek, & Araújo, 2014; Parmesan & Yohe, 2003;

Sillett, Holmes, & Sherry, 2000), causing shifts in their phenology and distribution, which potentially indicate adaptive reactions of organisms that are trying to cope with global change (Jonzén et al., 2006; Wong & Candolin, 2015). However, despite such shifts, many populations have showed sharp declines linked to climate change, which is therefore generating a massive biodiversity loss on a global scale (e.g., Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Urban, 2015).

Ecological theory foresees the synchrony of population fluctuations over wide areas due to spatial correlations in environmental stochasticity (the so-called Moran effect, Moran, 1953). This prediction has been confirmed by a series of empirical studies (e.g., Sæther et al., 2007; Stenseth et al., 1999), suggesting that populations of the same species exposed to similar climate oscillations show a similar demographic variation, and therefore a similar population trend.

However, other evidence shows a large intra-specific variation in populational responses to a similar environmental change (Rushing, Ryder, & Marra, 2016). Demographic parameters, for instance age and sex composition, affect the response of populations to an environmental change, because individuals of different categories may respond differently to environmental oscillations (Coulson et al., 2001). Indeed, recent evidence shows how the same climatic trend can have different or even opposite effects on the life-history traits of spatially segregated populations (e.g., Balbontín et al., 2009; Guéry et al., 2017), or of populations inhabiting different environments (Oliver, Brereton, & Roy, 2013; Oliver, Roy, Hill, Brereton, & Thomas, 2010; Rushing et al., 2016). Evidence of the intra-specific variation in climate sensitivity is, therefore, accumulating in many organisms (mammals: Coulson et al., 2001; Mason et al., 2011; Weladji & Holand, 2003; fishes: Crozier, Zabel, & Hamlet, 2008; trees: Benito-Garzón, Alía, Robson, & Zavala, 2011; Rehfeldt, Ying, Spittlehouse, & Hamilton Jr, 1999). However, whether this variation can emerge even among populations living close to one another remains an elusive question.

Birds are well-studied and monitored organisms, and long-term studies on their population fluctuations are common. However, only a few examples of different sensitivities to climate variations among neighboring bird populations are available, and they almost exclusively refer to Passerines. For instance, the laying date of very close populations of the Corsican Blue Tit (*Cyanistes caeruleus ogliastrae*) is differently affected by climate conditions (Lambrechts, Blondel, Maistre, & Perret, 1997; Porlier et al., 2012). The population-specific responses to the same climate variation suggest that the difficulty of identifying an optimum climate and/or environmental condition holds throughout the distribution range of a species (Jiguet et al., 2006; Moran, 1953). Consequently, climate variability can cause large differences in population trends, especially among populations that occupy different parts of the climatic niche of a species (Jiguet et al., 2006; Martínez-Meyer, Díaz-Porrás, Peterson, & Yáñez-Arenas, 2013). This fine-scale process of the responses to climate and/or environmental conditions may disrupt the Moran effect, even among populations that are not separated by geographical barriers. Evidence for the actual occurrence of this process is still flimsy, and studies based on long term (>10 years, Møller & Fiedler, 2010, Tavecchia, Oro, Sanz-Aguilar, & Béchet, 2017) data on population trends collected at a fine-grained spatial scale have

been invoked to fill this gap of knowledge (Merilä & Hendry, 2014).

This study analyzed two populations of the Lesser Kestrel (*Falco naumanni*, Fleischer 1818), which breed in Sicily (Southern Italy) and overwinter in sub-Saharan West Africa. They are an ideal model for investigating the differential effects of climate and environmental variations on trends in neighboring populations. Indeed, this species breeds at a relatively high density along an altitudinal gradient in Sicily (~1,000 pairs over >25,000 km²; Di Maggio et al., 2014; Sarà, 2008, 2010), and therefore it offers the opportunity to study populations occupying areas with different climatic and environmental conditions (see Methods), but that are also living less than 100 km to one another. This distance can be potentially covered by a Lesser Kestrel in a flight of a few hours (Hernández-Pliego, Rodríguez, & Bustamante, 2017), but it is much longer than the mean natal dispersal of this species, which is normally shorter than 8 km (Ortego, Calabuig, Aparicio, & Cordero, 2008; Serrano, Tella, Donazar, & Pomarol, 2003). In addition, previous research provided rich information on the climatic niche (Morganti, Preatoni, & Sarà, 2017) and on the life cycle (Limiñana, Romero, Mellone, & Urios, 2012; Sarà, Campobello, Zanca, & Massa, 2014; Serrano, Forero, Donazar, & Tella, 2004; Serrano, Oro, Ursua, & Tella, 2005) of different populations of the Lesser-Kestrel and on the susceptibility of their reproductive parameters to climate and environmental variation (Mihoub, Gimenez, Pilard, & Sarrazin, 2010; Rodríguez & Bustamante, 2003; Sarà, 2010).

This work is structured in three steps. First, we tested whether population trends and reproductive phenology differed between neighboring populations in a highland and a lowland habitat. Second, the trends in climatic and environmental variables both on the breeding and the wintering grounds were analyzed to assess whether the two populations have been exposed to divergent patterns of climate or environmental change in any phase of their life cycle. Third, we modeled year-to-year variation in the size of each population according to climate and environmental conditions.

2 | MATERIALS AND METHODS

2.1 | Study species

The Lesser Kestrel is a small raptor and a long-distance migrant that breeds in the open and dry cereal steppes of the Palearctic (Ferguson-Lee & Christie, 2001) and overwinters in sub-Saharan West Africa (i.e., Bounas, Panuccio, Evangelidis, Sotiropoulos, & Barboutis, 2017; Limiñana et al., 2012). It is a secondary-cavity nester that forms colonies of 2–45 pairs in cliffs or rural buildings, often in association with other species (Campobello, Hare, & Sarà, 2015; Campobello, Sarà, & Hare, 2012; Sarà, Campobello, & Zanca, 2012). Lesser Kestrels arrive in Sicily in late February-mid March;

egg-laying peaks in late May and juvenile fledging peaks in late June (Di Maggio, Campobello, & Sarà, 2013; Mascara & Sarà, 2006). Movements of breeding adults are limited mainly to within 3 km from their colony during nest attendance (Bondi & Sarà, 2016a; Cecere et al., 2018; Gustin, Giglio, Pellegrino, Frassanito, & Ferrarini, 2017; Tella, Forero, Hiraldo, & Donazar, 1998; Vlachos et al., 2015). Chicks are therefore mainly fed with prey collected in the immediate area surrounding the colony (Bounas & Sotiropoulos, 2017; Morganti, Franzoi, Bontempo, & Sarà, 2016). After breeding, they move to premigratory areas in Sicily, where they stay from late June to mid-October fattening before migration (Bounas & Sotiropoulos, 2017; Sarà et al., 2014). Migration of this species is quite fast, and the journey from pre-migratory areas to winter quarters takes only a few days. The autumn migration, in particular, is completed in less than 1 week (Bondi & Sarà, 2016b; Limiñana et al., 2012).

