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Breeding in natural nesting sites can improve the resilience of local Lesser Kestrel (*Falco naumanni*) populations to environmental changes

MAURIZIO SARÀ*[1,2] & ROSARIO MASCARA[3]
[1]*Section of Botany, Anthropology, Zoology at Department of Biological, Chemical and Pharmaceutical, Sciences and Technologies, University of Palermo, Via Archirafi, 18, Palermo, 90123, Italy*
[2]*Water Research Institute – National Research Council (IRSA-CNR), Via del Mulino, 19, Brugherio, 20861, Italy*
[3]*Naturalistic Museum of the Caltagirone District and of the 'Bosco di Santo Pietro' Oriented Nature Reserve, Via degli Achei, 95041, Caltagirone, Italy*

The identification of key habitats of threatened species and of extrinsic environmental factors that influence their resilience to human-induced environmental changes are the foundation for the definition of conservation objectives. Using the presence and numerical abundance data collected in a long-term survey (2000–24) of breeding colonies of Lesser Kestrel *Falco naumanni* in Sicily (southern Italy), we defined occupancy patterns (on a focal sample of 99 colonies) and estimated population size (on a regional sample of 198 colonies). Each colony was categorized according to covariates based on its landscape (lowland, highland) and location in natural (cliffs) or artificial (buildings) sites. Occupancy modelling highlighted the prevalence of higher, annually variable colonization rates compared with low, annually constant local colony extinction rates. The colonization rates of the natural highland sites have a magnitude equivalent to those of local extinction rates of the artificial lowland sites, implying that local extinction in lowland colonies is compensated by colonization of cliffs in highlands. Furthermore, highland natural sites tend to have higher occupancy rates than colonies located elsewhere on the island. Since 2000, the Sicilian population increased to a peak of 1365 estimated pairs in 2011, then decreased, halving in 2019. From 2020 to 2024, a new numerical growth is taking place, mainly in the highland population. The lowland population is currently limited by the collapse of the buildings in which they nest and by drought and heatwaves that reduce offspring survival, while the cliffs of the cooler and wetter highland are buffering the overall population decline. These findings suggest concrete conservation actions to halt the species' decline in the island. Installing thermally insulated nestboxes can mitigate the loss of lowland breeding sites and reinforce the highland population.

Keywords: global change, long-term study, natural-sites resilience, occupancy modelling, population modelling.

Long-term analyses of population dynamics, distribution and reproductive timing of focal species have provided key information on the effects that human activities (e.g. DDT, oil spills, longline fishing, timber harvest) have on bird populations (Thompson & Thompson 1991, Holmes & Sherry 2001, Clutton-Brock & Sheldon 2010, Campbell *et al.* 2012) and, recently, on those of climate change (Greenwood & Baillie 1991, Collins 2001, Clutton-Brock & Sheldon 2010). Through the use of population models and the definition of habitat requirements, long-term studies have also become increasingly useful for setting conservation goals and then evaluating conservation actions on threatened species (Pienkowski 1991, Margalida 2017).

*Corresponding author.
Email: maurizio.sara@unipa.it

Typically, individuals of the same species respond in similar ways to environmental changes (Liebhold *et al.* 2004) because conspecific populations exposed to similar climatic oscillations have similar dynamics (Post & Forchhammer 2002, Sæther *et al.* 2004). However, populations are not uniform entities and almost always show local demographic heterogeneity, because individual variations in survival and reproduction rates are transferred to the population level. This changes age and sex composition over the years, which in turn may affect the ecological response of each population to local environmental conditions (Sultan & Spencer 2002, Kendall *et al.* 2011). A clear example is the intraspecific variation in the response to habitat loss and fragmentation (Banks-Leite *et al.* 2022), whereby peripheral populations are generally more vulnerable to habitat changes than central populations (Orme *et al.* 2019, Hasui *et al.* 2024). Furthermore, evidence of intraspecific variation in climate sensitivity is accumulating, demonstrating that the same climate pattern can have different or even opposite effects on the life history traits of spatially segregated populations (Balbontín *et al.* 2009, Guéry *et al.* 2017) or of populations inhabiting different environments (Oliver *et al.* 2010, 2013, Lopez-Ricaurte *et al.* 2024, Ferrer Obiol *et al.* 2025). There is therefore good theoretical (Schreiber 2010) and empirical (Valladares *et al.* 2014, Hasui *et al.* 2024, Hernández-Matías *et al.* 2024) evidence of how environmental variation in space and time produces populations with different resilience within the species' range (Ferrer Obiol *et al.* 2025).

Resilience is one of the ways in which populations respond to environmental stress (Harrison 1979, Nimmo *et al.* 2015), and is usually intended to reflect the ability of an ecosystem to absorb disturbances without shifting to an alternative state and losing functions and services (Holling 1973). Whatever the cause of natural or human-induced change, long-term studies (Dunnet 1991) are among the few tools that can provide information on the resilience of bird populations and guilds to a given magnitude of perturbation (Jiguet *et al.* 2006, 2007, Karp *et al.* 2011). However, several aspects of inter-population resilience are still not well explored. For species of conservation interest, it is, for example, important to understand the extrinsic environmental factors that influence their resilience (Nimmo *et al.* 2015), as well as the temporal and spatial scales to which they respond, to target appropriate conservation actions and maximize their effectiveness at the population level (Ruggiero *et al.* 1994).

To our knowledge, only a few cases of different sensitivity between bird populations of the same species have been studied at small spatial scale, and most of them have involved climatic variation between neighbouring populations (Porlier *et al.* 2012, Morganti *et al.* 2019, Sauser *et al.* 2021).

