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# Causes of the recent decline of a Lesser Kestrel (*Falco naumanni*) population under an enhanced conservation scenario

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Lesser Kestrel *Falco naumanni* (Fleischer, 1818) populations have been one of the best monitored bird populations in Spain over the last 70 years. These populations suffered a sharp decline between the 1950s and 1990s. Since then, periodic censuses showed a population increase that lasted until the 2010s. In those years, numerous projects for the recovery of the species were also initiated (some EU LIFE Projects, among others), which have continued to the present day. However, despite conservation efforts, the Spanish Lesser Kestrel population, which includes about 40% of the European breeding population, has declined at a rate of 6% per year since 2012. In this study, we analysed changes in habitat and population size in 12 colonies located in La Mancha between 2003 and 2021 in order to identify possible causes of the current decline. This colonial species breeds in old buildings, and roof area (a proxy for house size) was the predictor that best accounted for the number of pairs in a colony in a given year. In addition, the extent of herbaceous crops (related to prey availability) explained a similar amount of colony size variance in 2021, whereas in 2003, the availability of large Orthoptera itself had a significant effect but a much lower effect size. The number of nestboxes affected positively the number of breeding pairs in 2021 but explained only 1% of the variance. The decline of the Lesser Kestrel population between 2003 and 2021 was largely explained by the decrease of the density of large orthopterans, their main prey. The model with the minimum Akaike Information criterion adjusted for small sample size (AICc) value also included a positive association with changes in roof area and a negative association with rabbit density (possibly through a hyperpredation phenomenon). Other top models (i.e. $\Delta$AICc $\leq$ 2 units) also showed negative effects of the loss of favourable land uses (pasture lands and herbaceous crops) on colony size, probably because this caused a reduction in the availability of large Orthoptera. These changes in land use occurred less often in areas protected by the Natura 2000 network, which may thus have contributed to the conservation of the Lesser Kestrel population. However, other conservation measures such as the installation of nestboxes were not as efficient as expected.

**Keywords:** *Falco naumanni*, habitat changes, land use, nest-site availability, population decline.

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The Lesser Kestrel *Falco naumanni* (Fleischer, 1818) is a small falcon that feeds mainly on insects in cereal fields and, with few exceptions, breeds in human constructions. The fate of its populations has been intricately linked to the development of agriculture over the last two millennia (Negro *et al.* 2020), and the population has probably thrived on Orthoptera pests, such as Moroccan locust *Dociostaurus maroccanus* (Thunberg, 1815) that periodically devastated crop fields in the Mediterranean basin and the Middle East (Latchininsky 1998), establishing a strengthened partnership with humans. Nevertheless, over the last century, coinciding with the development of intensive agriculture and the advent and widespread use of chemical inputs in agriculture (Rhoades 1963), the Lesser Kestrel population suffered a remarkable decline until the early 1990s (González & Merino 1990, Biber 1996). In the following two decades, its population experienced very noticeable increases in large areas of Southern Europe and North Africa and there was even evidence of an increase in genetic diversity at the local level (Ortego *et al.* 2007a). In line with these population trends, the International Union for Conservation of Nature and Natural Resources (IUCN) assessed the Lesser Kestrel as 'Threatened' until 1994, 'Vulnerable' until 2011 and since then as 'Least Concern' (BirdLife International 2018). Lesser Kestrel populations in Greece, Sicily and Portugal have continued to grow steadily in the last decade thanks to the continued support of management action (Morganti *et al.* 2019, Gameiro *et al.* 2020, Tsiopelas 2021). In Spain, however, which hosts about 40% of the European breeding population (Iñigo & Barov 2010), an extensive census revealed a severe decline of 6% per year since 2012 (Bustamante *et al.* 2020).

There is a consensus among researchers on the main threats to Lesser Kestrel populations on their breeding grounds, which include: foraging habitat loss, reduction in the availability of prey due to pesticide use and loss of nesting sites (Biber 1996, Atienza & Tella 2003, Pilard 2009), but there are few empirical studies that have analysed explicitly the association between any of these hypothesized factors and population changes (Sarà 2010, Morganti *et al.* 2019). Rather, the substantiation of these threats often comes from indirect evidence. For example, studies on habitat selection generally agree on habitat preferences for foraging (Donázar *et al.* 1993, Bustamante 1997, Parr *et al.* 1997, Tella *et al.* 1998, 2004, Franco & Sutherland 2004, Ursúa *et al.* 2005, Rodríguez *et al.* 2006, cf. Catry *et al.* 2012) or for colony foundation (Calabuig *et al.* 2010), but it is necessary to investigate relationships between the availability of favourable habitat and colony sizes, or to examine whether current colonies are constrained by the extent of favourable habitat to demonstrate explicitly that this threat is a direct cause of population decline.

With regard to pesticides, several studies have analysed their direct effects on Lesser Kestrel, which seem to be mild in recent years and insufficient to explain its population decline (Negro *et al.* 1993, Vergara *et al.* 2007, Goutner *et al.* 2015). More importance has been given to indirect effects of pesticide use, through a reduction in the availability of prey. However, studies on indirect effects are scarce and refer to occasional episodes of use of insecticides that are currently banned (Ortego *et al.* 2007b). To our knowledge, there is no widespread use of insecticides that can explain the current population decline, but herbicides are used to kill ruderal vegetation growing in fields and along roadsides, which can indirectly affect Orthoptera and other insects. In addition, other chemicals, such as nitrogen fertilizers, are widely used, and have been shown to have a strong impact on Orthoptera abundance (Nessel *et al.* 2021), so their indirect effects on Lesser Kestrel populations may need to be analysed.

In the case of nest-site scarcity, the empirical support is contradictory. It seems intuitive that the loss of nesting habitat could become a problem for the viability of Lesser Kestrel populations in the medium to long term (Calabuig *et al.* 2007). In fact, nest availability seemed to be a limit to rapid population growth in the 2000s in Portugal (Franco *et al.* 2005), whereas, in neighbouring Spain, available nest-sites were normally higher than the number of breeding kestrel pairs, and were not a scarce resource even in decreasing colonies at that time (Forero *et al.* 1996).

There may also be threats due to other factors, such as climate change (Morganti *et al.* 2019; but see Rodríguez & Bustamante 2003) or degradation of habitat quality in winter quarters in Sub-Saharan Africa. If so, we would expect differences between migrant and resident kestrels, which is not the case (Buchan *et al.* 2021).