2.2 | Study areas

We performed an extensive long-term survey (12 years, from 2003 to 2014) of two Lesser Kestrel populations, one breeding in a highland area in north-western Sicily at a mean altitude of 600 m above sea level (a.s.l.) (“highland population” hereafter) and the other breeding in the lowland surrounding the city of Gela in the south-eastern part of the island at a mean altitude of 200 m a.s.l. (“lowland” population hereafter; Figure 1). The two populations inhabited markedly different environmental conditions (Figure 1), and their breeding biology also differed. In the lowland, most

colonies (73%) occurred in rural buildings, while in the highland most (77%) were in natural cliffs (our own data). Furthermore, the two areas had different meteorological features (Sarà, 2008, 2010; Triolo, Campobello, & Sarà, 2011, Figure 1).

Although the breeding biology of different populations of this species is affected by general climate and environmental conditions of the area where they breed (Mihoub et al., 2010; Rodríguez & Bustamante, 2003; Sarà, 2010), the available evidence suggests that, within a population, breeding performances of individuals do not change with the microclimatic features of nesting cavities (Campobello, Lindström, Di Maggio, & Sarà, 2017) or between nests located in cliffs or in rural buildings (Liven-Schulman, Leshem, Alon, & Yom-Tov, 2004). For this reason, we did not consider the difference of nesting sites (cliffs or rural buildings) in the analysis. In addition, potential predators and nest-site competitors were almost the same in both areas. The Eurasian Kestrel *Falco tinnunculus*, the Barn Owl *Tyto alba*, the Little Owl *Athene noctua*, the Eurasian Jackdaw *Coloeus monedula*, and the Feral Dove *Columbia livia domestica* breed in both cliffs and rural buildings in both areas (our own observations). The Raven *Corvus corax*, the Common Buzzard *Buteo buteo*, and the large falcons *Falco peregrinus* and *Falco biarmicus* occurred in the highland area and in the hills a few hundred meters from the lowland area. Among other potential predators of the Lesser Kestrel listed in Tella, Hiraldo, Donazar, and Negro (1996), only the Red Fox (*Vulpes vulpes*) and rats (*Rattus* spp.) were present in Sicily. However, foxes were scarce in the intensive farmlands of the lowland area (Sarà et al., 2012), whereas in the

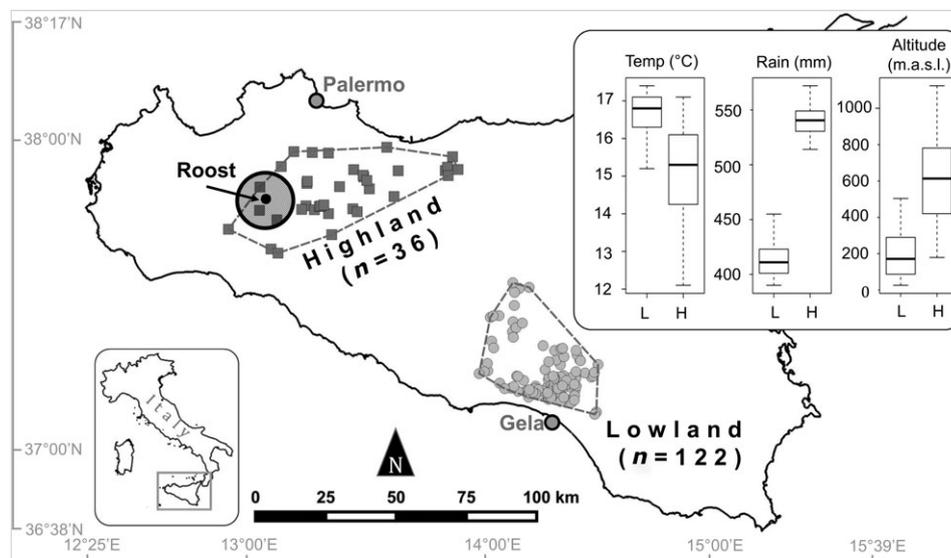


FIGURE 1 Distribution of the lowland and the highland population of the Lesser Kestrel in Sicily, Italy. The dashed contours indicate the minimum convex polygons used for calculating NDVI values for lowland (circles) and highland (squares) colonies. Boxplots show altitude, annual temperature, and rainfall for the lowland (L) and highland (H) colonies. Altitude data were extracted from a digital elevation model with cells of 20 m (available at sinanet.isprambiente.it). Temperature and rainfall data were obtained from the WorldClim datasets “Bio1” and “Bio12” (Hijmans et al., 2005) at a resolution of 30 arcsec (~1 km²), which report the mean temperature and rainfall per cell during the period 1950–2000 and are generally interpreted as “current climatic conditions.” The location of the pre-migratory roost with the 10 km buffer used for calculating the roost NDVI is also shown. “N” indicates the number of colonies that were monitored. NDVI, normalized difference vegetation index

highland area they were more abundant. However, because Lesser Kestrels in the highland population mainly breed in steep cliffs (Sarà M. and Zanca L. pers. comm.) foxes are unlikely to represent a threat in this area. Predation by rats was observed in no more than four of the lowland colonies (Sarà et al., 2012 and Sarà M. and Zanca L., pers. comm.) during 2005–2007 and ceased after this period, possibly because the buildings were no longer used for cereals and fodder storage. During our field observation period spanning more than 15 years (including a preliminary survey), we documented only a few cases of predation on nests of Lesser Kestrels in both habitats (Sarà M. and Zanca L., pers. comm.). Hence, we confidently assumed that the predator and/or competitor pressures were similarly distributed in the highland and the lowland populations and had a negligible role, if any, in shaping the population trends in our study areas.

2.3 | Colony size and reproductive phenology

Buildings and cliffs were used by single pairs for breeding, as well as by colonies of 2 to 45 pairs (Sarà et al., 2012). Following other authors (i.e., Serrano et al., 2003), we defined as a “colony” any breeding site where at least one pair of the Lesser Kestrel performed territorial behavior during the breeding season (April–July) at least in 1 year over the study period. We recorded the number of territorial pairs in each colony and year by counting any pair that displayed breeding-related behaviors, such as entering a hole, chasing off other individuals, mating or visiting active nests with eggs or chicks. Deserted breeding sites and nearby areas were also carefully inspected to confirm the absence of breeding pairs. It is, therefore, certain that we recorded the presence or the absence of breeding pairs at all colonies in the study areas (see Di Maggio, Campobello, Tavecchia, & Sarà, 2016, Sarà, 2008 for a similar approach). To assess the number of breeding pairs, each colony was visited at least twice during each breeding season, and the number of breeding pairs was counted during each visit. The average number of breeding pairs observed in the two visits was considered an estimate of the colony size in that year. Further details on the field methods were reported in Sarà (2010) and Di Maggio et al. (2013, 2014, 2016). This protocol was followed in each year between 2003 and 2014 in both study areas. Overall, we censused 122 colonies in the lowland area and 36 colonies in the highland area. Due to unpredictable limitations (e.g., adverse meteorological conditions or inaccessibility of nesting sites), some colonies were not visited twice in some years. In such a case, we did not estimate the size of these

colonies for that year (see the results section for the exact number of colonies with missing information).

We also aimed at describing the reproductive phenology of both populations. To this end, we selected 20 colonies in the lowland area and 9 in the highland area and obtained phenological data during 11 and 5 years, respectively (Table 1). In these colonies, we inspected nest cavities at least four times every tenth day between early-April and the end of June and recorded the number of eggs or nestlings at each visit. For late fledging nests, we added an extra-visit in July. Overall, we collected phenological data for 1,157 nests in the highland area and 53 nests in the lowland area. This sample size was considered sufficient to accurately describe the breeding phenology of the two populations.