The Lesser Kestrel *Falco naumanni* is a migratory small raptor that breeds in the open and dry cereal steppes of the Palaearctic (Ferguson-Lee & Christie 2001) and moves to sub-Saharan Africa in winter (Sarà *et al.* 2019). Once the most common European bird of prey (Ferguson-Lee & Christie 2001), during the mid-20th century it suffered a marked population collapse across its European range that prompted investigation in order to understand the causes of decline and orient conservation interventions (Rodríguez & Bustamante 2003, Iñigo & Barov 2010). Research revealed the species' links with traditional agriculture and proved it to be an excellent bioindicator of agricultural intensification of farmland (Tella *et al.* 1998, Franco & Sutherland 2004, Sarà 2010, Catry *et al.* 2012, Assandri *et al.* 2023). The Lesser Kestrel has thus become a species of European Union (EU) conservation interest, included in Annex 1 of the EC Directive 2009/147, and is the subject of two European and several national action plans, as well as the main target of a dozen projects funded by the EU LIFE programme (Iñigo & Barov 2010, Sarà 2021).

During the breeding season, the Lesser Kestrel nests in secondary cavities, and in Sicily (southern Italy) it forms colonies both on cliffs and rural buildings, often in association with other species (Campobello *et al.* 2012, Sarà *et al.* 2012) and with a peculiar population structure: most of the northwestern colonies of this island are located in natural cliffs, whereas the southeastern ones are settled in human buildings (Morganti *et al.* 2019). We wondered whether these two neighbouring Lesser Kestrel subpopulations had independent demographic trajectories that could influence their persistence on this Mediterranean island. Therefore, we used a long-term survey to investigate the occupancy, the population size trends, and the effects of landscape (lowland versus highland) and

location (natural versus artificial) of the breeding colony.

MATERIALS AND METHODS

Study area

Sicily is a typical area representative of the Mediterranean bioclimate of southern Europe occupied by the Lesser Kestrel. The island covers 25 832 km^2 and is the largest (8.6% of national surface) and one of the most populated (186.7 inhabitants per km^2 in 2022) administrative regions of Italy, from which it is separated by the 3-km-wide Strait of Messina. Almost 24.4% of the territory is mountainous, 61.4% is composed of highland and 14.2% of the surface is lowland. Natural deciduous forests and Mediterranean vegetation have been greatly reduced by centuries of anthropogenic impact and forests occupy only 8% of the territory, mostly in the northeastern part of the island, with European Beech *Fagus sylvatica* forests extending from 1200 to 1400 m above sea level (a.s.l.) and endemic Birch *Betula aetnensis* on the slopes of the Etna volcano between 1300 and 2100 m a.s.l. There is considerable habitat heterogeneity in hilly and flat inland areas, where cultivation zones (especially arable land with cereals and fodder, currently replaced by vineyards and olive orchards) alternate with woodlots of non-native species (*Pinus* spp. and *Eucalyptus* spp.), natural oak *Quercus* spp. evergreen woods, Mediterranean xeric grasslands and shrub vegetation. The climate is typically Mediterranean, but shows considerable variation between the higher and wetter northern and northwestern areas (> 1000 mm/year), which mostly fall within the sub-humid and dry meso-Mediterranean bioclimates, to the less elevated and arid (< 500 mm/year) southeastern areas, which mostly fall within the thermo-Mediterranean dry bioclimate.

Population survey

The Lesser Kestrel in Sicily is a summer breeding, migratory and partially wintering species, with few individuals, mostly in the southern part of the island (Morganti *et al.* 2017). Studies on the species were scarce and anecdotal in the mid-20th century (cf. Iapichino & Massa 1989). Only the population of the Gela Plain (south-east Sicily) has been studied in depth since the 1980s (Mascara 1984). Since 2000, standardized censuses were activated to analyse the distribution and breeding ecology of the species on the entire island (Mascara 2002, Mascara & Sarà 2006, Sarà 2010). Subsequently, since 2003, an intensive population survey with standardized protocols has allowed collection of data on reproductive biology and colony establishment, population dynamics and diet (Campobello *et al.* 2012, Sarà *et al.* 2012, Di Maggio *et al.* 2013, 2014, 2016, 2018). Today, the Sicilian population is characterized by a predominantly mountain-hill subpopulation that nests mainly on cliffs (77%), on average at 600 m a.s.l. in a cooler and wetter climate (hereafter the highland population); and by a second subpopulation of the more southeastern flat and low-hilly areas, nesting on average at 200 m a.s.l. in a warmer and drier climate and mainly (73%) in rural buildings, hereafter the lowland population (Morganti *et al.* 2019). Lesser Kestrels arrive in Sicily in March for the breeding season, but the two subpopulations have a different calendar, with the lowland population laying their eggs on average 3 weeks earlier than the highland one (Sarà 2010, Morganti *et al.* 2019).

The database of Lesser Kestrel colonies in Sicily, compiled by the authors, includes 235 sites where the species has been recorded. Of these, 198 colonies (84% of the total; hereafter referred to as the 'regional colony sample') were visited and georeferenced by the authors at least once during the study period (2000–24) to confirm the species' presence during the breeding season. The remaining 16% – consisting of artificial colonies with nestboxes and unverified reports of presence – was excluded from the study.

Within the regional colony sample, a subset of 99 colonies (hereafter the 'focal colony sample') was monitored with greater continuity (mean ± standard deviation (sd): 18 ± 4.4 years; range: 10–25 years). These included 64 colonies in lowland areas (52 in buildings and 12 on cliffs) and 35 in highland areas (nine in buildings and 26 on cliffs). In contrast, the remaining 99 colonies in the regional colony sample were monitored less frequently (mean ± sd: 4 ± 2.5 years; range: 1–9 years).