The European Union (EU) Natura 2000 network of protected areas was established over the last two decades to safeguard species and habitats of biodiversity conservation interest under the Birds Directive (79/409/EEC) and the Habitats Directive (92/43/EEC). Many Natura 2000 sites were designed to preserve the biodiversity of agro-ecosystems, the maintenance of habitats and, in particular, species such as the Lesser Kestrel (considered 'Vulnerable' at the time). It is of great concern that the latest decline of the Lesser Kestrel population has occurred after the establishment of protected areas in the Natura 2000 network and despite the reinforcement of conservation measures directly targeting this species, such as numerous EU LIFE projects, as well as national, regional and local actions for captive breeding, reintroduction, construction of 'primillares' (small buildings similar to pigeon lofts, provided with nesting holes for Lesser Kestrels), installation of nestboxes, etc. This raises the question of whether the causes of population decline have been well identified or adequately addressed in conservation programmes.

In this study, we examined changes between 2003 and 2021 at 12 Lesser Kestrel colonies in La Mancha, Spain. In both years, and for the same sites, we obtained detailed data on kestrel population, land use around each colony, building conditions (i.e. nest-site availability) and density of Orthoptera, which is the main prey of the kestrel to feed nestlings (Rodríguez & Bustamante 2008; P.J. Cordero, A. Gómez & J.M. Aparicio, in prep.). The aim was to contrast three possible causes, not mutually exclusive, explaining population changes: changes in habitat, Orthoptera abundance or availability of nest-sites. In the course of this study, we found a dramatic increase of rabbit *Oryctolagus cuniculus* (Linnaeus, 1758) populations to the point of being considered an emerging pest in some districts (Barrio *et al.* 2011). Their high population levels affect the vegetation structure, accelerating the collapse of buildings and attracting large numbers of birds of prey. Although its impact needs further study, we have included rabbit density as an explanatory variable in our analyses. In addition, we examined the role of the Natura 2000 network in preserving favourable habitats for the Lesser Kestrel and whether this has contributed to the conservation of populations in the study area.

# MATERIAL AND METHODS

## Study area and species

The study was conducted on a Lesser Kestrel population located in La Mancha, provinces of Ciudad Real and Toledo, Central Spain (39°20′N, 3°15′W, at 600–800 m asl). The maximum temperature averages 32–35 °C in summer and frequently exceeds 40 °C. Mean temperatures range from 24–26 °C in July to 4–6 °C in January. Annual precipitation is typically between 300 and 400 mm, concentrated mainly in spring and autumn (Perez González & Sanz Donaire 1998). The study area is approximately 1000 km$^2$ and was set in a plain used for agriculture, cultivated mainly with barley, wheat and vineyards. Other minor habitats include scattered olive groves, almond and pistachio trees, pine plantations and pasture lands. In this area, we carried out a thorough monitoring of the Lesser Kestrel population between 1991 and 2007 (Hernández *et al.* 2007) and revisited the colonies in 2021.

Lesser Kestrels form breeding colonies of up to 60 pairs located in abandoned farmhouses. Natural nest-sites are normally located under tiled roofs (94%) and, in a minor proportion, inside wall holes (6%) in the studied colonies. Therefore, one measure of the potential of a building to house kestrel nests is its size and in particular its roof area suitable for breeding. In addition, in our study colonies, 14% of pairs bred in artificial nestboxes. Lesser Kestrels are migrants in our study area and normally arrive between January and March, depending on the year and age (Calabuig *et al.* 2008), laying between three and six eggs in one clutch per year. Egg-laying normally takes place through late April and May (range 15 April–6 June; Aparicio & Bonal 2002). Diet is based on insects, particularly Orthoptera, which are the main prey fed to nestlings (Bonal & Aparicio 2008).

## Estimations of colony size

In April, before egg-laying by kestrels, we surveyed the colonies to take a first census of the population. In that period, kestrel pairs usually stay near their nest-sites and sometimes go into the nesting hole, making it easy to locate and count the pairs present in the colony. Surveys were conducted before 11:00 or after 17:00 h in order to detect the maximum number of kestrels at a colony, as they are usually feeding in the surroundings in the middle of the day. Two or three observers thoroughly surveyed a colony by telescope for 1 or 2 h, depending on kestrel activity and building size, to assess breeding activity. A survey session ceased when no new pair appeared in the colony after 30–40 min. This procedure was repeated two or three times on different days. From 30 April onwards, we also inspected other holes apparently appropriate for the Lesser Kestrel, especially those with pellets, feathers or other vestiges indicating the presence of kestrels (Aparicio *et al.* 2007).

## Land use

Land use was established for all parcels within 1 km around each colony. We used this distance because 80% of the prey captures take place within this radius around the colony when kestrels are feeding the nestlings (Bonal & Aparicio 2008). In 2003, the use of each agricultural parcel was determined visually by driving or walking around the kestrel colonies in March and April and noting this on cadastral maps. This information was then processed using digitized maps in ArcMap. In 2021, we used SIGPAC, a Digital Land Parcel Identification System (LPIS) existing in Spain for the management of EU agricultural aids (https://sigpac.mapama.gob.es/fega/visor/) and downloaded land use information from databases provided by the JCCM (accessible at http://pagina.jccm.es/agricul/sigpac_datos/localidades.php). We also used satellite images from Sentinel-2, which provides information at a spatial and temporal resolution of 10 m and 5 days, respectively, in order to discern arable land use, especially to distinguish between cereal crops and fallow land. The parcels were classified into nine uses: 'Herbaceous crops' (including cereals and leguminous crops), 'Fallow lands' (which are arable lands but not cultivated in the last season and generally ploughed), 'Vineyards', 'Olive groves', 'Nut trees' (pistachio and almond trees), 'Pine plantations', 'Pasture lands', 'Abandoned lands' (which had not been cultivated for the previous 3–10 years) and 'Non-productive lands' (on soils without vegetation or Orthoptera; this buildings, roads, solar farms, the water or salt crust of lagoons).

## Orthoptera sampling

In both years, 2003 and 2021, we carried out an extensive Orthoptera sampling around 12 Lesser Kestrel colonies. Sampling was carried out between 16 June and 5 July, between 10:00 and 18:00 h, with temperatures above 25 °C. The sampling plots were concentrated in an area of 1-km radius around each colony, as we have previously found that 80% of the prey captures for nestling delivery took place within this area (Bonal & Aparicio 2008). We sampled 10–14 plots per colony, with the number of plots per habitat proportional to its coverage. In 2021, we repeated the sampling on the same plots as in 2003, but added some new habitats that were not present before, such as pistachio crops.