The protocol for nest inspections was established on the basis of information collected in 2000 on nests that were visited daily during laying and incubation. We candled eggs to check the embryo development and revealed that, in our populations, eggs were laid every 24 to 40 h; incubation lasted for 29 to 31 days, and chick rearing lasted for 30 to 32 days (Sarà et al., 2012). In all cases, the monitored nests occurred in rural buildings, because nests in natural cliffs were inaccessible, but there is no reason to suspect that the timing of egg-deposition and embryo or chick development markedly differed in natural cliffs. This intensive study also allowed us to describe body size and plumage development of nestlings of a known age. This information was then used to estimate nestling age and hatching and laying date of the other broods in the study colonies (see Campobello et al., 2017, Mascara & Sarà, 2006, Sarà et al., 2012 for further details).

Before the autumn migration, Lesser Kestrels perform a communal roost in premigratory areas (Sarà et al., 2014). The largest roost in Sicily was located at Rocca d'Entella (Figure 2). In 2010–2012, about 84–94% of the individuals of this species breeding in Sicily congregated in this roost, including birds coming from several lowland colonies, as was supported by resighting of color-ringed birds (Sarà et al., 2014) and through satellite telemetry (Bondi & Sarà, 2016b). During this period, Lesser Kestrels feed within a radius of 10 km from the roost (Sarà et al., 2014).

2.4 | Life-cycle

For the purposes of the present study, we divided the annual life-cycle of the Lesser Kestrel into four stages and analyzed climatic and/or environmental variables for each of them that may have direct or indirect influences on population dynamics (Figure 2).

TABLE 1 Phenological differences in laying date between lowland and highland populations of the Lesser Kestrel in Sicily

Population	N sampling years	N colonies	N nests	Median laying date	Earliest laying date	Latest laying date
Lowland	10	20	1,157	26 April	7 April	7 June
Highland	5	9	53	17 May	4 May	28 May

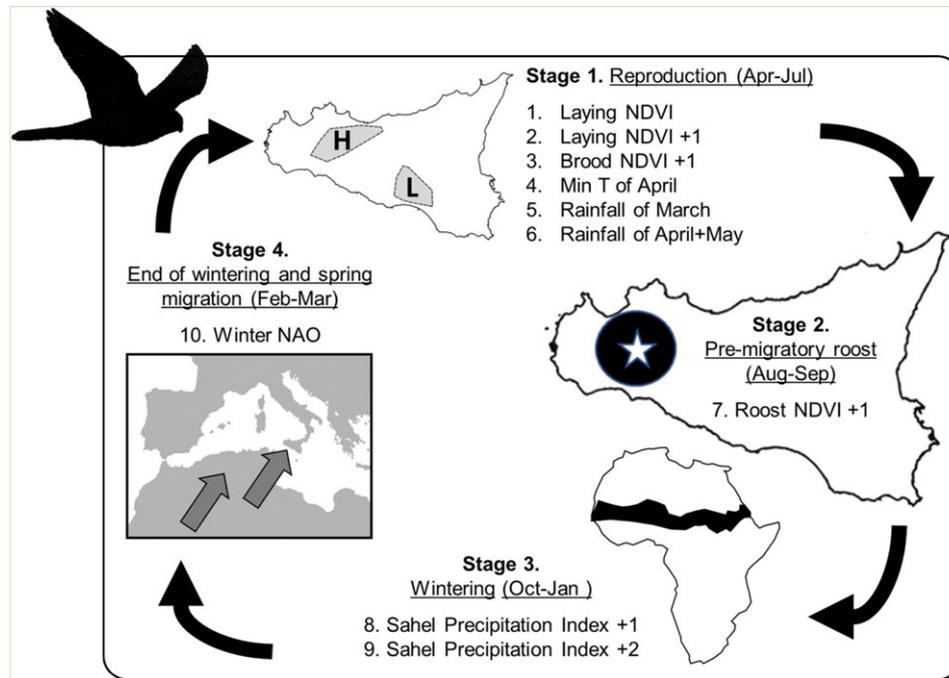


FIGURE 2 Main phases of the life cycle of Lesser Kestrels in Sicily, Italy. For each phase, key climatic and environmental variables are indicated. T, Temperature; NAO, North Atlantic Oscillation index; NDVI, normalized difference vegetation index. The effect of the variables on Lesser Kestrel population size was tested with a lag of one (+1) or 2 years (+2) (see the main text) separately for the highland (H) and the lowland (L) population. The left insert with gray arrows shows general migration directions followed by Lesser Kestrels during spring migration

The occupancy rate of colonies is known to be sensitive to spring rainfall and the temperature of the breeding areas (Di Maggio et al., 2016; Mihoub et al., 2010, 2012; Rodríguez & Bustamante, 2003). Specifically, to account for these potential effects, following Rodríguez and Bustamante (2003) and Morganti, Preatoni, and Sarà (2017), we used the cumulated rainfall of March, the sum of April and May cumulated rainfall, and the monthly mean minimum temperature of April as predictors (stage 1, Figure 2). Rainfall and temperature data for the lowland area were collected by a weather station located in the town of Gela (37°04'N, 14°15'E), while data for the highland area were collected in Prizzi village (37°43'N, 13°25'E). All weather data were gathered from SCIA website (Sistema nazionale elaborazione e diffusione dati climatici; www.scia.isprambiente.it). Although laying and hatching occurred later in the highland than in lowland (see result section), Lesser Kestrels were normally observed in both study areas from the beginning of March. Likely, colony occupancy and courtship stages were a bit longer in the highlands, but the scarcity of available observations did not allow us to test the differences in their length between the two areas. In addition, these stages are less defined and more variable from year to year and among colonies or even among individuals, than for example, egg laying or hatching. For these reasons, we decided to consider weather variables accounting for conditions in March–May as predictors of colony occupancy rate in both areas.

To model the potential effect of local environmental conditions during the breeding season, we used normalized difference vegetation index (NDVI) values for the lowland and

the highland areas. NDVI is a satellite-derived index of primary productivity (Gordo & Sanz, 2008; Pettorelli et al., 2005), and it can be considered a proxy of the abundance of food supply and also for insectivorous birds like the Lesser Kestrel, because insect abundance depends on plant productivity (Sanz, Potti, Moreno, Merino, & Frias, 2003). Georeferenced NDVI raster maps of Sicily representing NDVI values every 16 days with a resolution of 500 m per pixel were downloaded from the online platform MRTWeb (United States Geological Survey [USGS], 2015; MODIS product MOD13A1 V6; data available at <https://lta.cr.usgs.gov/NDVI>) and processed in QGIS 2.4.0 (QGIS Development Team, 2018). Since the breeding phenology of the Lesser Kestrel differed between the two studied populations by about 15 days (see result section and Sarà, 2010) and NDVI values were explicitly supposed to influence clutch size and the survival of both adults and chicks, we calculated NDVI variables for the highland and the lowland population during different periods of the year. Specifically, to measure the NDVI during the laying period (“laying NDVI”; Figure 2), we selected images corresponding to 21 April (20 April in leap years) for the lowland and 7 May (6 May in leap years) for the highland, as these dates corresponded to the peak of laying in the two areas. Similarly, to measure the NDVI during the peak of the chick-rearing period (“brood NDVI”), we selected images corresponding to 9 June (8 June in leap years) for the lowland and to 24 June (23 June in leap years) for the highland. We emphasize that these were the only variables considered in this study that were calculated over different time spans for the highland and the

lowland populations, because we hypothesized that Lesser Kestrel population dynamics could be sensitive to NDVI values during the peak of laying and chick rearing, which occurred at different times in the two areas.