Details of the population sampling protocols and ringing schemes are given in Sarà (2010), Sarà *et al.* (2012), Di Maggio *et al.* (2016) and Morganti *et al.* (2017). For the purposes of this study, two or three visits were generally carried out on

clear and non-windy days from mid-April to late May and then from late May to late June, depending on the breeding calendar of the two subpopulations (median laying date of lowland population: 26 April, and of highland one: 17 May, Morganti *et al.* 2019) to ascertain the breeding establishment of the colonies and/or to count the installed (i.e. breeding and non-breeding) pairs. Therefore, the database includes both presence/absence data (P/A, assessment of an active colony or colony desertion) and abundance data (counts of installed pairs observed in the colony site).

Occupancy modelling

Dynamic occupancy models (MacKenzie *et al.* 2002, 2003) have been developed to estimate temporal changes (multi-stage) in occupancy of Lesser Kestrel employing the focal colony sample (two visits per year to the 99 colonies during the 25-year study period). Multi-stage occupancy models derive the following parameters from the data: occupancy (ψ), the probability that a nest-site is occupied in the first and following survey year; colonization (γ), the probability that an unoccupied site becomes occupied between years; local extinction (ε), the probability that an occupied site becomes deserted between years; and detection (p), the probability that breeding birds are detected each year given that the colony is occupied. The naive estimate of occupancy is instead the annual proportion of surveyed sites where the species was present, derived directly from field data, and is compared with the modelled occupancy.

Statistical computing of the multi-stage modelling of occupancy was run by PRESENCE 2.13.47 (Hines 2006). Models with alternative parameterizations were then compared using Akaike's Information Criterion (AIC, Burnham & Anderson 2002).

The Lesser Kestrel is a colonial species (Ferguson-Lee & Christie 2001) and for skilled observers, the probability of discovering the presence or verifying the real absence of a colony is very high, resulting in almost zero possibility of recording false negatives and false positives. In the multi-stage modelling, the detection p was therefore kept constant (.) over years.

Four candidate models were constructed separately for preliminary exploration of the constant (.) or year-specific (y) colonization and local extinction probabilities (Table 1a). The most parsimonious model (k = 4), with constant colonization and extinction probabilities over the 25 years, is therefore: ψ, $\gamma_{(.)}$, $\varepsilon_{(.)}$, $p_{(.)}$ and the overparameterized model (k = 50), among those considered, has both year-specific colonization and extinction probabilities: ψ, $\gamma_{(y)}$, $\varepsilon_{(y)}$, $p_{(.)}$.

Settlement in lowland (LOW) or highland (HIGH) areas and breeding in cliffs, i.e. natural sites (hereafter NAT), or in buildings, i.e. artificial sites (hereafter ART), were considered potential drivers of occupancy and population size, worthy of exploration. The four interactive 'site × area' effects of the covariates (NAT × HIGH, NAT × LOW, ART × HIGH and ART × LOW) are more informative than single covariates at a time and also reduce the number of possible combinations to explore, avoiding over-fitting the models. We then characterized each colony with a dummy variable (1/0) that expressed one of the four possible combinations between its breeding site and area. The interactive effect of these covariates on occupancy, colonization and local extinction was then introduced in a complementary manner in a second family of candidate models (Table 1b). The effect of covariates was interpreted in terms of odds ratio (OR), a constant parameter across different values of the predictor variable. The ORs are expressed by the exponential function of the regression coefficients β and define the effect size, i.e. they represent the one-unit change in covariate values at each site (Jones & Peery 2019). Finally, the occupancy probabilities estimated by the top-ranked model have been used to calculate the average rate of change in occupancy between years (occupancy turnover) over the 25 years of the survey, as: ($\lambda = \psi_{t+1}/\psi_t$); where λ is the change in occupancy, ψ_{t+1} is the estimate of occupancy at year $t + 1$, and ψ_t is the estimate of occupancy at year t (MacKenzie *et al.* 2003).

Abundance modelling

We estimated the size of the population in the study period by modelling the annual counts (maximum number of installed pairs assessed through a minimum of two visits each year) using TRIM 3 (TRends for Indices and Monitoring bird data, version 3), a software developed for the analysis of count data obtained from the monitoring of wildlife populations. This method assumes a

Poisson distribution and a log link function, takes into account data overdispersion and serial correlation, and is also robust to the presence of a high percentage of missing counts (Van Strien *et al.* 2004, Pannekoek & van Strien 2005). Time series (2000–24) of Lesser Kestrel pair counts in the regional colony sample (n = 198) were analysed using Poisson regression and producing log-linear estimates of population and annual trends. Linear time trends in TRIM 3 were entered by looking for 'change-points', i.e. significant turning points in each year, allowing for their automatic deletion (when there are not enough observations to estimate the parameters between two points of change), and through stepwise selection to produce the most parsimonious pattern of change-points. The same effects of the covariate interactions used to estimate occupancy were also included in the models in the way expected by the software (one covariate site × area, and four dummy variables for each level of the covariate as: NAT × LOW = 1; NAT × HIGH = 2; ART × HIGH = 3; ART × LOW = 4). The use of covariates allowed us to analyse trends in population size across natural and artificial sites of lowland and highland.

Table 1. Multi-stage occupancy modelling of Lesser Kestrel in Sicily.