In 2003, we used a variant of Onsager and Henry's (1977) method to estimate the density of Orthoptera, which yields reliable density estimates when sampling is extensive and carried out by different people. This method consists in putting wire rings of 0.1 $m^2$ (35.68 cm in diameter) spaced at an interval of 10 m along transects. The wire rings delimit an area inside which the number of grasshoppers can be seen and counted by a person with sufficient clarity to distinguish between motion inside and outside the circle. In each plot we placed 48 rings of 0.1 $m^2$ in a net of six lines of eight rings, spaced at approximately 4-m intervals along lines. Each patch was sampled by a group of three people, counting the number of Orthoptera within the rings, as well as the number in 1-m-wide transects following the lines between rings. As both methods, using rings and transects, reported similar Orthoptera density estimates ($R^2 = 0.91$, $n = 123$, $P < 0.0001$), in 2021 we only used the transect survey method, which is less time-consuming and does not require the use of rings. Transects (60 m long, measured by GPS) were sampled by the same four people, who walked along them (10 m apart) at the same time. They counted the number of Orthoptera seen jumping/moving within 1 m on each side of their path. At each transect, we recorded Orthoptera species and sex, whenever possible, as well as number of specimens and body size estimated visually. Orthoptera were classified according to size as small (< 0.5 g), medium (0.5 to < 1 g) and large (≥ 1 g), although only large Orthoptera were considered for density estimates because they are the main food for Lesser Kestrel nestlings in the study area (P.J. Cordero, A. Gómez & J.M. Aparicio, in prep.).

## Rabbit abundance

Rabbit abundance is usually estimated through latrine counts along a certain track length (Virgós *et al.* 2003). Relative abundance of rabbits was surveyed in the same plots and transects in which we sampled Orthoptera. Any sign of rabbit activity (warrens, tracks, faecal pellets, scratches and observation of animals) and the number of latrines (Palma *et al.* 1999) was recorded. The abundance of rabbits was estimated in 2021 using an index which included number of latrines, burrows and presence/absence of rabbit signs in neighbouring plots (i.e. 100 m around the sampling area). This index ranged from 0 to 5, where 0 = absence of rabbits on the sampled plot and neighbouring plots, 1 = presence of rabbits on neighbouring plots, 2 = up to five latrines per sampling track, 3 = more than five latrines per sapling track, 4 = up to five rabbit burrows on the sampled plot, and 5 = more than five rabbit burrows on the sampled plot. The mean index of abundance of rabbits for a colony was estimated as the mean value of the indices of the sampled plots within 1 km of the colony.

## Statistical methods

To examine the change in the population from 1991 to 2021, the number of pairs in a colony in a given year was standardized relative to its annual maximum. Population size was estimated as the mean of the relative sizes of each colony. The population size was then adjusted for the year according to polynomial functions of increasing order until the highest adjusted $R^2$ was obtained.

We used paired *t*-tests for comparisons of colony size (i.e. number of pairs per colony) and Orthoptera abundance between 2003 and 2021, and chi-square tests to compare frequencies of changes in the land use type of parcels between 2003 and 2021 depending on whether they were included in the Natura 2000 network. Multiple linear regression analyses were used to see which rabbit abundance indices were associated with land use or Natura 2000 land cover characteristics and also to investigate the factors affecting colony size. In the latter case, we evaluated a number of independent variables such as roof area, Orthoptera abundance and number of nestboxes (see Table 1 for complete details) as predictors, or their increment from 2003 to 2021 when analysing changes in colony size for the same period. Changes in colony size as well as predictor variables were estimated as the logarithm of the ratio, i.e. log (value in 2021/value in 2003). Some of these variables such as Orthoptera abundance 1 km around colonies and favourable habitat fraction (herbaceous crops and/or pasture land) were strongly correlated with each other and in these cases only one was included in each model.

Beyond the selection of a model that can best predict dependent variables, our goal was to determine the importance of each predictor. Therefore, it made sense to distinguish between two separate steps: model selection and predictor comparison (Azen *et al.* 2001, Wang *et al.* 2013). In the first step, we used generalized linear models (GLMs) with normal distribution of errors and identity link and compared all different models (including Null models) that involved up to three potential predictors. These were compared using Akaike's Information Criterion adjusted for small sample size (AICc) to select the best models (i.e. those with $\Delta$AICc $\leq 2$ units, Burnham & Anderson 2002) from the candidate set, as those models with the lowest AICc value (Burnham & Anderson 2002). Although the AICc takes into

**Table 1.** Variables used in analyses of factors affecting colony size in 2003 and 2021, as well as the changes in colony sizes over that period. In the latter analyses, the differences in the variables detailed in this table were used, except for 'rabbit index' and 'Natura 2000', which were used with the values recorded in 2021.

| Variable | Description |
|---|---|
| Colony size | Number of breeding Lesser Kestrel pairs in a colony |
| Roof area | Roof area with breeding possibilities for Lesser Kestrels |
| Large Orthoptera density | Number of large Orthoptera (mass ≥ 1 g) per square metre averaged over the plots sampled in a colony |
| Large Orthoptera 1 km | Estimation of the number of large Orthoptera (mass ≥ 1 g) within 1 km of a colony |
| Nestboxes | Number of operative nestboxes in a Lesser Kestrel colony |
| Herbaceous crops | Land area within 1 km of a colony that includes herbaceous crops |
| Pasture lands | Land area within 1 km of a colony that includes pasture lands. |
| Favourable habitat | Land area within 1 km of a colony that includes herbaceous crops or pasture lands |
| *i*-use | Land area within 1 km of a colony devoted to the use '*i*', where '*i*' = each of the land uses considered in this study (i.e. *i* = fallow lands, vineyards, etc.) |
| Rabbit index | Rabbit abundance index |
| Natura 2000 | Proportion of area within 1 km of a colony included in Natura 2000 |

account the number of parameters included in a model and allows us to compare models with different numbers of predictors, we checked for possible overfitting by calculating the predicted $R^2$ value of each selected model. The predicted $R^2$ is a form of leave-one-out cross-validation that summarizes a model's ability to predict new data. Predicted $R^2$ is calculated by removing each observation from the dataset, estimating the regression equation and determining how well the model predicts the removed observation. A substantially lower predicted $R^2$ is an indication that the model may be overfitted and/or excessively dependent on individual data points (Deforest *et al.* 2020). The statistical significance of predicted $R^2$, as well as of each of the predictors, was tested using 1000 bootstrap iterations.

We tested the existence of multi-collinearity among independent variables using the variance inflation factor (VIF), which varies from 1 (when independent variables are uncorrelated) to infinite. In our analyses all VIF values were $\leq 1.21$. As this value falls well below 10, the commonly considered cut-off indicative of excessive multi-collinearity (O'Brien 2007), we were fairly confident of statistical independence among the predictors, and this allowed us to apply the Pratt index (Pratt 1987, Thomas *et al.* 1998), which is an $R$-square based statistic that has been shown to be useful to assess the contribution of a predictor to the variance explained by a linear regression model in the absence of collinearity (Liu *et al.* 2014, Thomas *et al.* 2018). Thus, the proportion of variance of the dependent variable explained by a predictor can be estimated by multiplying the Pratt index by the $R^2$ of the model. In this case we use predicted $R^2$ to obtain a more conservative estimate of the variance explained. To estimate these statistics, we use the linear regression module when the variable is continuous and normally distributed. In this case, it yields the same coefficients as GLM and, in addition, performs multi-collinearity diagnostics and provides standardized regression coefficients to estimate the Pratt index. All statistical analyses were done in SPSS v.26 and bootstrap resampling was performed in Excel (Microsoft) using VBA macros.

