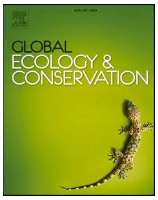
Global Ecology and Conservation 52 (2024) e02988

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



The effects of land use changes on site occupancy and breeding success of the barn owl (*Tyto alba*) from 1993 to 2020

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ARTICLE INFO

Keywords:
Agricultural intensification
Urban expansion
Land use change
Barn owl fitness

ABSTRACT

Land use changes, driven by human activities such as agricultural intensification and urban expansion, have drastic effects on biodiversity. As these changes are anticipated to continue, understanding species' adaptations to their evolving habitats is essential to find solutions for effective conservation efforts and sustainable management. In this study, we investigated how long-term changes in the agricultural landscape influence the breeding performance of a population of barn owls (*Tyto alba*) residing in nest boxes using data collected from 1993 until 2020. Specifically, we assessed how agricultural intensification, urbanization, and site availability affected barn owls' site occupancy and breeding success. Our results reveal that nest boxes surrounded by more agricultural fields are more likely to be occupied and have higher fledging success. Additionally, nest boxes installed higher on the barn were more likely to be occupied. Owls laid more eggs in nest boxes facing North than South or East. Clutches laid in nest boxes installed at higher altitudes were smaller. Finally, nest boxes with a higher density of surrounding nest boxes were less likely to be occupied and had smaller clutches. These insights show barn owls high reliance on the agricultural landscape surrounding their nesting sites, but also the importance of nest box characteristics to optimize their breeding success.

1. Introduction

Over the past decades, the environment has undergone profound transformations, shaped by the ever-increasing human population and the various strategies and decisions that societies have implemented in response to this growth. Landscapes, once characterized by the ecological richness of wildlife species, are now altered by anthropogenic activities. Among these, agricultural landscapes are perhaps the most affected (Stoate et al., 2009), undergoing a shift towards more intensive farming practices, a prevalence of monocultures with larger field sizes, and a substitution of natural surfaces by cultivated areas. Unfortunately, this intensification comes at a considerable environmental cost, notably with the decrease of biodiversity in agricultural landscapes (Robinson and Sutherland, 2002; Benton et al., 2003; Herzog et al., 2012; Wilson et al., 2016; Sirami et al., 2019). Among the most affected species are farmland birds, which have experienced a dramatic decline worldwide in the past few years (Bowler et al., 2021, Antoniazza et al., 2018). Nearly three

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https://doi.org/10.1016/j.gecco.2024.e02988
Received 15 March 2024; Received in revised form 2 May 2024; Accepted 14 May 2024

years after a study published in the journal Science revealing that North America had lost 3 billion breeding birds since 1970 (Rosenberg et al., 2019), the 2022 State of the Birds Report for the United States (North American Bird Conservation Initiative, 2022) found that bird declines are continuing in almost every habitat, except wetlands. Grassland birds are experiencing the most severe declines among all habitats, a trend closely associated with intensified agricultural practices (Donald et al., 2006; Newton, 2004). The situation is similar in Europe, where land-use change tends to be a strong driver of bird population decline (Bowler et al., 2021; Silva et al., 2024). Therefore, it is essential to find solutions that not only meet the increasing demand for agricultural production but also actively preserve agricultural biodiversity.

Together with agricultural intensification, urban areas also keep growing, both in size and density, leading to habitat fragmentation and resource depletion. While some species have demonstrated a remarkable capacity to adapt to urban environments, described as urban exploiters by Blair (1996), the majority of species are restricted to increasingly small and isolated natural habitats. Many studies analyzed how bird species thrive in urban environments. Møller (2009) found that bird species better adapted to urban environments have specific characteristics (e.g. large breeding ranges, high propensity for dispersal, high rates of feeding innovation, and short flight distance when approached by a human), while Sol et al. (2014) found a phylogenetic signal for urbanization tolerance, implying that some families are more tolerant than others, such as *Sturnidae, Corvidae* or *Columbidae*. To develop efficient conservation strategies in such constantly changing environments, it is essential to understand how species respond to these changes.