To represent primary productivity in the premigratory period, we used NDVI values in a radius of 10 km around the Rocca d'Entella roost ("roost NDVI") from the image corresponding to 13 August (12 August in leap years; stage 2, Figure 2), because the peak occupancy of the roost was around mid-August (Sarà et al., 2014). We considered that NDVI data in a single period could represent conditions affecting the dynamics of the populations from both areas, because the phenology of the pre-migratory period is almost the same among all Sicilian colonies.

Sahel precipitation index (hereafter SPI), defined as the anomalies with respect to the 1901–2016 mean (in millimeter of rain) between June and October (JISAO, 2018), was used as a measure of the ecological conditions in the wintering quarters (stage 3, Figure 2). Indeed, during wintering, the food abundance of insectivorous raptors depends upon precipitation, which is known to affect the survival of Lesser Kestrel yearlings (Mihoub et al., 2010) and can determine shifts in the breeding phenology of adults through carry-over effects (Schlaich et al., 2016).

Finally, the North Atlantic Oscillation (NAO) index between December and March ("winter NAO") was used to assess general ecological conditions experienced by birds during spring migration (stage 4, Figure 2). Winter NAO is one of the most used predictors in studies of the effects of climate variability on the migration ecology of European birds (e.g., Gordo, Barriocanal, & Robson, 2011; Guéry et al., 2017; Sæther et al., 2004; Saino et al., 2004, but see Haest, Hüppop, & Bairlein, 2018 for criticism on its use). Although the spring migration of the Lesser Kestrel spans only few days (stage 4, Figure 2), the winter NAO index calculated during this period is a good proxy of the general winter and early spring meteo-climatic conditions over large areas of the Northern Hemisphere (see e.g., Guéry et al., 2017; Wang, Ting, & Kushner, 2017).

Autumn migration could have been included as a further stage in the annual life cycle of the Lesser Kestrel, because it is probably one of most energy-demanding life phases for any migratory bird (Newton, 2008). However, autumn migration of the Lesser Kestrel lasts less than 1 week (Bondi & Sarà, 2016b; Limiñana et al., 2012), and it is unlikely that mortality during this short time span can be high enough to influence population trends.

2.5 | Statistical analyses

2.5.1 | Reproductive phenology and population trends

Differences in breeding phenology between the two populations were evaluated by comparing the median laying date in the subsamples of colonies where this variable was recorded by means of a Wilcoxon rank test.

We estimated population trends in both areas separately using *rtrim* (Bogaart, Van der Loo, & Pannekoek, 2016), an R package based on the popular TRIM software (TRends for Indices and Monitoring bird data, Pannekoek & van Strien, 1996) that models yearly counts assuming a Poisson distribution and a log link function and accounting for data overdispersion, if necessary. This method is robust to the presence of a high proportion of missing counts (i.e., missing information on the size of a given colony in a given year), as was the case of our dataset (missing data were 40.6% for lowland colonies and 20.2% for highland colonies). In the trend estimation, *rtrim* imputes missing data with values estimated by considering the absolute value of the specific colony and the general trend of the whole group of colonies in that year. This allows us to estimate the number of pairs at each area and year even in the presence of missing counts. Specifically, we used model 2 of *rtrim*, which assumed all years as possible changing points in the population trend and takes into account the overdispersion of the data (Pannekoek, van Strien, & Bogaart, 2018). The *rtrim* model 2 also allowed us to compute the *SE* of the estimated number of breeding pairs and the variance-covariance matrix among the estimates in different years that were used in subsequent analyses (see below).

We also tested whether the number of breeding pairs at each area varied non-monotonically through time by fitting models that included both the linear and the squared term of year as predictors. To account for the differences in the uncertainty of the annual population size estimates obtained from the *rtrim* model, we weighted the observations based on the inverse of the variance of the yearly effect estimates (weight = $1/SE^2$). This use of weights is a common way to account for differences in the uncertainty of the dependent variable in linear models (Draper & Smith, 2014), because in this way more precise yearly estimates have larger importance in the model fitting than less precise ones.

2.5.2 | Climate, environmental conditions and their temporal trends

According to the known sensitivity of this species to climate conditions in the breeding areas (see above), we hypothesized that weather conditions during spring (i.e., minimum temperature of April, cumulated rainfall of March, cumulated rainfall of April and May; see stage 1 in Figure 2) may influence the number of breeding pairs in the same year in which they are measured. Similarly, the laying NDVI may affect the number of breeding pairs, because under unsuitable environmental conditions, Lesser Kestrels that have failed laying will abandon colonies very early and thus escape our observation. The laying NDVI could also determine adult survival to the following breeding season through carry-over effects, particularly in an income breeder, such as the Lesser Kestrel (Dunn, 2006). Hence, the laying NDVI was entered in the analyses both with a nonlagged effect

(i.e., we hypothesized that the laying NDVI value of year i could affect population size in year i through effects on early nest desertion), and with a lagged effect of 1 year (laying NDVI lag+1, i.e., the laying NDVI value of year i could affect population size in year $i + 1$ through effects on adult survival). In contrast, the brood NDVI and the roost NDVI (stages 1 and 2 Figure 2), which described environmental conditions after breeding pairs established, were hypothesized to influence the annual survival of yearlings and adults and therefore population size in the following year (i.e., we hypothesized that the brood NDVI and the roost NDVI value of year i could affect population size in year $i + 1$).

The scarcity of Sahel rainfalls may affect the winter survival of both adult and juvenile Lesser Kestrels (Mihoub et al., 2010, stage 3 Figure 2). Adult winter survival will reverberate on the size of the breeding population in the next spring, while survival of juveniles will affect the size of the breeding population 2 years later, as most Lesser Kestrels breed for the first time in their second year of life (Ferguson-Lee & Christie, 2001). We, therefore, modeled the effect of winter rainfalls on population size by using SPI with both a lag of 1 year (SPI lag + 1, i.e., we hypothesized that SPI value of year i could affect population size in year $i + 1$) and of 2 years (SPI lag + 2, i.e., we hypothesized SPI value of year i could affect population size in year $i + 2$).

Finally, the winter NAO values were hypothesized to affect survival during return migration (stage 4, Figure 2) and colony size in the following spring. For instance, we hypothesized that the winter NAO 2012 (i.e., the mean monthly NAO index registered in the period December 2012–March 2013) could influence population size recorded in April to May 2013.

To test whether the abovementioned climate and environmental conditions changed during the survey period, we first fitted linear models assuming a Gaussian error distribution with the function *lm* (*stats* package) in R 3.4.1 (R Core Team, 2017) with year included as a covariate. We then inspected the residuals of the models in search of possible temporal autocorrelation by using the function *acf* (*stats* package of R) and, whenever we detected it (i.e., when data of successive years were not independent), we fitted generalized least square models with the *gls* function (*nlme* package; Pinheiro & Bates, 2017) assuming a first-order temporal autocorrelation of residuals (i.e., AR1 structure). No variable showed temporal autocorrelation of an order higher than one, or other deviations from the assumptions of the linear model (details not shown).