Rank	Model	AIC	ΔAIC	AIC w	*k*
(a)					
1	**ψ, $\gamma_{(y)}$, $\varepsilon_{(.)}$, $p_{(.)}$**	1433.23	0.00	0.999	27
2	ψ, $\gamma_{(.)}$, $\varepsilon_{(.)}$, $p_{(.)}$	1446.59	13.36	0.001	4
3	ψ, $\gamma_{(y)}$, $\varepsilon_{(y)}$, $p_{(.)}$	1452.46	19.23	0.000	50
4	ψ, $\gamma_{(.)}$, $\varepsilon_{(y)}$, $p_{(.)}$	1463.89	30.66	0.000	27
(b)					
1	ψ, $\gamma_{(y,\ NAT\ \times\ HIGH)}$, $\varepsilon_{(.,\ ART\ \times\ LOW)}$, $p_{(.)}$	1427.03	0.00	0.671	29
2	$\psi_{(y,\ NAT\ \times\ HIGH)}$, $\gamma_{(y,\ NAT\ \times\ HIGH)}$, $\varepsilon_{(.,\ ART\ \times\ LOW)}$, $p_{(.)}$	1428.98	1.95	0.253	30
3	ψ, $\gamma_{(y,\ ART\ \times\ LOW)}$, $\varepsilon_{(.,\ NAT\ \times\ HIGH)}$, $p_{(.)}$	1433.16	6.13	0.042	29
4	**ψ, $\gamma_{(y)}$, $\varepsilon_{(.)}$, $p_{(.)}$**	1433.23	6.20	0.040	27
5	ψ, $\gamma_{(y,\ ART\ \times\ HIGH)}$, $\varepsilon_{(.,\ NAT\ \times\ LOW)}$, $p_{(.)}$	1435.74	8.71	0.012	29
6	ψ, $\gamma_{(y,\ NAT\ \times\ LOW)}$, $\varepsilon_{(.,\ ART\ \times\ HIGH)}$, $p_{(.)}$	1436.39	9.36	0.008	29

(a) Ranking of the models used for the preliminary evaluation of the effects of constant (.) or year-specific (y) colonization (γ) and local extinction (ε) probabilities, always keeping the probability of detection (p) constant. (b) Ranking of the occupancy models with covariate effect. The top model of (a) (in bold) is reinserted into (b) as a reference point. ART, artificial (buildings) breeding sites; HIGH, colony in highland; LOW, colony in lowland; NAT, natural (cliffs) breeding sites. ΔAIC is the difference in Akaike Information Criterion values between each model and the model with the lowest AIC; w is the AIC model weight; and k is the number of parameters in the model.

RESULTS

Occupancy models

The four occupancy models used in the preliminary analysis tested the effect of annual variability (Table 1a). The model with annual variation of colonization and constant local extinction over the course of the survey fit the data better, ranking in first place (ΔAIC = 0.00) and with the AIC weight greater than the reverse, with constant colonization and variable local extinction over the years. Even the simplest model (k = 4) and the most parameterized model (k = 50) had no data support because of their ΔAICs and AIC weights (Table 1a). The top model was maintained and compared with a second group of five candidate models, with complementary combinations of covariates on occupancy, colonization and local extinction (Table 1b).

The top ranked model with lowest AIC (1427.03) and highest weight (0.671) compared with the others means that the highest support for the data occurred when local extinction and detection did not change over years, while colonization did, thus confirming the strong importance of the annual variation of colonization in the occupancy of the Lesser Kestrel found in the first exploration of Table 1a. Furthermore, the strongest support for the data occurred when the probability of colonization depended on the effect of colonies in highland cliffs compared with other (cliffs or buildings) elsewhere; and when the probability of local extinction depended on the effect of the colonies in the buildings on the lowland compared with those elsewhere. Indeed, the local extinction in buildings on the lowland was balanced by colonization in highland cliffs, as the estimated effect size of the two covariates, in terms of ORs, was equivalent (0.640 and 0.609 respectively, Table 2). Models that combine the effect of covariates differently (e.g. ART × HIGH instead of NAT × HIGH, etc., cf. model 1 versus model 5 in Table 1b) on colonization and local extinction also have null support for the data.

The probability of occupancy in the first year was $\psi = 0.488 \pm 0.056$ standard error (se). This probability changed over the years, reaching a peak of 0.836 ± 0.005 se in 2012, and then decreasing, with an upward oscillation in 2020, until reaching a value of 0.605 ± 0.008 se at the end of the survey period (Fig. 1). Nonetheless, the occupancy turnover (κ) had much stronger fluctuations, especially in the phase of demographic increase (2004–12) and subsequently in 2020–22 (Fig. 2).

Between all years, the average total probability that Lesser Kestrels colonize a previously unoccupied colony (γ) was 0.202 ± 0.003 se with a maximum peak of 0.553 ± 0.005 se in 2012. Similarly, the probability that a previously occupied Kestrel colony became locally extinct (ε) varied between 0.083 and 0.107 with an average, annually constant, probability of 0.087 ± 0.002 se.

The second model, being < 2 ΔAIC units, is also considered a plausible explanation of the information contained in the focal colony data, albeit with a lower AIC weight (0.253, Table 1b). Compared with the first, it differed due to the inclusion of the effect of the covariates on occupancy. In this case, the effect size that natural colonies in the highland have on occupancy was 1.12 times higher than that in another colony elsewhere. The naive estimates provide an occupancy trend that is quite close to the modelled one, but which was more sensitive to variable sampling over the years (Fig. 1).

Abundance modelling

Results from linear modelling of the population trend of the 198 colonies of the regional sample revealed a significant effect of covariates (site × area: Wald test = 79.16, df = 24, $P = 0.000$). The overall slope of the linear estimate over the 25 years was 1.020 ± 0.006 se, corresponding to a statistically significant ($P < 0.01$) moderate population increase of 2.0% per year.