# RESULTS

## Local changes

### Lesser kestrel population

In the study area, the Lesser Kestrel population increased throughout the 2000s but seems to have decreased throughout the 2010s. The population data fit a third-degree polynomial model (Adjusted $R^2 = 0.86$) better than any other model (Adjusted $R^2$ for second- and fourth-degree polynomials of 0.68 and 0.75, respectively), which predicts a population peak around 2012 (Fig. 1). In particular, 10 of the 12 colonies included in this study decreased from 2003 to 2021, whereas the other two increased. The average colony size in 2003 was 19.8 pairs (± 5.4 se), and 12.0 pairs (± 3.1 se) in 2021. Mean colony decline was significant (paired $t$-test: $t = -2.71$, df = 11, $P = 0.02$) and the total number of these colonies decreased by 39.4%.

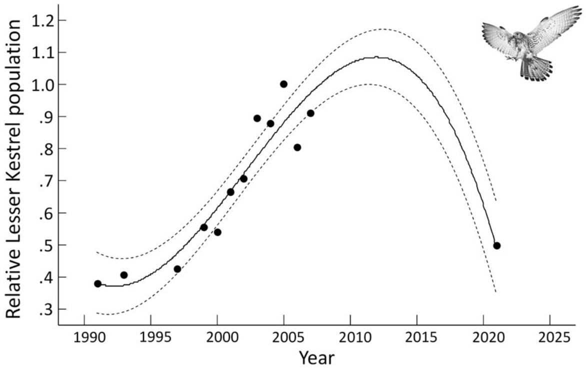

**Figure 1.** Evolution of the Lesser Kestrel population between 1991 and 2021. Dots indicate population size relative to the maximum registered population. The solid line indicates the population estimate by regression fit to a third-degree polynomial function and the dashed line the 95% confidence interval.

### Buildings and nestboxes

All Lesser Kestrel colonies included in this study were located in rural buildings. Nine of the 12 buildings have not been managed by their owners in recent years, so their deterioration has followed a natural process. In these buildings, on average, 23% of the roof area has disappeared over the last 20 years (Fig. 2). The other three buildings, which were managed by their owners, have had different fates. The original roofs of two of them have been almost completely demolished and, in both cases, nestboxes have been placed on the walls. The other building was acquired by an association for nature conservation (A.N. ESPARVEL), which is repairing the roofs in poorer condition but maintaining suitable nesting holes for Lesser Kestrels, so that it has had the same roof area since 2003.

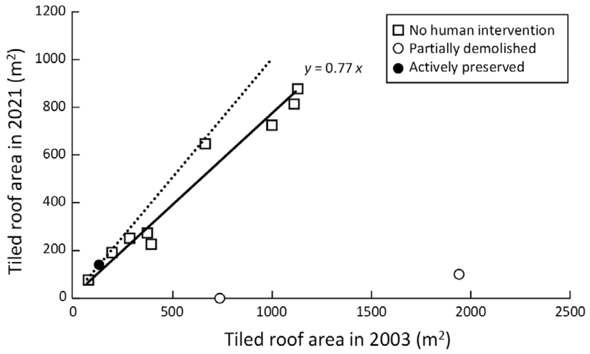

**Figure 2.** Relationship between roof area in 2003 and in 2021. The shape and colour of the dots indicates the type of human intervention. The solid line is the regression function of the expected changes in 2021 compared with 2003 in buildings without human intervention. The dotted line represents a situation of no change in roof area.

The average number of nestboxes per colony was 5.67 (± 4.13 se) in 2003 and increased to 9.83 (± 4.34 se) in 2021. In this time period, four colonies were provided with 8, 15, 16 and 24 nestboxes, respectively. Two colonies, which already had nestboxes in 2003, have lost three nestboxes, and 10 of them have not been replaced. Finally, the colony managed by the conservation association has maintained approximately 50–60 nestboxes during all these years.

### *Land use and Orthoptera abundance*

Arable land still occupied most of the territory in 2021 (Fig. 3). Nevertheless, since 2003, land use has changed dramatically. Overall, the extent of abandoned land, nut tree crops (almond and pistachio), olive trees and non-productive land (occupied by intensive farms and photovoltaic power stations) has increased, whereas pasture and herbaceous crops have decreased (Fig. 3a). In total, 142 ha of arable crops and 108.7 ha of pasture lands have been lost, i.e. 6.7% of the total area. The percentages relative to the area occupied in 2003 represent losses of 12.1% for herbaceous crops and 34.7% for pasture lands.

Changes in land use have occurred unevenly in the colonies (Fig. 3b). Shifts from herbaceous crops or pasture land to less favourable uses for Lesser Kestrels (nut tree crops, abandoned or non-productive land) were less likely if the property was included in the ecological network Natura 2000 than if it was not (10.2% vs. 32.7%; $\chi^2_1 = 7.63$; $P = 0.006$).

In 2021, the number of large Orthoptera (i.e. ≥ 1.0 g) per hectare was higher in pasture and herbaceous crops than for any other land use, but there was a sharp decline in large Orthoptera once these herbaceous crops were harvested and the land become cereal stubble (Fig. 4). Comparing densities of large Orthoptera within the same sampling plots between 2003 and 2021, we found no significant changes whenever land use was maintained (mean increase: 0.005 ± 0.004, df = 81, $P = 0.24$). However, their densities dropped significantly (mean increase: –0.0126 ± 0.004, df = 22, $P = 0.005$) when pasture and herbaceous crops were transformed into abandoned lands or other woody crops.