2.5.3 | Effects of climate and environmental conditions on population size

We modeled the effect of climate and environmental conditions (see Figure 2 for the complete list) on the size of Lesser Kestrel populations in the two study areas using the statistical approach proposed by Sicurella, Musitelli, Rubolini,

Saino, and Ambrosini (2016). As a first step, we calculated the year-to-year variation of both the series of predictors and the dependent variables (i.e., the number of breeding pairs in each year and study area), with the aim to remove the potential confounding effects due to the presence of temporal trends or temporal autocorrelations in both the dependent variable and the predictors. These new variables were named adding the prefix “ Δ ” to the name of the original variable, that is, lowland Δ Pairs was the year-to-year difference in the number of breeding pairs in the lowland study area. In contrast, we referred to the actual yearly counts and predictors as “original” variables. Similar to Sicurella et al. (2016), we opted to use the differences in population size between two consecutive years (Δ -variables), instead of the ratio between the population sizes in two consecutive years (λ), because the Δ variables were normally distributed (Shapiro–Wilk test for the lowland: $W = 0.98$, $p = 0.985$; and for the highland: $W = 0.92$, $p = 0.348$), while λ values were not (for the lowland: $W = 0.84$, $p = 0.037$; and for the highland: $W = 0.95$, $p = 0.682$). In addition, the use of Δ -variables allowed us to take into account the uncertainty of the yearly estimates of population size obtained from the *rtrim* models (see below). The Δ -variables showed no temporal trend (the effect of years: $|t_0| \leq 1.566$; $p \geq 0.152$ in all cases) and no temporal autocorrelation (the absolute value of the temporal autocorrelation of order 1 was <0.5 in all cases) with the only exception of lowland Δ Pairs, which still showed a significant temporal trend (effect of year: -17.03 ± 5.66 SE, $t_0 = -3.018$, $p = 0.015$). This indicated that the lowland population followed a nonlinear trend (Figure 3).

We then modeled the Δ Pairs using all the considered original climatic and environmental variables listed in Figure 2 as predictors, as well as the Δ -variable for each predictor. These analyses were run separately for each study area. According to this approach, a null variation in a given Δ -variable should result in a null variation of Δ Pairs. In contrast, the original variables were entered in the models for detecting possible “threshold effects” of a predictor on Δ Pairs (see Sicurella et al., 2016, where they used a similar analytical methodology for further details). To assess how this can occur, suppose, for instance, that the number of breeding pairs decreases when rainfall in the Sahel is below a given threshold value and that identical below-threshold values are registered in two consecutive years. In such a case, the Δ -variable for Sahelian rainfall will assume a value of zero for that pair of years, but Δ Pairs will be negative, because the population decreased in the two successive years due to drought. In this hypothetical case, the two Δ -variables (i.e., Δ Pairs and Δ Sahel) would result as unrelated, while in reality an ecological process was operating: the rainfall was below the minimum threshold to produce favorable conditions for the Lesser Kestrel. To account for this eventuality, it was also necessary to introduce the original variables as predictors in the models. Finally, we included calendar year

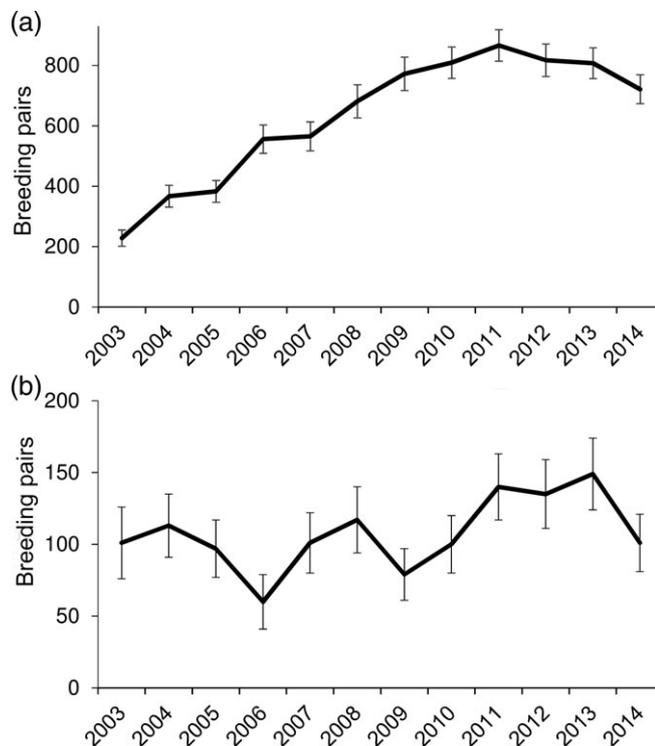


FIGURE 3 Trend of (a) the lowland and (b) the highland population of Lesser Kestrels in Sicily, Italy between 2003 and 2014 expressed as the number of breeding pairs. Whiskers represent *SE* of the yearly estimate as calculated by *rtrim*

as a further predictor in the analyses to account for potential variations in the year-to-year differences of population size. We note that an effect of year would imply that the difference in population size between consecutive years changed through time and therefore the population size changed nonlinearly.

Prior to model fitting, we explored the degree of autocorrelation among predictors using the *corrplot* package (Wei & Simko, 2017), and when we found a pair of variables whose absolute value of the Pearson correlation coefficient was >0.7 , we excluded one of them (see Figures S1 and S2 in the supporting Information). We then relied on an information theoretic approach to select the best model for each set of data (Burham & Anderson, 2002). In particular, we used the *dredge* function (*MuMIn* package; Barton, 2016) for automatically fitting models based on different combinations of predictors. Since our data series was limited in length (i.e., 11 year-to-year differences) while the number of possible predictors was large (21, including Δ -variables, original variables and “year”; see Figure 2), we avoided the overfitting of models by imposing a maximum of three predictors in each model. In this way, the ratio between the number of observations and that of predictors was ≥ 3.6 , that is, above the threshold of 3 that is recommended to avoid overfitting (Forstmeier & Schielzeth, 2011). We stress that our procedure generated models by combining the set of predictors in all possible ways, therefore testing all possible models with zero (i.e., null model), one, two or three

predictors. The overall number of models tested for each study area therefore depended on the number of predictors included in the procedure for each area (12 for the lowland and 10 for the highland area, after that collinear predictors were removed) and was equal to 299 models for the lowland population and 176 models for the highland population (see the result section).

In these models, the dependent variable ΔPairs was the year-to-year difference in the number of breeding pairs estimated by *rtrim*, and thus it was affected by uncertainty, since it was a difference of *estimated* values. We accounted for such uncertainty by weighting the regression models by the inverse of the variance of ΔPairs [i.e., $\text{weight} = 1/\text{Var}(\Delta\text{Pairs})$], which was calculated as:

$$\text{Var}(\Delta\text{Pairs}) = \text{Var}(\text{Pairs}_i) + \text{Var}(\text{Pairs}_{i+1}) + 2\text{Cov}(\text{Pairs}_i, \text{Pairs}_{i+1})$$

where Pairs_i and Pairs_{i+1} are population sizes in years i and $i+1$ estimated by *rtrim* and $\text{Var}(\text{Pairs}_i)$, $\text{Var}(\text{Pairs}_{i+1})$, and $\text{Cov}(\text{Pairs}_i, \text{Pairs}_{i+1})$ are the variances of estimated population sizes in the 2 years and the covariance between them, respectively. Both of these values were obtained from the variance-covariance matrix of the *rtrim* model.