The overall trend of change in population size is shown in Figure 3 (top). At the beginning of the survey in 2000, the model estimated 471 pairs in the 198 colonies and the population almost doubled in a few years, with 790 pairs in 2006 (with an increase of 25% between 2003 and 2004 and 36% between 2004 and 2006, significant change-points in Fig. 3 top) up to a peak of 1365 pairs in 2011. From 2011 to 2016 there was a statistically significant decline, indicated by the change-point in 2019, of approximately 4% per year, until the population was almost halved in 2019 with 743 pairs. From 2019, the population began a new statistically significant phase of increase (4.4% per year) until the estimate of 1024 pairs in 2024. However, the total population fluctuated widely with discordant and independent trajectories of the subpopulations breeding in the natural and artificial colonies of highland and lowland (Fig. 3 middle and below). The increase phase observed from 2019 to 2024 was concentrated mostly in the natural and artificial sites of the highland, while the population of the analogous sites of the lowland was more or less constant and was approximately halved compared with the previous period (Fig. 4).

DISCUSSION

This study describes small-scale spatial–temporal fluctuations in occupancy and population size of a kestrel species that is of conservation interest. The results enable identification of habitats that promote its persistence (Benton *et al.* 2003, Vickery & Arlettaz 2012) and evince the importance of

Table 2. Effects of covariates on Lesser Kestrel colonization, local extinction and occupancy resulting from the multi-stage occupancy modelling reported in Table 1b, and expressed in estimates (β coefficients) transformed into odds ratios (ORs) obtained from the two models within ΔAIC of 2.

Parameter	Covariate	β	se	OR
1st model				
Colonization	NAT × HIGH	−0.446	0.241	0.640
Local extinction	ART × LOW	−0.496	0.199	0.609
2nd model				
Occupancy	NAT × LOW	−0.079	0.263	0.924
	ART × HIGH			
	ART × LOW			
Occupancy	NAT × HIGH	0.113	0.504	1.120
Colonization	NAT × HIGH	−0.448	0.241	0.639
Local extinction	ART × LOW	−0.496	0.199	0.609

The ORs are invariant across years, so they are not affected by the overall level of colonization or local extinction in a particular time period. Abbreviations of covariates as in Table 1. ART, artificial (buildings) breeding sites; HIGH, colony in highland; LOW, colony in lowland; NAT, natural (cliffs) breeding sites; se, standard error. ΔAIC is the difference in Akaike Information Criterion values between each model and the model with the lowest AIC.

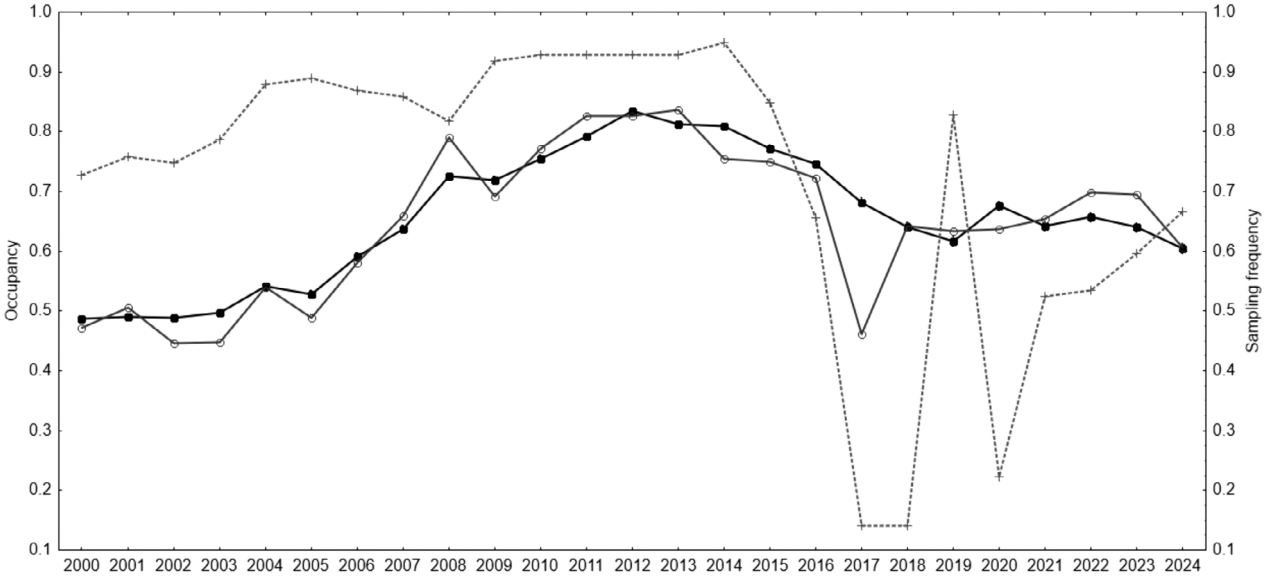

Figure 1. Changes in Lesser Kestrel occupancy (ψ) over the 25 years of the survey on the focal colony sample in Sicily. The solid black line is the estimated ψ (mean $\pm$ se) from the top model; the solid grey line with empty squares is the naive estimate of occupancy. The dashed grey line is the proportion of surveyed colonies represented on the right-hand *y*-axis.