Among the many species coping with the challenges posed by land use changes, the barn owl (*Tyto alba*) emerges as an exemplary study species. This nocturnal raptor lives in agricultural landscapes (Perrins and Snow, 1998), preying on small mammals, and nesting in barns and buildings (Roulin, 2020, Perrins and Snow, 1998). This dual reliance on both agricultural lands and urban areas makes the barn owl an ideal model for investigating how they are impacted by agricultural and urban changes. Furthermore, this species can contribute to natural pest control in agricultural fields (Meyrom et al., 2009; Donázar et al., 2016; Luna et al., 2020; Montoya et al., 2021), limiting small mammal populations that could otherwise cause significant crop damage (Peleg et al., 2018). In fact, during the breeding season alone, a breeding pair can consume up to 1000 prey items to feed their nestlings (George and Johnson, 2021, Schalcher et al., 2023). Therefore, understanding the adaptation of this bird to land use changes is essential. Previous studies have already explored this. Frey et al. (2011) studied a Swiss barn owl population from 1987 to 2009, estimating the influence of landscape features comprising urban areas and agricultural fields on barn owl breeding performances. Yet they did not account for environmental change, considering it as stable during the studied period, limiting insights into its impact on barn owls breeding success. Hindmarch et al. (2012) investigated the effect of landscape features, focusing on grasslands, urban areas, and roads, on a Canadian barn owl population. However, their study was constrained by limited data, having only two observation years, in 1990 and 2007.

The core objective of the present study is to evaluate the impact of land use change, specifically focusing on the agricultural intensification, urban areas expansion, and nest box density, on barn owl site occupancy and breeding success since the 1990s. On one hand, site occupancy provides insights into barn owl habitat preferences, helping to identify key habitat features influencing nest site selection. On the other hand, analyses on breeding success provide reliable measurements of the influence of habitat characteristics on barn owl reproductive success. By examining both variables together, we aim to assess which land uses correspond to high-quality habitats for the barn owl, focusing as much on the selection of breeding sites as on breeding performances, as advised by Johnson (2007).

We used data collected through a research project initiated in the early 1990s in Switzerland: On the Swiss Plateau, nearly 400 nest boxes have been gradually installed on farms since 1993 by scientists from the University of Lausanne in collaboration with the Swiss Ornithological Institute, with farmers' agreement. In the present study, we analyzed data accumulated since the start of this project to present days, encompassing variables such as agricultural land use change, urban area development, nest box density, and nest box characteristics. Through a multifaceted approach, we seek to gain a comprehensive understanding of how land use changes have influenced barn owl breeding success, to provide the best conservation strategies targeting this species. We expect landscape homogenization to adversely affect the breeding success of barn owls. Indeed, landscape heterogeneity enhances prey density and accessibility (Arlettaz et al., 2010; Gentili et al., 2014; Serafini et al., 2019; Sirami et al., 2019), suggesting that habitats with more diverse structures are likely to support better breeding outcomes. Regarding urban expansion, given barn owls' adaptation to human settlements, we expect a limited impact from the intensification of urban areas. However, this aspect has not been thoroughly investigated previously over the long term, and it is crucial to determine whether there is a threshold beyond which urbanization begins to negatively affect this species. Finally, our study aims at examining the influence of nest box characteristics and site density on barn owl breeding parameters. Research in other regions has explored similar dynamics, such as in the Hula Valley in Israel, where the location of nest boxes has been found to influence occupancy, nest boxes placed on trees showing higher occupancy, followed by nest boxes on poles in the shade and finally nest boxes on poles in the sun (Charter and Rozman, 2022). Similarly, in the Napa Valley in the USA, nest boxes constructed of wood and placed higher off the ground were more likely to be occupied (Wendt and Johnson, 2017). Despite these insights, the nest boxes and environmental conditions in our study differ from these examples. As such, we do not have specific predictions, but rather aim to elucidate the overall impact of nest box characteristics and site density on barn owl populations within our study context.

2. Material and methods

2.1. Study area and data collection

The present study focuses on a wild population of barn owls residing in nest boxes in Western Switzerland (Fig. 1 A-B). The study area of approximately 1'000 km^2 is mainly dominated by agricultural fields and urban areas comprising predominantly villages, the preferred habitat of the barn owl (Bunn et al., 1982).

Nest boxes are installed on barn walls, either inside with the flying hole facing the outside, or outside the barn (Fig. 1C). There can be up to two nest boxes installed in the same barn. Each barn with nest boxes, either one or two, is considered as a breeding site in this present paper. Nest boxes are usually installed between 4 and 10 m above the ground. They have been installed progressively since the 1990 s, reaching a total of 379 nest boxes at 310 different breeding sites nowadays.