Models were then ranked according to their values of the Akaike Information Criterion (AIC), corrected to account for sample size (AICc) from the lowest (best) to the highest (worst) (Symonds & Moussalli, 2011). All the models with $\Delta\text{AICc} < 2$ with respect to the model with the lowest AICc, were considered to have similar support from the data (Symonds & Moussalli, 2011), and their model coefficients were averaged (Johnson & Omland, 2004). Inspection of residuals of the final conditional average models so obtained revealed the presence of a potential outlier only for the highland dataset. This outlier, corresponding to year 2011, had a Cook's distance >1 in the standardized residual vs. leverage plot, and was removed from the final analysis (details not shown).

Eventually, since the use of (slightly) different sets of predictors for the models of the two populations may potentially affect the results of the model selection procedure, we checked for the robustness of final models by repeating the selection procedure starting from the same set of the predictors for both areas and found identical results (details not shown).

3 | RESULTS

3.1 | Reproductive phenology and temporal trends of population size

Median laying date occurred ~ 20 days earlier in the lowland than in the highland area (Wilcoxon test: $W_{1208} = 7.33$, $p < 0.001$; Table 1).

Yearly estimates (\pm SE) of the number of breeding pairs obtained from *rtrim* for both areas are shown in Figure 3. The lowland population followed a reversed U-shaped trend during the study period (linear term: 0.01 ± 0.01 SE, $t_9 = 6.140$, $p < 0.001$; quadratic term: -7.38 ± 1.21 SE, $t_9 = -6.128$, $p < 0.001$), with a peak in 2011. Indeed, from the 228 ± 27 (mean \pm SE) pairs estimated for 2003, the lowland population increased up to 866 ± 52 pairs in 2011 (linear trend for the 2003–2011 period: 82.01 ± 4.53 SE, $t_7 = 18.11$, $p < 0.001$), and then stabilized in the 2012–2014 period (temporal trend: -49.49 ± 21.91 SE, $t_1 = -2.26$, $p = 0.265$).

In contrast, the size of the highland population fluctuated with no temporal trend (linear term: -0.01 ± 0.01 SE, $t_9 = -0.711$, $p = 0.495$; squared term: 0.48 ± 0.68 SE, $t_9 = 0.712$, $p = 0.494$). Estimated population size was 101 ± 25 pairs in 2003 and reached a minimum of 60 ± 19 in 2006 and a maximum of 149 ± 25 in 2013.

3.2 | Temporal trends of climate conditions and NDVI

Temporal trends of variables accounting for climatic conditions and NDVI are reported in Figures 4 and 5. The plots showed that NDVI values tended to increase weakly over the study period in all areas and phases (laying, brood, and roost). However, the increase was statistically significant for brood NDVI in the lowland area ($t_{11} = 2.837$, $p = 0.016$) and for the roost NDVI ($t_{11} = 2.452$, $p = 0.032$) and was nearly significant for the laying NDVI in the lowland ($t_{11} = 2.057$, $p = 0.064$) and for the brood NDVI in the highland ($t_{11} = 2.012$, $p = 0.069$) and was nonsignificant for the laying NDVI in the highland ($t_{11} = 1.614$, $p = 0.135$). Rainfall and temperature did not show any significant trend for all analyses ($|t_{11}| \leq 1.614$, $p \geq 0.135$), with the exception of March rainfall which showed a significant increase in the highland area ($t_{11} = 2.432$, $p = 0.033$) and a nearly-significant increase in the lowland area ($t_{11} = 1.842$, $p = 0.093$). Winter NAO did not show any trend ($t_{11} = 0.029$, $p = 0.977$), while SPI showed a nearly-

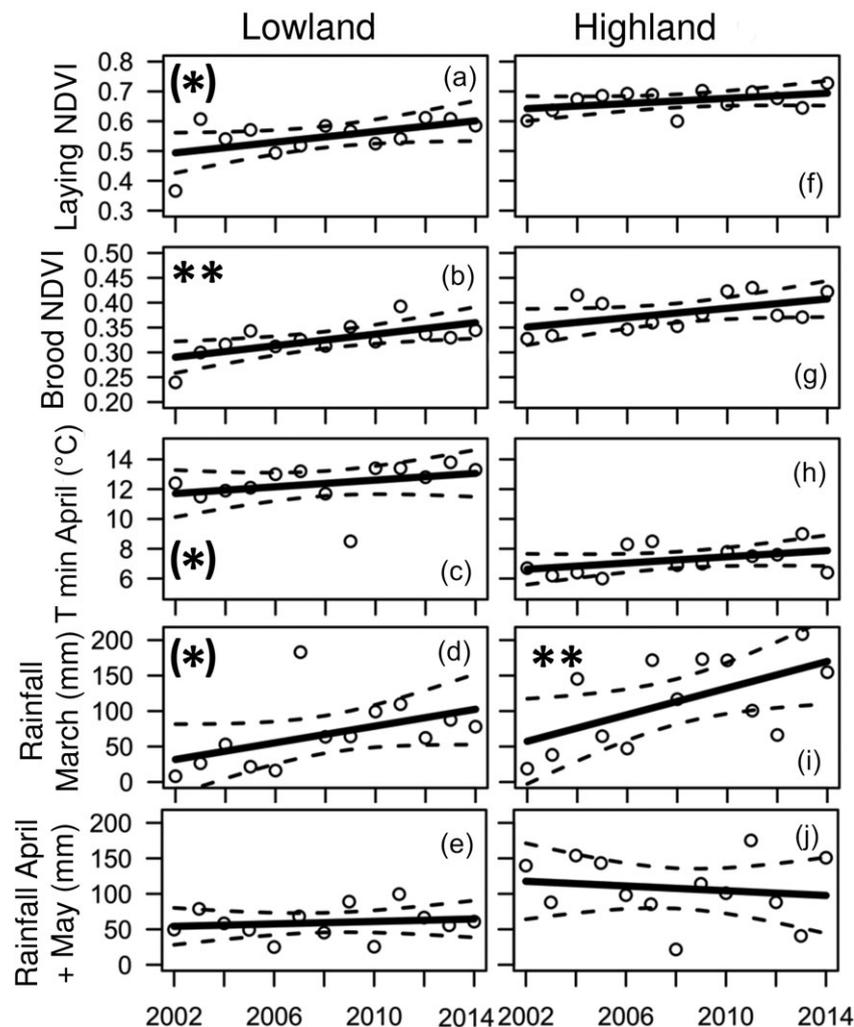


FIGURE 4 Trends of environmental and climatic variables experienced by the lowland (left column) and the highland (right column) populations of Lesser Kestrels between 2002 and 2014. NDVI, normalized difference vegetation index. Letters indicate the trend of: Laying NDVI (a–f); brood NDVI (b–g); minimum temperature of April (c–h); cumulated rainfall of March (d–i); cumulated rainfall of April and May (e–j) **Linear trend significant ($p < 0.05$).