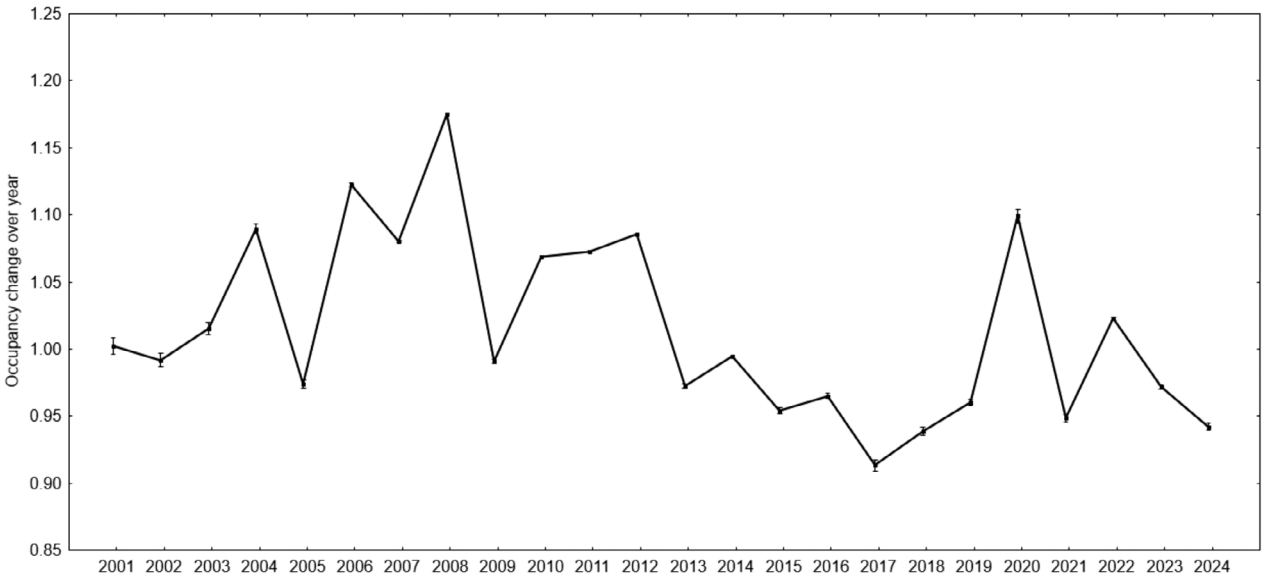

Figure 2. Fluctuations in occupancy turnover, or λ, the average rate of change in occupancy, over the 25 years of survey on the focal sample of Lesser Kestrel colonies in Sicily.

semi-natural habitats in the local resilience of the Lesser Kestrel (Rösch *et al.* 2023).

Several complex factors interact to generate the dynamics of patch occupancy, but generally the ability to disperse over long distances, especially of adult birds, and the extension of the range, are the factors that offer the greatest probability of colonizing new areas between consecutive seasons, while small population sizes increase the probability of local extinction in areas inhabited in previous years (Gaston & Blackburn 2002). Habitat structure is another major factor that determines