For each nest box, we extracted five characteristics that can possibly impact barn owls' site occupancy and breeding success: (1) the orientation, referring to the direction in which the nest box entrance faces, specifically categorized as North, East, South, or West; (2) the height above the ground in meters where the nest box is installed in or on the barn; (3) the altitude above sea level where the nest box is located; (4) the number of nest boxes present at the breeding site (either one or two); (5) whether the nest box was occupied by a barn owl pair the preceding year or not.For the current study, only nest boxes installed before 1993 and that remained in place until 2021 were selected, ensuring a consistent temporal framework for the analyses (n=89). Among those nest boxes, the majority were facing East (n=54), followed by North (n=18), and South (n=13), and only four were facing West. Due to this bias in the dataset, we decided to remove the four nest boxes facing West from the analyses. Moreover, the vast majority are placed inside barns (n=74). It was thus decided to remove the 15 nest boxes placed outside barns for the same reasons. Consequently, the final analyses were conducted on 48 distinct breeding sites, encompassing a total of 72 nest boxes, as some nest boxes are placed at the same site (Fig. 1 A).

Every year, each nest box was monitored every month between March and August to assess if it was occupied or not, i.e. if a clutch

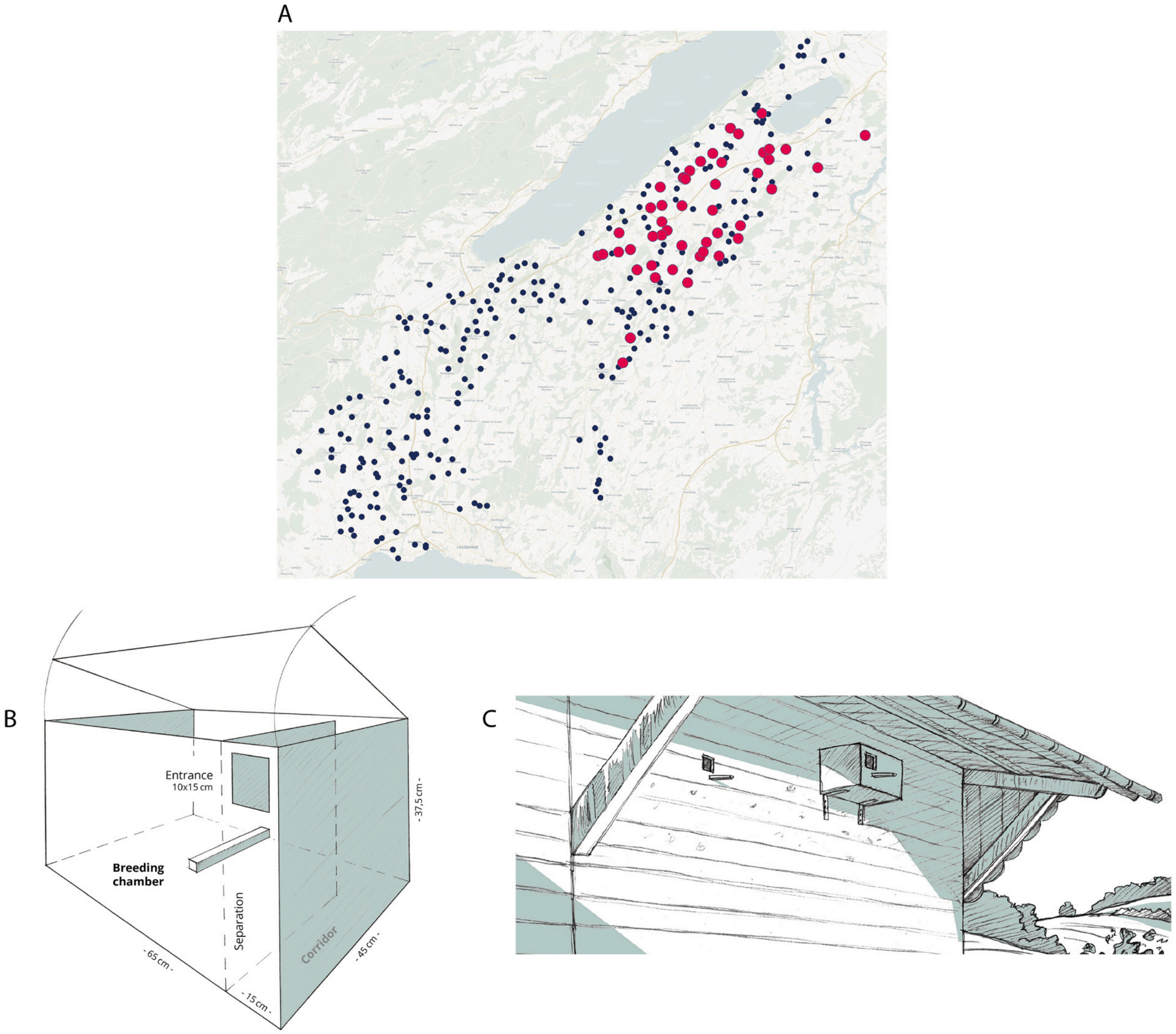

Fig. 1. Study area and nest box characteristics: (A) Map of the study area, with all nest boxes represented in black dots, and nest boxes selected for the present study in pink. (B) Scheme of a nest box, with internal dimensions. (C) Representation of the installation of two nest boxes, one inside the barn with the flying hole facing the outside (on the left) and one installed outside the barn (on the right). ©Laurent Willenegger for the artwork from Roulin (2020).

was present. Then, following Frey and colleagues' protocol (2011), breeding parameters were collected, including the clutch size, and the number of fledglings that survived until they were able to fly (over 55 days of age). Barn owls can produce several clutches per year. The first clutch represents the actual selection made by barn owl pairs throughout the winter. If this clutch fails or is abandoned, they can produce a replacement clutch. Finally, they can produce a second clutch after successfully completing the first one. For each clutch, the male and female identity was recorded, as well as the laying date, which is defined as the date when the first egg was laid, calculated according to the first-hatched nestling wing length, assuming a period of 32 days for incubation (Béziers and Roulin, 2016).

2.2. *Surrounding environment*