*Linear trend near to significance ($0.05 < p < 0.09$)

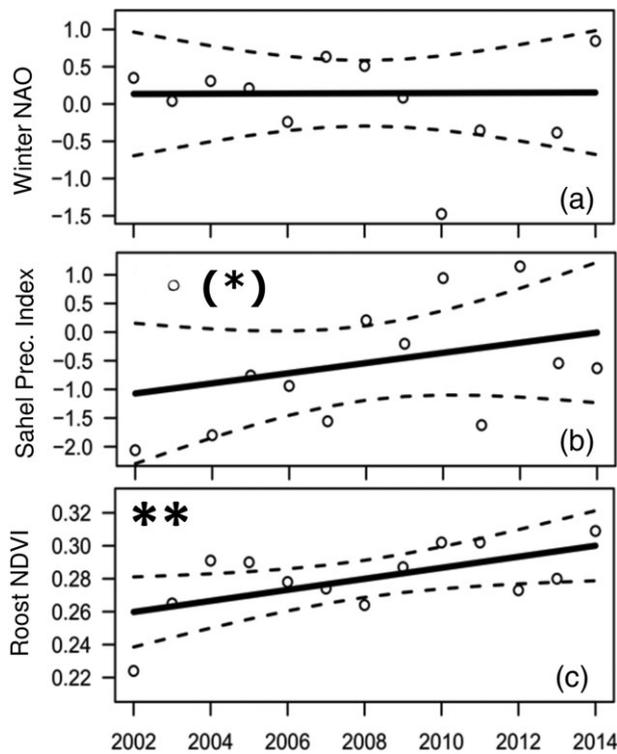


FIGURE 5 Trends of environmental and climatic variables experienced by Lesser Kestrels breeding in both study areas during the postbreeding and wintering stages between 2002 and 2014. NAO, North Atlantic Oscillation; NDVI, normalized difference vegetation index. (a) Trend of winter NAO; (b) trend of Sahel precipitation index; (c) trend of roost NDVI. **Linear trends were significant at the 0.05 level. * Linear trend near to significance ($0.05 < p < 0.09$)

significant increase over the study period ($t_{11} = 1.869$, $p = 0.084$).

3.3 | Effects of climate and NDVI oscillations on population trends

The set of models in which we studied the association between Δ Pairs and the climatic and NDVI predictors indicated significant and specific relations for each breeding population. For the lowland population, a single best-supported model was selected (Table S1), which included

SPI lag+2 with a positive effect and year with a negative effect as predictors (Table 2, Figure 6). In contrast, for the highland population, the selection procedure retained four well-supported models (Table S2), from which we calculated an average model. This latter included winter NAO index and Δ laying NDVI, both with a negative effect and Δ rainfall in March with a positive effect as predictors (Table 2, Figure 6). Both models explained a substantial part of the variance in the observed populations ($R^2 = 0.73$ and $R^2 = 0.78$, respectively; Table 2).

4 | DISCUSSION

4.1 | Sensitivity to climatic and environmental factors

In this study, we documented the temporal trends of the two Lesser Kestrel populations, respectively, inhabiting the eastern lowland and the western highland of Sicily, Italy, and we investigated the climatic and environmental variables that explained oscillations in the size of those populations.

We found that the lowland population showed a reversed U-shaped trend, increasing until 2011 and then stabilizing (at least until 2014, when the annual censuses ended) and that its year-to-year variability was positively related to the amount of rainfall 2 years before in the Sahel (the wintering area). We hypothesized that this lagged effect may have arisen because Sahel conditions are known to affect the survival of juvenile Lesser Kestrels (Mihoub et al., 2010), which, in turn, would reverberate on population size 2 years later, because the Lesser Kestrel starts to reproduce at an age of 2 years (Ferguson-Lee & Christie, 2001). This finding is consistent with those of a study on a French population, in which Sahel rainfall positively correlated with survival probability of juveniles, but not with that of adults (Mihoub et al., 2010). In contrast, the highland population did not show any temporal trend and the year-to-year variations in its size were related to both climatic (winter NAO and March rainfall) and environmental proxies (Laying NDVI) experienced during spring migration and in the breeding areas. Population increased in years with abundant rainfall in

TABLE 2 Estimates of the final linear models explaining the influence of climatic and/or environmental variables on population trends of the Lesser Kestrel in Sicily (Italy) during the 2003–2014 period

Population	Factor	Estimate	SE	95% CI	<i>t</i>	<i>p</i>	
Lowland	Intercept	40,300.66	8,028.08	24,565.62, 56,035.70	5.02	<0.001	
	$R^2 = 0.73$	Sahel precipitation index (−2)	44.91	13.66	18.13, 71.67	3.29	0.011
	Year	−20.02	4	−27.86, −12.19	−5.01	<0.001	
Highland	Intercept	−2.26	5.07	−12.19, 7.67	−0.45	0.671	
	$R^2 = 0.78$	Winter North Atlantic Oscillation	−18.89	10.51	−39.49, 1.71	−1.8	0.123
	Δ Laying NDVI	−436.28	86.7	−606.21, −266.34	−5.03	0.003	
	Δ Rainfall March	0.25	0.01	0.12, 0.37	3.99	0.007	

Note. For the lowland population, a single model was selected based on AICc, while for the highland population, a set of models resulted selected and eventually averaged. SEs and 95% CI of the estimates are also shown. R^2 indicate the proportion of variance explained by the model. The dependent variable is the year-to-year difference in the number of breeding pairs (Δ Pairs).

CI: confidence interval; NDVI: normalized difference vegetation index.

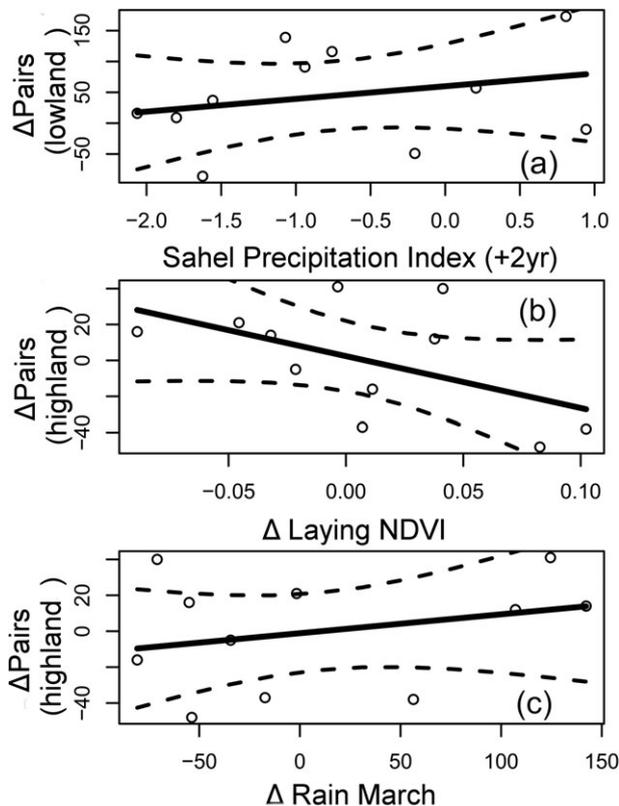


FIGURE 6 Relationships between the selected climatic or environmental variables and the population oscillations of Lesser Kestrel in the lowland and the highland area. Coefficients of the corresponding models are reported in Table 2. NDVI, normalized difference vegetation index. (a) Relation between the Δ Pairs of the lowland population and the Sahel precipitation index of 2 years prior to the population estimation; (b) relation between the Δ Pairs and the Δ Laying NDVI of the highland population; (c) relation between the Δ Pairs and the Δ rainfall of March for the highland population