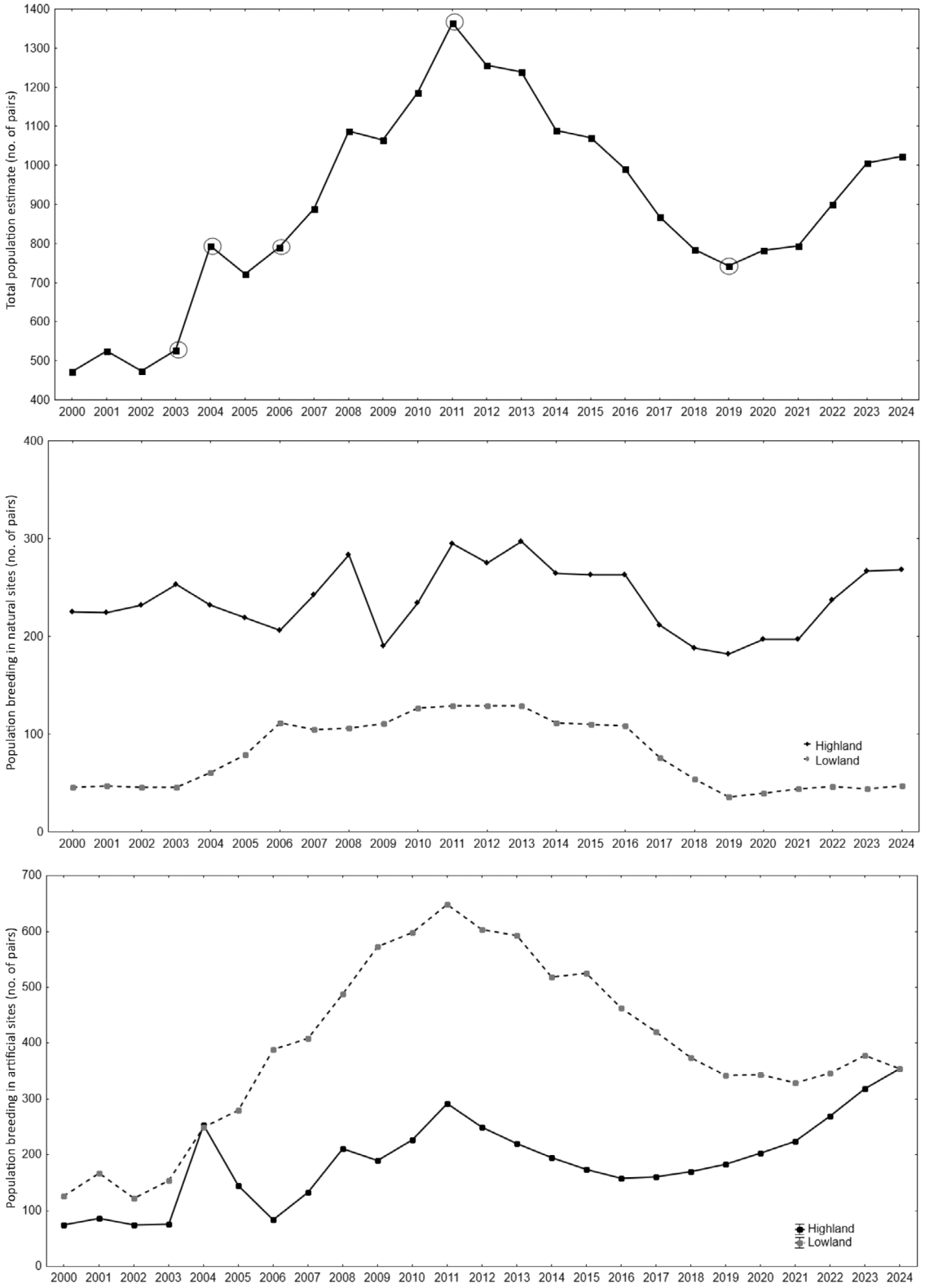

Figure 3. Population abundance estimates, from the TRIM model, on the total colony sample (n = 198) of the Lesser Kestrel in Sicily during 25 years (2000–24) (top). Grey circles highlight statistically significant change-points in population abundance. The total population estimate is further split into abundance estimates for natural sites (middle) and for artificial sites (bottom) of lowland and highland.

the occupancy rates of bird communities (Hingee *et al.* 2022), and its changes induce species-specific extinction and colonization rates with strong temporal and spatial variations in colonial species (Barbraud *et al.* 2003). The summer-breeding Lesser Kestrel leaves the breeding colonies each year for a trans-Sahelian migration, and returns the following year at these breeding sites. Every year, the quality and availability of nesting and foraging areas, together with the processes of adult and juvenile dispersal and the attractive cues from conspecifics, govern the formation of the colony network (Serrano *et al.* 2003, 2004, Aparicio *et al.* 2007, Calabuig *et al.* 2008a). Our occupancy models suggest that in this long-distance migrant the process of colonization, with a fairly large and annually variable rate (0.202–0.553), of the same or new breeding colonies, has priority over their local extinction, which has a constant and smaller rate over time (0.087). The variability of colonization rates would depend on both remote and local limiting factors; Morganti *et al.* (2019) found that Sahel rainfall 2 years before each annual survey significantly affected population variation in the lowland, while rainfall in March and primary productivity in the breeding areas affected population variation in the highland. Based on these findings, Morganti *et al.* (2019) proposed that non-breeding survival in the Sahel limits the lowland population, whereas local climate conditions inducing prey availability during breeding limit the reproductive output of the highland population.

A noteworthy aspect of the occupancy modelling is the equal magnitude of the two parameter estimates. Regardless of the overall levels of colonization and local extinction in a given year, local extinction in artificial lowland colonies would be compensated for by a similar amount of colonization in natural highland ones. The fine-grained environmental sensitivity of the two subpopulations, whose central points between the respective colonies are approximately 100 km apart, would therefore drive the long-term occupation of the Lesser Kestrel, annually orienting the extent and strength of colonization at the small geographical scale of Sicily.

On a broader perspective, after the demographic collapse of this species in the mid-20th century (Rodríguez & Bustamante 2003, Iñigo & Barov 2010), in the following decades the population began to increase over much of the range. In accordance with this demographic improvement, the International Union for Conservation of Nature and Natural Resources (IUCN) has progressively downgraded the species from 'Threatened' (1994) to 'Vulnerable' (2011) and then to 'Least Concern' (BirdLife International 2021). In Spain, where most of the European population breeds, the population peak is estimated to have occurred in 2012, but subsequently the population began to decline again by 6% per year (Bustamante *et al.* 2020, Aparicio *et al.* 2023).

In Sicily we can reasonably assume that the population has fluctuated in a similar way to the continental population, because in the mid-20th century it seemed to be more common than the Common Kestrel *Falco tinnunculus* (Mebs 1957) and occurred in large colonies (Krampitz 1958). About 30 years later, in line with the European collapse, it was considered uncommon and about 200 breeding pairs were estimated (Iapichino & Massa 1989). Between the end of the 20th and the beginning of the 21st century, the Sicilian population began to increase, at least judging from the only quantitative studies available for the Gela Plain (Mascara 1984, Mascara & Sarà 2006). Indeed, in that period the current models show an overall growth in occupancy rates and population size, and are also congruent with a shorter 12-year survey of the Sicilian population (Morganti *et al.* 2019). After the peak in 2011, models agree in supporting a decline until 2019 and a recent recovery phase, albeit with fluctuating occupancy, in 2020–24.

The Lesser Kestrel has the ability to spread in suitable habitats, forming large networks of colonies year after year, as in southeastern Spain (Tella *et al.* 1998), southern Portugal (Catry *et al.* 2009) or southern Italy (La Gioia *et al.* 2017). Our results suggest that during positive population fluctuations, the Lesser Kestrel would expand, tending to saturate all available breeding habitats in Sicily; by contrast, in the negative phases, the population would shrink in areas with better habitats. The latter increasingly coincide with the less hot and dry

Figure 4. The progressive deterioration of artificial sites in the lowlands. Top left, Conca d'Oro colony in 2005 (eight pairs) and top right in 2024 (five pairs). Bottom left, La Torre colony in 2010 (23 pairs) and bottom right, the same colony in 2024 (10 pairs).

areas of the highlands, which also offer a wide availability of cliffs as a nesting substrate.