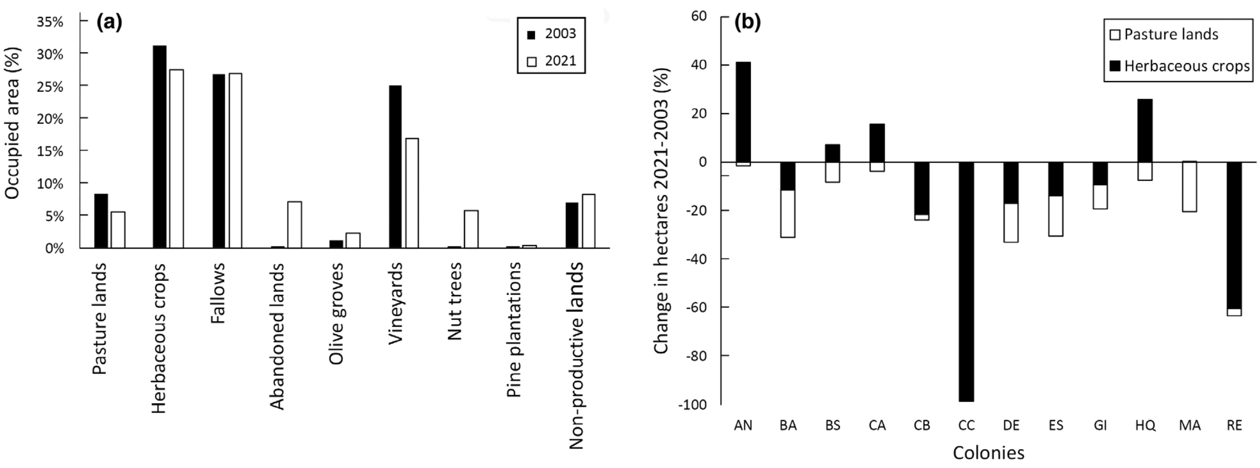

**Figure 3.** (a) Land use in 2003 and 2021 within 1 km of 12 Lesser Kestrel colonies. (b) Absolute changes in area occupied by herbaceous crops and pasture lands in each colony.

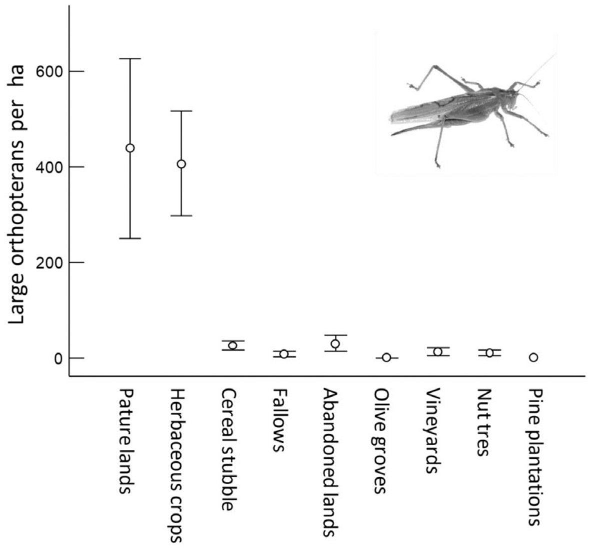

**Figure 4.** Mean (± se) density of large Orthoptera by land use in 2021.

*Rabbits*

Rabbits were already present in moderate numbers in 2003. Unfortunately, we did not monitor the rabbit population in 2003 because its abundance was much lower and did not attract our attention as a possible factor that could affect the conservation of the buildings, the vegetation structure or, indirectly, the Lesser Kestrel population. However, in recent years, their populations have experienced outbreaks in some parts of the study area. In 2021, rabbit burrows were concentrated on pasture lands and other uncultivated land including around buildings, where colonies of Lesser Kestrels are established. Farmers had put fences around rabbit burrows to prevent them from invading their land, and high rabbit numbers were completely cleared of plants in some areas, changing the vegetation (species composition and structure).

Rabbit abundance index in the vicinity of a colony was positively related to the area of non-productive land ($\beta = 0.73$, $t = 4.76$, $P = 0.001$) and negatively related to the proportion of land around the colony included in Natura 2000 ($\beta = -0.50$, $t = 2.93$, $P = 0.017$; Regression model: $r^2 = 0.79$, $F_{2,9} = 16.9$, $P = 0.001$).

## Factors affecting colony size

The best GLM predicting colony size in 2003 included the independent variables 'Roof Area' and Orthoptera abundance ('Large_Orthop_1km'). However, we cannot rule out the model including 'number of nestboxes' as a predictor, because differences in AICc between models were small (Table 2). In 2021, the best GLMs predicting colony size included 'Roof Area', 'Herbaceous crops' and 'Nestboxes' as predictor variables (Table 2). In both years, 2003 and 2021, roof area was the independent variable that accounted for the most variance for colony size (23–29% in 2003 and 26–37% in 2021; Table 3). Moreover, the magnitude of its effect was fairly stable over the years on average;

**Table 2.** Top models (i.e. ΔAICc ≤ 2) for the effects explaining Lesser Kestrel colony size in 2003 and 2021, as well as changes in colony size over that period. Models are ranked according to the Akaike Information Criterion corrected for small samples (AICc). The ΔAICc indicates AICc differences between a particular model and the best-fitting model. Akaike weights ($\omega_i$) indicate the contribution of each model to the average of all candidate models. See Table 1 for definition of variables.

| Model | Predictors | AICc | ΔAICc | $\omega_i$ |
|---|---|---|---|---|
| Colony size in 2003 | | | | |
| 1 | Roof area + Large Orthoptera 1 km | 104.38 | 0 | 0.39 |
| 2 | Roof area + Nestboxes | 104.51 | 0.13 | 0.37 |
| 3 | Roof area | 105.42 | 0.91 | 0.23 |
| Colony size in 2021 | | | | |
| 1 | Roof area + Herbaceous crops + Nestboxes | 87.34 | 0 | 0.73 |
| 2 | Roof area + Herbaceous crops | 89.32 | 1.98 | 0.27 |
| Change in colony size (2021–2003) | | | | |
| 1 | ΔLarge Orthoptera density + ΔRoof Area + Rabbit index | 8.32 | 0 | 0.31 |
| 2 | ΔLarge Orthoptera density + ΔFavourable habitat | 8.53 | 0.22 | 0.28 |
| 3 | ΔLarge Orthoptera density + ΔHerbaceous crops | 9.77 | 1.45 | 0.15 |
| 4 | ΔLarge Orthoptera density | 9.94 | 1.62 | 0.14 |
| 5 | ΔLarge Orthoptera density + ΔRoof area | 10.04 | 1.72 | 0.13 |

**Table 3.** Regression parameter of top models explaining colony sizes in 2003 and 2021, as well as changes in colony size over that period. $P^*$ indicates probability values for Predicted $R^2$ and for the effect of predictors, which were estimated using leave-one-out-cross-validation.