To estimate the impact of the surrounding environment on barn owl breeding parameters, we extracted three variables, namely the intensification of urban areas and agricultural fields and the density of surrounding breeding sites. Those three variables were extracted within a 1.5 km radius around each breeding site, corresponding to the rounded average home range size of barn owls (Almasi et al., 2013; Séchaud et al., 2021).

2.2.1. *Urban areas*

To determine the intensification of urban areas, we extracted the proportion of urban areas around each breeding site. We obtained aerial photos (50 cm resolution) of our study area from the Swiss Federal Office of Topography for the years 1993, 1998, 2007, and 2020. Using QGIS software 3.12.0 (QGIS Development Team, 2009), urban areas were manually delimited on the aerial photos. Any isolated building, city, or village was considered as urban area. The proportion of urban area in the 1.5 km radius was then extracted for each breeding site for the 4 years using the package *sf* in R (Pebesma, 2018). We then applied a linear interpolation between each year to estimate values for every year from 1993 to 2020 using the *approx* function in R.

2.2.2. *Agricultural fields*

The agricultural intensity level was determined by the number of fields surrounding each breeding site. A higher number of fields was supposed to be associated with increased field margins, which typically indicates less intensive agricultural use. Conversely, fewer fields suggest larger, more consolidated farming areas that are often more intensively cultivated. To extract the average number of fields around each breeding site, an algorithm able to detect field boundaries based on pixel greyscale values from the same aerial photos as urban areas was developed (Fig. S1). To do this, the pixel values of each photo were normalized to range from 0 to 255. A Gaussian blur with a sigma of 2 was applied to enhance between-fields contrast while minimizing within-fields variance (Canny, 1986; Wells, 1986). Forests, that were provided by the Swiss TLM3D catalogue (Swiss Topographic Landscape Model, n.d.) and urban areas, obtained as described in the above paragraph, were then assigned greyscale values of 0 to account only for agricultural fields. The number of fields was determined by analyzing the variance of greyscale values within a moving pane of 5 pixels on 6 transects of 1.5 km around the breeding site, at angles of 0°, 60°, 120°, 180°, 240°, and 300°, to capture a comprehensive and representative sample of the agricultural landscape surrounding each breeding site. To obtain an average number of fields around each breeding site, the mean of the 6 transects was extracted. This process was done for the years 1993, 1998, 2007, and 2020. Similar to urban area calculation, we then performed a linear interpolation using the *approx* function in R to estimate the mean number of fields for every year from 1993 to 2020.