March and low NAO index values (i.e., wet winters for the Mediterranean area, Ottersen et al., 2001) but decreased in years of high productivity in late April (as indicated by high laying NDVI values). NDVI is an index of “greenness” of an area, and is regarded as a good proxy of insect abundance (Sanz et al., 2003; Schlaich et al., 2016). A positive relationship between the laying NDVI values and population sizes was, therefore, expected. However, we found a puzzling negative effect. To explain this pattern, we can hypothesize that vegetation structure is a main determinant of foraging suitability for insectivores (see e.g., Atkinson, Buckingham, & Morris, 2004; Devereux, McKeever, Benton, & Whittingham, 2004), and that dense and tall vegetation decreases the foraging efficiency of Lesser Kestrels (Catry, Franco, & Moreira, 2014). This hypothesis is supported by the observation that excessive irrigation correlates with the decrease of foraging activity of the Lesser Kestrel (Ursúa, Serrano, & Tella, 2005), which seems not able to feed over very tall vegetation (above ~80–100 cm height; Morganti et al., 2018). The results of our model thus suggest that wet conditions in winter and early spring (boosting insect abundance), associated with rather dry conditions in May

(avoiding excessive vegetation growth) are probably ideal for the highland population of the Lesser Kestrel.

One limit of the present study is that the potential contributions of quality and availability of foraging habitats and breeding sites to population trends in the two areas were not taken into account. In the lowland, the habitat type in the immediacy of the colony influences the diet of the chicks (Morganti et al., 2016) and the adults (Di Maggio, Campobello, & Sarà, 2018), and the breeding success (Di Maggio et al., 2016; Sarà et al., 2012), while in the highland the availability of cavities may pose a strong limit to population size for a secondary-cavity nester like the Lesser Kestrels (i.e., Newton, 1994). However, our models, despite being based on climatic and environmental variables only, were able to explain a rather large amount of variance in the oscillations of both populations and included different sets of predictors, thus suggesting that the sensitivity of the two population to climate and environmental oscillations actually differs.

4.2 | Proximate and ultimate causes of the intra-specific differences

Population oscillations of migratory species integrate conditions experienced by individuals during their entire life cycle (Sillert et al., 2000). For Afro-Palaearctic migratory birds, ecological conditions in the Sahel, such as the abundance or the spatial and temporal distribution of food resources, are the key drivers of survival probability of wintering populations (Zwarts, Bijlsma, van der Kamp, & Wymenga, 2009). However, according to our results, this was true only for the lowland population but not for the highland, for which the variability of winter conditions in the Sahel seems less important than the variability of environment conditions experienced during spring migration and at the onset of reproduction. Movement tracks of Lesser Kestrel gathered with satellite telemetry showed that individuals breeding in different areas of southern Italy (including Sicily) mixedly wintered in the same area of the Sahel (M. Sarà, unpublished data). It is, therefore, very unlikely that individuals breeding in the two study areas segregated in different Sahel regions during winter. For the highland population, environmental conditions in the breeding area may be decisive for population size and dominant over effects of Sahelian conditions. Therefore, the high impact of conditions experienced in the breeding area may mask effects of environmental conditions experienced in the Sahel. The lowland population breeds in a climatically optimal area for the Lesser Kestrel, while the highland population in a suboptimal one (Morganti, Preatoni, & Sarà, 2017). Indeed, an high breeding success has been observed in the lowland area (La Gioia, Melega, & Fornasari, 2018; Mascara & Sarà, 2006). Conditions in the breeding areas seem, therefore, not limiting for the lowland population, while they may limit juvenile survival during winter, similar to what occurred in a French population

(Prugnolle, Pilard, Brun, & Tavecchia, 2003). In contrast, the highland population, which likely lives at the edges of the climatic niche of the species during breeding, may be limited mainly by spring climatic conditions in its breeding area.

A recent study on an American passerine, the Wood Thrush *Hylocichla mustelina*, described how trends of populations occupying the core of the breeding area were mainly determined by conditions experienced in the wintering quarters, while the loss of breeding habitats was the main determinant of abundance for peripheral populations (Rushing et al., 2016). It, therefore, adds to a growing body of evidence supporting the hypothesis that different populations may show different sensitivity to climatic and environmental factors (e.g., Balbontín et al., 2009; Balestrieri et al., 2018; Mainwaring & Hartley, 2016; Morganti, Rubolini, Caprioli, Saino, & Ambrosini, 2017). In some cases, an ultimate mechanism underlying the observed differences in climate sensitivity could also be identified. For instance, different populations of the Great Tit *Parus major* have different genetically determined reaction norms that link laying dates to perceived temperature (Husby et al., 2010). Similarly, different reaction norms determine the laying date of two populations of Corsican Blue Tits living only 6 km apart from one another (Porlier et al., 2012). Our study opens a new question about whether similar differences in reaction norms are also occurring in the Lesser Kestrel and other nonpasserines and suggests that environmental sensitivity between neighboring populations is probably more widespread in wild animal populations than was suspected before.

4.3 | Conservation consequences

Climate change is threatening the long-term persistence of many populations of migratory birds (Jiguet, Gadot, Juliard, Newson, & Couvet, 2007; Møller, Rubolini, & Lehtikoinen, 2008; Panuccio, Martin, Morganti, Onrubia, & Ferrer, 2017; Stephens et al., 2016). In this scenario, our findings suggest that the fate of populations with different climate sensitivity may also differ. Indeed, increasing Sahel desertification (IPCC, 2014) and spring droughts in south-eastern Sicily will mainly impact the lowland population (Morganti, Preatoni, & Sarà, 2017). Because of global warming, we also expect a range shift of living organisms northward and toward higher altitudes (e.g., Lenoir & Svenning, 2015), including the Lesser Kestrels breeding in Italy (Morganti, Preatoni, & Sarà, 2017). Global warming should thus favor the long-term persistence of the Lesser Kestrel in the current mesic highlands of Sicily, where the reduction in the spring rainfalls forecasted by climate models for the Mediterranean region (Heinrich & Gobiet, 2012; Quesada, Vautard, Yiou, Hirschi, & Seneviratne, 2012) will mitigate the negative effect of the excessive spring “greenness” that seems to

limit the highland population. We can, therefore, forecast that the highland population (or more generally higher altitude and latitude populations) of the Lesser kestrel may persist at unknown population size under future climate conditions, while those inhabiting more xeric habitats, like our lowland population (or more generally lower altitude and latitude populations of this species), may suffer substantial reduction under future climate conditions. Indeed, the very recent declines of the species registered in core breeding areas such as Andalusia (−50% between 2012 and 2017, Garrido, de las Heras, & Martos, 2018) seem to confirm our worries about Lesser Kestrel populations living in dry climates.

A primary challenge for future research will be to assess how and to what extent different populations of the same species are differentially affected by anthropogenic impacts. Although difficult to determine, detailed knowledge of population-specific environmental sensitivity would increase our ability to predict the adaptive capacity of a species, eventually improving the design of well-balanced networks of areas devoted to conservation.

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CONFLICTS OF INTEREST

The authors declare no competing interests.

Author contributions

Field data collection: M.S. and M.M.; Data analysis: M.M., R.A. and M.S.; Manuscript writing: M.M., M.S. and R.A.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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