| Predictor | Value | se | β | $t$ | $P$ | $P^*$ | VIF | Pratt Index | % Variance |
|---|---|---|---|---|---|---|---|---|---|
| Colony size in 2003 | | | | | | | | | |
| Model 1: Adjusted $R^2$ = 0.57; $F_{2,9}$ = 8.37; $P$ = 0.009. Predicted $R^2$ = 0.35; $P^*$ = 0.007. | | | | | | | | | |
| Intercept | −47.2 | 22.9 | | | | | | | |
| Roof area | 0.027 | 0.007 | 0.805 | 3.895 | 0.004 | 0.006 | 1.10 | 0.82 | 29 |
| Large_Orthopt_1km | 1.882 | 0.800 | 0.486 | 2.354 | 0.043 | 0.048 | 1.10 | 0.18 | 6 |
| Model 2: Adjusted $R^2$ = 0.57; $F_{2,9}$ = 8.23; $P$ = 0.009. Predicted $R^2$ = 0.29; $P^*$ = 0.01. | | | | | | | | | |
| Intercept | −2.06 | 6.49 | | | | | | | |
| Roof_area | 0.028 | 0.070 | 0.807 | 3.877 | 0.004 | 0.008 | 1.10 | 0.82 | 53 |
| Nestboxes | 0.631 | 0.272 | 0.481 | 2.321 | 0.045 | 0.140 | 1.10 | 0.18 | 11 |
| Model 3: Adjusted $R^2$ = 0.38; $F_{1,10}$ = 7.70; $P$ = 0.02. Predicted $R^2$ = 0.23; $P^*$ = 0.029. | | | | | | | | | |
| Intercept | 4.89 | 6.91 | | | | | | | |
| Roof_area | 0.023 | 0.008 | 0.66 | 3.877 | 0.02 | 0.029 | 1.00 | 1.00 | 23 |
| Colony size in 2021 | | | | | | | | | |
| Model 1: Adjusted $R^2$ = 0.79; $F_{3,8}$ = 14.96; $P$ = 0.001. Predicted $R^2$ = 0.65. $P^*$ = 0.001. | | | | | | | | | |
| Intercept | −11.06 | 3.90 | | | | | | | |
| Roof area | 0.025 | 0.005 | 0.722 | 4.793 | 0.001 | 0.005 | 1.20 | 0.57 | 37 |
| Herbaceous crops | 0.13 | 0.032 | 0.572 | 4.043 | 0.004 | 0.004 | 1.06 | 0.42 | 27 |
| Nestboxes | 0.304 | 0.108 | 0.425 | 2.817 | 0.023 | 0.011 | 1.21 | 0.01 | 1 |
| Model 2: Adjusted $R^2$ = 0.63; $F_{2,9}$ = 10.43; $P$ = 0.005. Predicted $R^2$ = 0.48; $P^*$ = 0.006 | | | | | | | | | |
| Intercept | −5.04 | 4.34 | | | | | | | |
| Roof area | 0.019 | 0.006 | 0.566 | 3.036 | 0.014 | 0.025 | 1.04 | 0.54 | 26 |
| Herbaceous crops | 0.117 | 0.042 | 0.516 | 2.767 | 0.022 | 0.014 | 1.04 | 0.46 | 22 |
| Change in colony size (2021–2003) | | | | | | | | | |
| Model 1: Adjusted $R^2$ = 0.80; $F_{3,8}$ = 15.38; $P$ = 0.001. Predicted $R^2$ = 0.65; $P^*$ = 0.001. | | | | | | | | | |
| Intercept | −0.059 | 0.087 | | | | | | | |
| ΔLargeOrthopt_density | 13.952 | 2.675 | 0.714 | 5.215 | 0.001 | 0.002 | 1.01 | 0.64 | 41 |
| Rabbit index | −0.147 | 0.054 | −0.378 | −2.76 | 0.025 | 0.034 | 1.02 | 0.19 | 13 |
| ΔRoof area | 0.186 | 0.065 | 0.392 | 2.878 | 0.021 | 0.046 | 1.00 | 0.17 | 11 |
| Model 2: Adjusted $R^2$ = 0.69; $F_{2,9}$ = 13.219; $P$ = 0.002. Predicted $R^2$ = 0.61; $P^*$ = 0.001. | | | | | | | | | |
| Intercept | −0.244 | 0.07 | | | | | | | |
| ΔLargeOrthopt_density | 13.728 | 3.316 | 0.705 | 4.14 | 0.003 | 0.001 | 1.02 | 0.72 | 44 |
| ΔFavourable lands | 0.004 | 0.002 | 0.415 | 2.447 | 0.037 | 0.022 | 1.02 | 0.28 | 17 |
| Model 3: Adjusted $R^2$ = 0.66; $F_{2,9}$ = 11.488; $P$ = 0.003. Predicted $r^2$ = 0.57; $P^*$ = 0.001. | | | | | | | | | |
| Intercept | −0.279 | 0.07 | | | | | | | |
| ΔLargeOrthopt_density | 14.066 | 3.477 | 0.719 | 4.045 | 0.003 | 0.001 | 1.01 | 0.76 | 43 |
| ΔHerbaceous crops | 0.004 | 0.002 | 0.378 | 2.127 | 0.062 | 0.043 | 1.01 | 0.24 | 14 |
| Model 4: Adjusted $R^2$ = 0.54; $F_{1,10}$ = 13.643; $P$ = 0.004. Predicted $R^2$ = 0.43; $P^*$ = 0.003. | | | | | | | | | |
| Intercept | −0.307 | 0.08 | | | | | | | |
| ΔLargeOrthopt_density | 14.851 | 4.021 | 0.76 | 3.694 | 0.004 | 0.003 | 1.0 | 1.0 | 43 |
| Model 5: Adjusted $R^2$ = 0.65; $F_{2,9}$ = 11.131; $P$ = 0.004. Predicted $R^2$ = 0.58; $P^*$ = 0.001. | | | | | | | | | |
| Intercept | −0.234 | 0.078 | | | | | | | |
| ΔLargeOrthopt_density | 14.819 | 3.467 | 0.758 | 4.238 | 0.002 | 0.001 | 1.00 | 0.81 | 47 |
| ΔRoof area | 0.175 | 0.085 | 0.368 | 2.055 | 0.07 | 0.014 | 1.00 | 0.19 | 11 |

colonies increased by 2.8 breeding pairs every 100 $m^2$ of roof (Fig. 5). ‘Herbaceous crops’ accounted for 22–27% of the variance in colony size only in 2021, whereas ‘Orthoptera abundance’ explained 6% of the variance in colony size in 2003 (model 1) and 20% in 2021 when this variable replaced ‘Herbaceous crops’ in the model. The number of nestboxes explained as much variance in colony size as Orthoptera abundance in 2003, but only 1% in 2021 in the best of the models. On average, each nestbox contributed to the increase of kestrel colonies by 0.63 (± 0.27 se) pairs in 2003 and 0.30 (± 0.11 se) pairs in 2021 (Table 3).