2.2.3. *Surrounding breeding sites density*

To estimate whether the number of breeding sites surrounding each nest box could have an impact on barn owl breeding success and site occupancy, we extracted for each selected site the density of surrounding breeding sites in a radius of 1.5 km. As nest boxes were installed progressively since the 1990 s, we extracted this density every year, accounting for all available breeding sites, not only the ones selected in this study. This density metric was determined by summing the reciprocals of the distances to surrounding breeding sites, calculated as follows: $Density = \sum_{i=1}^{n} \frac{1}{d_i}$; where n is the number of surrounding breeding sites, and d_i represents the distance from the focal site to each breeding site. In our analysis, we differentiated the density measurements into two distinct categories for a more nuanced understanding. Firstly, we calculated the overall density of available breeding sites, encompassing all surrounding breeding sites, regardless of their occupancy status. This provided a broad view of the breeding site environment. Secondly, we focused specifically on barn owl breeding density, by calculating the density of only those breeding sites that were occupied, either before the laying date or simultaneously depending on the analysis.

2.2.4. *Climatic data*

Finally, as the analysis focuses on a 30-year period, it is essential to account for climatic variables. We thus extracted both daily temperature (minimal, maximal, mean) and average daily sum of precipitation data for every selected breeding site each year (MeteoSuisse, 2023).

2.3. *Statistical analyses*

The goal of this study is to understand what environmental factors impact barn owl site occupancy and breeding success. This was done through three sets of analyses, each one of them focusing on a specific response variable.

We first determined the factors influencing barn owl breeding parameters by focusing only on the first clutches of each breeding pair of the season. The reasons for this choice are threefold: second clutches typically occur near the first one or based on nest box availability rather than their specific characteristics, since many nest boxes are already occupied by pairs completing their first breeding attempt. Furthermore, the breeding success of second clutches is impacted by many confounding factors, such as the laying date of the first clutch or the size of the first clutch, and thus depends less on the environment (Béziers and Roulin, 2016). Finally, the probability of doing a second clutch depends on the parents' experience (Béziers and Roulin, 2016). For each first clutch, we extracted two breeding success variables: (1) the clutch size, defined as the number of eggs laid, and (2) the fledging success, corresponding to the proportion of eggs that hatched and survived until they were able to fly (over 55 days). For the clutch size, a linear mixed model (LMM) from the function *lmer* from package *lme4* (Bates et al., 2015) was used. Fledging success was modeled with a weighted generalized linear mixed model (GLMM) with a binomial family using the function *glmer* from the package *lme4* (Bates et al., 2015), with clutch size as weights. To disentangle between success and failure, we also run the model accounting only for successful clutches, i.e. clutches with at least one fledgling.

For the two global models, the predictors remained constant. The fixed factors included the surrounding environment (i.e. the number of fields interpolated, the proportion of urban areas interpolated, and the density of surrounding breeding sites), and nest box characteristics (i.e. the orientation, the height, the altitude, the number of nest boxes present at the site (one or two), whether the nest box was occupied the year before or not), as well as control variables, including climatic data (for the clutch size: average minimal daily temperatures and average daily sum of precipitations since 01st October the year preceding the laying date to the laying date; for the fledging success: number of extreme days (days above the average maximal temperature of the period) and average daily sum of precipitations from hatching date to 100 days after laying date), and laying date. We included the female ID, male ID, nest box ID, and year as random intercepts in the models to account for the non-independency of data and repeated measures. To understand the distinct impacts of the two variables of density of surrounding breeding sites, namely the density of available breeding sites and the density of breeding barn owls, we conducted our analysis in two separate runs. Each run included one of these variables, allowing us to isolate and compare their respective effects on the response variables.

We then determined the factors influencing site occupancy. A breeding site was defined as occupied in a given year if at least one barn owl's egg was found at the site, regardless of whether it was a first, replacement, or second clutch, and not occupied otherwise. In cases with double nest boxes at the same breeding site, occupancy was mutually exclusive; if one box was occupied in a given year, the other was not. To ensure analytical robustness and to avoid potential bias introduced by the mutual exclusion, we calculated occupancy based on the following criteria: if one of the nest boxes was occupied, that record was retained; if neither of the nest boxes was occupied, one record was randomly selected. This random selection was important to maintain the unbiased nature of the data. It is important to note that there were 12 instances where both nest boxes at the same site were simultaneously occupied within the same year, representing 0.8% of the data. In these rare cases, both records were retained to accurately reflect the site occupancy dynamics.