The original nesting substrate of this cavity-nesting bird is rocky outcrops (Ferguson-Lee & Christie 2001), but today more than 95% of colonies of this species in southern European countries are found on buildings. The Lesser Kestrel's urbanization and use of buildings dates back at least two millennia and was probably facilitated by the large availability of cavities in buildings surrounded by cereal steppes rich in their preferred invertebrate prey (Negro *et al.* 2020). The limited availability of natural sites, such as in some areas of the Iberian Peninsula (Franco *et al.* 2005, Negro *et al.* 2020), could therefore have favoured this process. Besides, it is known that in the absence of alternative breeding sites, the availability of human constructions is a limiting factor for Lesser Kestrels, as in La Mancha (Spain), where in 2003–21 there was a significant loss of breeding habitat as the result of the deterioration or demolition of old buildings (Aparicio *et al.* 2023). In most of Sicily, the Lesser Kestrels instead have a large availability of cliffs and therefore a portion of the breeding population has been maintained in small or medium-sized cliffs. Over time, the species' urbanization process in the island has been limited to isolated and abandoned human buildings and there have never been colonies in cities or villages. Interestingly, in the Gela Plain, most of the population in the past bred in rocky cliffs (72.7% in Mascara 1984) and the increase phase coincided with the colonization of human buildings (83.3% in Mascara & Sarà 2006). The attractiveness and availability of abandoned rural buildings, together with their climatic suitability (Morganti *et al.* 2017) and the productivity of insects in artichoke cultivation (Di Maggio *et al.* 2018), have therefore made the Gela Plain the core area of the Lesser Kestrel on the island. This territory, which covers approximately 12% of the species' range, hosts on average 66% of the installed (breeding and non-breeding) pairs recorded each year.

In addition to the predominant effect of colonization, our modelling results suggest that artificial sites in lowland areas also have a worrying rate of constant colony extinction. This is happening not only because of changes in traditional agriculture (Catry *et al.* 2012, Di Maggio *et al.* 2018, Assandri *et al.* 2022) but also because they are increasingly exposed to two other main causes of deterioration of the Lesser Kestrel's breeding environment. The first is the progressive collapse of buildings, which has repercussions on population dynamics (Franco *et al.* 2005, Catry *et al.* 2009, Aparicio *et al.* 2023). The second is represented by the heavy impacts on the reproduction resulting from the increasing frequency and intensity of extreme events such as droughts and heatwaves (Marcelino *et al.* 2020, ISAC 2022, Corregidor-Castro *et al.* 2023), produced by anthropogenic climate change (IPCC 2023). Exposure to elevated temperatures affects the survival of offspring both directly, causing lethal hyperthermia in the nest (Corregidor-Castro *et al.* 2023), and indirectly on its growth due to the reduced prey availability

and/or foraging opportunities by parents (Marcelino *et al.* 2020). Recent northward range shifts in both breeding and non-breeding distributions suggest that European populations are responding to climate change and that the Gela Plain and other southern breeding areas are becoming increasingly less suitable (Morganti *et al.* 2017, Ferrer Obiol *et al.* 2025). Pairs that fail to breed often disperse to other colonies the following season, so that colonies suffering from a high failure rate will have fewer breeding pairs and may even be abandoned within a few years (Serrano *et al.* 2001, Calabuig *et al.* 2008b). In this scenario, it can be argued that every year, part of the lowland population moves to the cliffs of the highland, where they find a good availability of holes and crevices that buffer extreme temperature changes and improve the survival of eggs and offspring. Adults base their settlement on the productivity of conspecifics, and colonies with higher average reproductive success are occupied faster than less productive ones (Aparicio *et al.* 2007, Calabuig *et al.* 2008a), so we could argue that in recent years the occupancy rates of natural colonies would be increasing because of their higher reproductive success compared with artificial sites. These arguments suggest carrying out field experiments (Krebs 1991) that verify whether the two nesting environments (artificial under the tiles and natural inside the crevices) present a truly different microclimate that favours better reproductive success.

The basic information collected during the long-term study highlighted the drivers that determine the spatial–temporal change of local populations, already providing a precise indication of how the semi-natural habitats of meso-Mediterranean bioclimate highlands are becoming crucial for the Lesser Kestrel, as they constitute a buffer zone with respect to the progressive local extinction in the lowlands with dry thermo-Mediterranean bioclimate. Artificial habitats can become ecological traps, as for the Common Kestrel in Vienna (Sumasgutner *et al.* 2014), and this seems to be the risk for the core area of the Lesser Kestrel in the Gela Plain. To halt numerical decline and avoid the contraction of the species' range on the island, conservation actions urgently need to be implemented. The provision of nestboxes (Gameiro *et al.* 2020), thermally insulated and carefully positioned to cope with high temperatures and heatwaves (Catry *et al.* 2011, Corregidor-Castro *et al.* 2023), could potentially mitigate the loss of nesting sites in the lowlands and also reinforce some colonies in the highlands. However, any programme aimed at installing nestboxes should be designed and implemented with caution in areas where corvid species co-occur (Papakosta *et al.* 2023), as these may act as competitors to Lesser Kestrels and usurp the artificial structures provided.

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AUTHOR CONTRIBUTIONS

Maurizio Sarà: Conceptualization; writing – original draft; writing – review and editing; investigation; methodology; formal analysis; data curation. **Rosario Mascara:** Investigation; data curation; writing – original draft; writing – review and editing.

CONFLICT OF INTEREST

The authors have no conflicts of interest.

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