Furthermore, we analysed the factors predicting the change in colony size from 2003 to 2021 and found that all GLMs with ΔAIC ≤ 2 included the ΔLarge Orthoptera density variable as the main

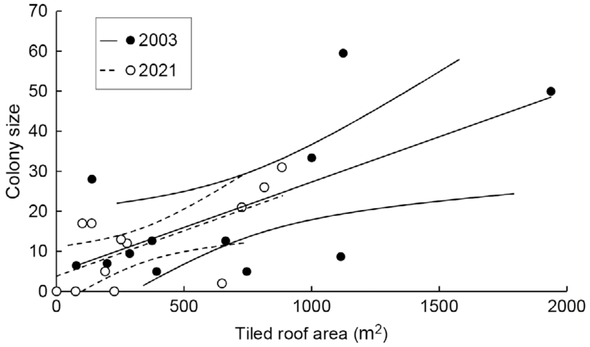

**Figure 5.** Lesser Kestrel colony sizes in relation to roof area of building suitable for breeding. Black and grey lines represent the regression lines and 95% confidence intervals of the mean for 2003 (solid line) and 2021 (dashed line).

predictor, explaining 41–47% of the variance of changes in colony size. The best GLM also included the predictors 'rabbit index' and 'changes in roof area', which explained 13% and 11%, respectively, of the variance in changes in colony size. The rabbit abundance index had a negative effect on changes in colony size, whereas the effects of changes in roof area were positive, i.e. colonies decreased more where the rabbit index was higher and changes in roof area were smaller. Models 2 and 3 in rank order included changes in favourable lands for Lesser Kestrel or change in area of herbaceous crops, which accounted for 17% and 14% of the variance in their respective models (Table 3).

## DISCUSSION

In one of the best-preserved populations of Lesser Kestrels in Europe, located in Castilla-La Mancha (Spain), we found that after an increase throughout the 1990s and 2000s (Ortego *et al.* 2007a), there has been a severe decline in recent years (39.4% since 2003). This population trend observed in La Mancha is similar to that for the Lesser Kestrel in Spain as a whole (Bustamante *et al.* 2020). If we take into account that the population peak is estimated to have occurred around 2012 (Fig. 1), the decline since then could be close to 60% in just 10 years, which would match the annual decrease rate of 6% estimated by Bustamante *et al.* (2020) from 2012 to 2019 for the whole of Spain. The rate of decline is worrying, as it is even greater than the estimated population decline in the second half of the 20th century. However, it is also true that the recovery capacity of the Lesser Kestrel population is high, as demonstrated by the population growth throughout the 1990s and 2000s, when the population doubled in just 15–20 years in La Mancha (Ortego *et al.* 2007a) as well as in other Mediterranean regions (Catry *et al.* 2007, Sarà 2010, Cherkaoui *et al.* 2013). The core of the problem therefore lies in the persistence of the causes currently driving the population decline.

It has been hypothesized that two of the main threats to the kestrel are the loss of nesting sites and foraging habitat (Bustamante 1997, Franco *et al.* 2005, Sarà 2010). Our results show that in the last two decades there has been a significant loss of nesting habitat. On average, 1.1% of roof area favourable for kestrel breeding is lost each year due to a process of natural deterioration of the buildings. In addition, two of 12 colonies have been almost completely restructured or demolished over these two decades. Adding these two phenomena together, approximately 2% of nesting habitat is lost annually. Furthermore, we found that there is a close association between roof area and colony size and, similarly, changes in roof area affect changes in colony size. We therefore show that, in this species, nesting habitat can become a real threat. However, we know little about building dynamics, especially how many more are available in a territory or how many new buildings are colonized by Lesser Kestrels each year.

One way to mitigate the loss of nesting habitat is the supplementation of nestboxes (Franco *et al.* 2005); in fact, the Lesser Kestrel population in Portugal increased from 2003 to 2007 in the colonies where artificial nest-sites were provided, but not in others (Catry *et al.* 2009). By contrast, in this study population the effects were unclear. In 2003, with a low number of nestboxes per colony, each additional nestbox increased the colony by 0.67 pairs, which seemed quite optimistic. However, as the number of boxes increased in successive years up to 2021 by almost double, the nestbox effect became less strong and each nestbox contributed to increase the colony size by just 0.30 pairs (i.e. less than half of what it did in 2003), so that there was no relationship between nestbox increase and changes in colony size. This lack of relationship could occur: (1) if the Lesser Kestrel population is limited by other causes than nest-site availability (Forero *et al.* 1996), (2) nestboxes are not well designed or (3) their maintenance has not been adequate to increase the kestrel population. Franco *et al.* (2005) found that two towers built specifically to provide cavities for Lesser Kestrels to breed in were not occupied due to an inadequate size of inner cavity chambers and, when some of these were enlarged, their occupation was successful.

There are few studies addressing the suitability of nestbox designs (but see Pomarol 1996) and some widely used designs have not been previously tested. In the colonies we examined, most of the nestboxes installed in the walls had entrance holes 6 cm in diameter, much smaller than the 17 × 14 cm entrance of natural nests (Negro & Hiraldo 1993), and thus they were mostly occupied by Jackdaws *Corvus modedula* rather than kestrels. In fact, the increase in the number of nestboxes from 2003 to 2021 is also associated with an increase in the Jackdaw population. In consequence, nestboxes could play an unexpected role in facilitating the occupation of other species (Gameiro *et al.* 2022) that, in certain cases, may be competitors of the Lesser Kestrel (Bijlsma *et al.* 1988), but also an ally in the defence against predators (Campobello *et al.* 2012, 2015). We have observed that the nestboxes, due to their extremely closed structure, accumulate too much debris (feathers, pellets and even sticks and ropes if they have hosted Jackdaws, in much larger quantities than 'natural' nest-sites) which, in a few years, prevented them from being occupied. Thus, the success of the nestboxes depends to a large extent on regular maintenance; however, this is not always possible.

The other major threat to the Lesser Kestrel, the most important for some authors, is the loss of foraging habitat due to changes in land use and agricultural intensification. Several studies on habitat selection of Lesser Kestrels agree that the preferred habitats are grasslands and cereal crops during the nestling period (Donázar *et al.* 1993, Vlachos *et al.* 2014, Christakis & Sfougaris 2021, Assandri *et al.* 2022). In our study area, 12.1% of herbaceous crops and 34.7% of pasture lands have been lost between 2003 and 2021 in favour of abandoned land, woody crops or non-productive areas (photovoltaic farms, intensive livestock farms, etc.). This loss of foraging habitat could affect the availability of Orthoptera in the vicinity of Lesser Kestrel colonies because herbaceous crops and pasture lands concentrate the highest densities of large Orthoptera (at least 10 times more than any other use; Fig. 2, see also Rodríguez & Bustamante 2008) and these insects account for about 90% of the prey delivered by kestrels to their nestlings in the study area (P.J. Cordero, A. Gómez & J.M. Aparicio, in prep.).