A GLMM with a binomial family was used using the function *glmer* from the package *lme4* (Bates et al., 2015). The predictors used were kept constant and aligned with those used in the first clutch level analyses (namely surrounding environment and nest box characteristics), except for the climatic data which were annual means (annual average minimal temperatures, annual average maximal temperatures, annual average precipitations). As the orientation and the height can vary between nest boxes at the same site, the nest box ID nested in the site ID was used as random intercepts in the models, in addition to the year for repeated measures. Again, we ran twice the model, once with the density of available breeding sites and once with the density of barn owl breeding.

All statistical analyses were conducted with R 4.2.1 (R Core Team, 2022), with RStudio (R. Team, 2022) as the graphic user interface. Models were fitted, checked for collinearity between predictors, and assumptions were verified using the *performance* package (Lüdecke et al., 2021) and by visually inspecting the residual diagnostic plots. The effects were considered significant when

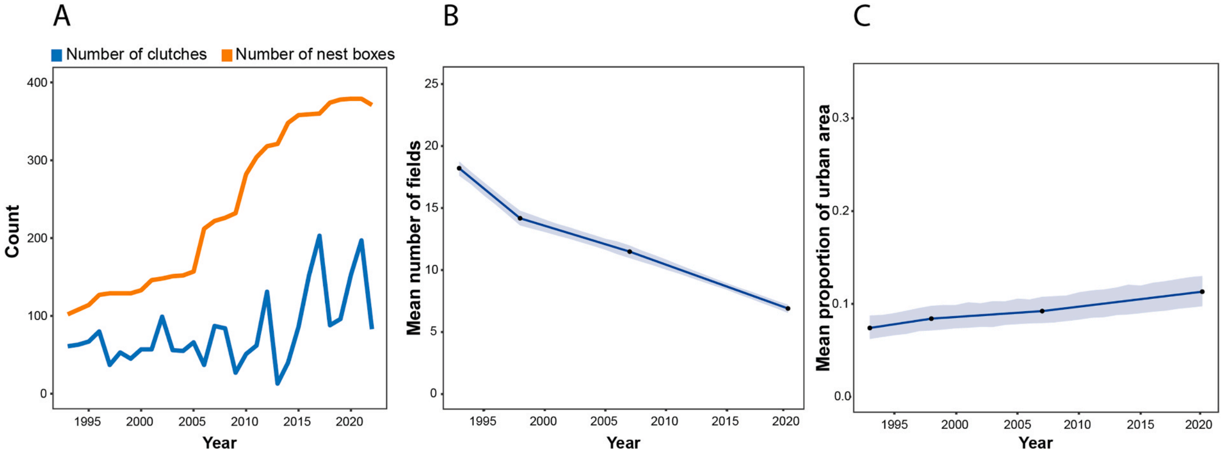

Fig. 2. Evolution of the number of nest boxes, clutches, agricultural fields, and proportion of urban areas over time: (A) Number of clutches (in blue) and number of nest boxes (in orange) from 1993 to 2020; (B) number of agricultural fields and (C) proportion of urban area within a radius of 1.5 km around the breeding sites from 1993 to 2020, with blue shaded area representing the 95% confidence interval of the estimated means (solid blue line), while the black dots represent the mean for the 4 years extracted.

their p-values were smaller than 0.05. Non-significant variables were removed step by step from the global model, making sure the Akaike information criterion (AIC) decreased when removed, to obtain the final model. If the AIC increased when a variable was removed, it was kept in the final model, even if not significant. In all models, linear predictors were z-scores standardized, involving a centering around a mean of zero and scaling to units of one standard deviation. This procedure allows direct comparison across variables. Spatial autocorrelation was assessed for each model by plotting residuals against spatial coordinates, and no evidence of spatial autocorrelation was detected across all models.

3. Results

Since 1993, a growing number of nest boxes have been installed, starting with 129 nest boxes in 1993 and ending up to 379 nest boxes in 2020 (Fig. 2A). As previously explained, for the present study, only nest boxes installed before 1993 and remained in place until 2021 were selected. The following analyses are then conducted on 72 nest boxes at 48 distinct breeding sites.

The habitat around the breeding sites changed substantially between 1993 and 2020. The number of agricultural fields decreased from 18 fields (*SD=2*) on average in 1993–6 fields (*SD=1*) in 2020, thus showing a 66.6% decrease (Fig. 2B). The proportion of urban areas, on the other hand, increased from 7.4% (*SD=5.3%*) in 1993–11.3% (*SD=7.3%*) in 2020, thus showing a 52.7% increase (Fig. 2C).

3.1. *Breeding parameters*

3.1.1. *Clutch size*

Regarding the clutch size, barn owls laid on average 5.8 eggs (*SD* = *1.6*). The density of surrounding breeding sites tended to negatively impact the clutch size, with clutches decreasing by approximately 0.15 eggs per unit increase in density (Table 1, Fig. 3A). However, this was not the case when accounting for the density of occupied breeding sites (*scaled breeding barn owl density: Est=-0.01, SE=0.14, t=-0.08)*. Moreover, clutch size was impacted by nest box characteristics: Clutches were larger by roughly one egg in nest box facing North compared to South or East (*North: mean=6.57, CI: 6.02–7.11; East: mean=5.74, CI: 5.46–6.03; South: mean=5.75, CI: 5.31–6.20;* Table 1, Fig. 3B). No significant difference was observed between East and South orientations. Altitude is also essential, with an estimated decrease of 0.25 eggs for every 100-meter increase in altitude (Table 1, Fig. 3C). Finally, each 10-day delay in laying date led to an increase in clutch size by around 0.07 eggs (Table 1). We found no evidence of an effect of the other variables tested, namely the proportion of urban area, the number of agricultural fields, the height of the nest box, the number of nest boxes at the site, whether the nest box was occupied the previous year or not, and the climatic data on the clutch size (Table 1).

3.1.2. *Fledging success*

The second model focused on the fledging success (Table 2). On average, 69% of eggs hatched and reached fledging (*SD=30%*). An

Table 1
Analyses for clutch size: Results of fitting linear mixed models to the clutch size, before and after step-selection. Nest box ID, year, female ID, and male ID were added as random intercepts. Significant terms ($p<0.05$) are written in bold. The model is based on 406 broods in 64 different nest boxes at 47 distinct sites between 1993 and 2020.

Parameter	Global model			Final model		
Variable	Estimates (SE)	t	p	Estimates (SE)	t	p
Clutch size						
(Intercept)	6.58 (0.33)	19.78	<0.001	6.57 (0.27)	24.56	<0.001
Scaled proportion of urban areas	-0.09 (0.10)	-0.84	0.404	Rd		
Scaled number of agri. fields	-0.09 (0.11)	-0.84	0.402	Rd		
Scaled density of surr. breeding sites	-0.15 (0.08)	-1.85	0.065	-0.15 (0.08)	-1.89	0.059
East orientation	-0.84 (0.27)	-3.15	0.002	-0.82 (0.26)	-3.16	0.002
South orientation	-0.79 (0.34)	-2.36	0.019	-0.81 (0.31)	-2.62	0.009
Scaled heigth [m]	-0.09 (0.09)	-1.00	0.317	Rd		
Scaled altitude	-0.19 (0.09)	-2.01	0.045	-0.16 (0.08)	-1.99	0.047
Nb of nest boxes at the site	0.07 (0.20)	0.33	0.744	Rd		
Occupied previous year	-0.10 (0.16)	-0.64	0.523	Rd		
Scaled minimum T° previous winter	0.02 (0.16)	0.11	0.912	Rd		
Scaled mean precip. previous winter	-0.08 (0.15)	-0.53	0.597	Rd		
Scaled laying date	0.20 (0.12)	1.64	0.102	0.21 (0.08)	2.72	0.007
Random Effects						
	σ^2		1.52	σ^2		1.54
	$\tau_{00\ \mathrm{F\_ring}}$		0.54	$\tau_{00\ \mathrm{F\_ring}}$		0.51
	$\tau_{00\ \mathrm{M\_ring}}$		0.06	$\tau_{00\ \mathrm{M\_ring}}$		0.05
	$\tau_{00\ \mathrm{nestid}}$		0.01	$\tau_{00\ \mathrm{nestid}}$		0.00
	$\tau_{00\ \mathrm{year}}$		0.29	$\tau_{00\ \mathrm{year}}$		0.28
Model fit						
	Observations		406	Observations		406
	Marginal R^2		0.065	Marginal R^2		0.088
	AIC		1529.1	AIC		1502.2