Some studies on habitat selection have shown that Lesser Kestrels positively select fallow land at certain times of the year (Franco *et al.* 2004, de Frutos *et al.* 2010, Christakis & Sfougaris 2021). In this study, however, fallow land had a very low density of Orthoptera and any other invertebrates on the sampling dates. This is because fallow land is usually ploughed in the second half of spring, at least in our study area. Ploughing removes vegetation and the possibility of harbouring insects for some period of time, at just the nestling stage when the demand for food by the kestrel is at its highest. Farmers consider that ploughing fallow land at this time is essential to prevent the growth and fruiting of weeds with the spring rains. This creates a difficult conflict between farmers' interests and the conservation of the Lesser Kestrel.

On the other hand, the density of large Orthoptera on abandoned land was higher than on fallow lands or woody crops, although much lower than on pasture lands or herbaceous crops (Fig. 3b). Abandoned lands were arable lands until 3–10 years ago. The change of Orthoptera communities on these lands is interesting, as they become richer over time and will probably become as rich in diversity and abundance as the pasture lands. In fact, we observed a positive correlation between age of abandonment and densities of medium and small Orthoptera, but no correlation with large ones. We observed that quite a few adult kestrels used these abandoned fields to feed themselves (P.J. Cordero, A. Gómez & J.M. Aparicio unpubl. data); however, the scarcity of large prey makes them still little suitable for feeding nestlings, as this raptor is a single prey loader (Bonal & Aparicio 2008).

We considered Orthoptera abundance around colonies and favourable habitat fraction (herbaceous crops and/or pasture land) as predictors of colony size or changes in colony sizes. As both variables were strongly correlated, only one or the other was included in each model. In 2021, herbaceous crops were more closely associated with colony size compared with Orthoptera abundance, whereas both colony size in 2003 and changes in colony size from 2003 to 2021 were better predicted by Orthoptera abundance or changes in

Orthoptera abundance than by area of favourable habitat. Nevertheless, it seems reasonable that changes in the area of favourable habitat also underlie the effects of Orthoptera abundance on Lesser Kestrel populations. The subtle differences in the factors included in the 2003 and 2021 models may be due to the fact that in 2021 herbaceous crops were almost exclusively cereals, whereas in 2003 these crops also included an important fraction of legumes, which may be less favourable for Lesser Kestrels than cereal crops. In an experimental study promoting the establishment of new colonies in the study area, Calabuig *et al.* (2010) found that the probability of occupation of experimental breeding patches increased with the relative cover of cereal crops. However, cereal crops can also be an ecological trap when breeding time is late, because food availability varies greatly around harvest time (which usually takes place in the second fortnight of June and the beginning of July). Harvesting increases foraging opportunities, but prey abundance declines rapidly, as cereals, once harvested, are converted into low-quality stubbles with high Orthoptera mortality and dispersal (Catry *et al.* 2014, Gustin *et al.* 2017).

In other populations, colony size is also associated with habitat composition, although favourable habitat varies between populations and cereal crops are not always the best habitat for Lesser Kestrel populations (Catry *et al.* 2012). In Sicily, a non-traditional crop, such as artichokes, is a more favourable habitat for the Lesser Kestrel than cereal crops (Di Maggio *et al.* 2016, 2018). By contrast, in Turkey, there was a positive correlation between the size of Lesser Kestrel colonies and habitat composition, as the percentage of semi-natural habitats within 1 km of each settlement and, furthermore, colony size were correlated with lizard numbers (Parr *et al.* 1997), which, in this region, could be a major source of food for the Lesser Kestrel as in neighbouring Greece and Central Asia (Cramp & Simmons 1980).

In recent years, the rabbit population has exploded in some localities of the study area. We found a negative statistical correlation between rabbit abundance and changes in the Lesser Kestrel population. Although this correlation is only noticeable in multivariate models controlling for large grasshopper density, rabbit abundance explained 13% of the variance in the decline of Lesser Kestrel populations after correcting for possible overfitting effects. This possible effect of rabbit abundance on kestrels may follow two paths. On the one hand, overgrazing by rabbits can have many direct effects on vegetation, and indirect effects on Orthoptera abundance, and ultimately affect the Lesser Kestrel population. However, the effect of rabbits on kestrels may more probably occur through a process of hyperpredation (Taylor 1979, Smith & Quin 1996, Courchamp *et al.* 2000, Zhang *et al.* 2006), as the increase in rabbits attracts birds of prey such as Buzzards, Booted Eagles, harriers, Black Kites and even Goshawks (Aparicio & Cordero 2018), which may opportunistically prey on kestrels, especially on nestlings when they start to stay longer periods on the rooftops begging for food from their parents or initiate flight exercises. This last hypothesis would be in agreement with other studies which show a negative relationship between abundance of breeding Lesser Kestrels and presence of larger raptors (Tella *et al.* 2004). Nevertheless, a more specific study will be needed to analyse these effects of rabbit numbers.

In conclusion, the reduction in the availability of large Orthoptera is the main cause of the decline in Lesser Kestrel populations in recent years. This reduction in available prey seems to be caused by changes in land use, particularly due to the loss of uses favourable for the kestrel (herbaceous crops and pasture land). The availability of nesting sites, measured as roof area for nesting, is the main factor explaining colony size in both 2003 and 2021, and the second most important factor explaining changes in the Lesser Kestrel population, together with rabbit density, which is negatively associated with changes in kestrel colony sizes. Protection measures such as the inclusion of some areas within the Natura 2000 network may have slowed down changes in land use and thus alleviated the decline of Lesser Kestrel populations. Conservation actions based on the construction of ‘primillares’ or nestboxes are not being as efficient as expected in mitigating the loss of nesting sites in the study area. Future research should investigate the causal relationships behind this association between rabbit abundance and changes in colony size, and also analyse whether the increase in artificial nest-sites is facilitating the establishment of other species such as Jackdaws, inducing changes in the ecosystem and in competitive relationships with the Lesser Kestrel.

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## AUTHOR CONTRIBUTIONS

**José Miguel Aparicio:** Conceptualization (equal); formal analysis (lead); investigation (equal); methodology (lead); writing – original draft (lead); writing – review and editing (equal). **Alberto Muñoz:** Investigation (equal); writing – original draft (supporting); writing – review and editing (equal). **Pedro J. Cordero:** Investigation (equal); writing – original draft (supporting); writing – review and editing (equal). **Raúl Bonal:** Conceptualization (equal); investigation (equal); writing – original draft (supporting); writing – review and editing (equal).

## CONFLICT OF INTEREST

None.

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## ETHICAL NOTE

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## Data Availability Statement

Data are available on request from the authors.

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