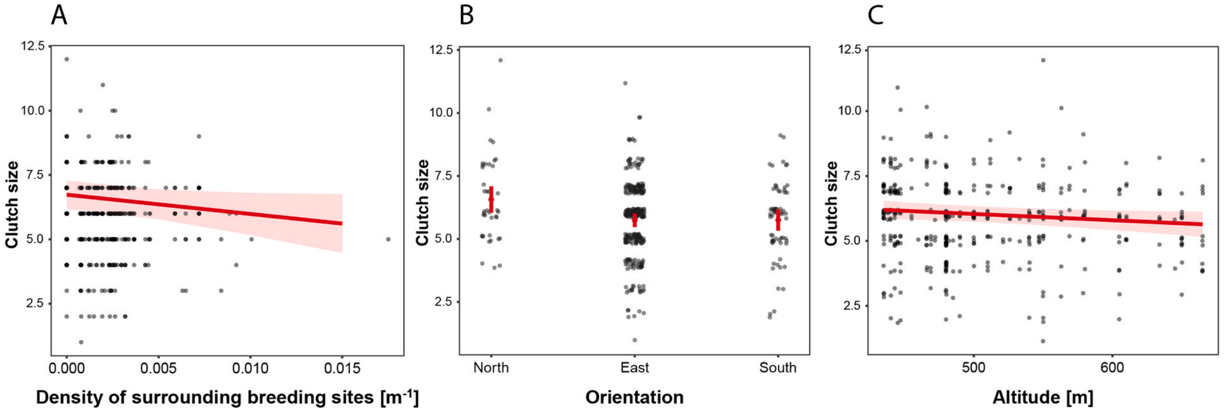

Fig. 3. Factors influencing clutch size: (A) the association between the density of surrounding breeding sites and clutch size, with the red shaded area representing the 95% confidence interval around the estimated means in solid red line, while the data are shown in black; (B) clutch size categorized by orientation, the data being shown in black, the red dots representing the predicted mean and the bars the 95% confidence intervals; (C) the correlation between altitude and clutch size, with the red shaded area representing the 95% confidence interval around the estimated means in solid red line, while the data are shown in black. The graphs present unscaled relationships for interpretative clarity, despite models utilizing scaled predictors.

increase in the proportion of urban areas was positively associated with fledging success, with fledging success exceeding 75% in nest boxes surrounded by at least 20% of urban area (Fig. 4A). This result was consistent when accounting only for successful clutches (*scaled proportion of urban areas: Est=1.14, SE=0.07, t=2.04, p=0.042)*. The number of agricultural fields was also positively associated with fledging success, as fledging success was higher in nest boxes surrounded by more agricultural fields (Fig. 4B). However, this result was not consistent when accounting only for successful clutches (*scaled number of fields: Est=1.06, SE=0.09, t=0.66, p=0.51*). Nest boxes occupied the previous year tended to have 6% lower fledging success than non-occupied nest boxes, and this was consistent when accounting only for successful clutches (*occupied previous year: Est=0.77, SE=0.1, t=-1.98, p=0.047*). Mean precipitations during the fledgling period decreased fledging success, which dropped below 75% when precipitation exceeded 3 mm per day on average (Fig. 4*C)*. This result was consistent when accounting only for successful clutches (*scaled mean precipitations: Est=0.84, SE=0.06, t=-2.3, p=0.021*). Finally, successful clutches laid later in the season had decreased success odds, falling below 75% of success for clutches

Table 2

Analyses for fledging success: Results of fitting weighted generalized mixed model with binomial family to the fledging success, before and after step-selection. Nest box ID, year, female ID, and male ID were added as random intercepts. Significant terms (p<0.05) are written in bold. The model is based on 406 broods in 64 different nest boxes at 47 distinct sites between 1993 and 2020.

Parameter	Global model			Final model		
Variable	Estimates (SE)	t	p	Estimates (SE)	t	p
Odds ratio of fledging success						
(Intercept)	5.06 (1.65)	4.98	<0.001	3.09 (0.43)	8.10	<0.001
Scaled proportion of urban areas	1.27 (0.14)	2.23	0.026	1.21 (0.10)	2.21	0.027
Scaled number of agri. fields	1.27 (0.13)	2.37	0.018	1.27 (0.12)	2.45	0.014
Scaled density of surr. breeding sites	1.12 (0.10)	1.29	0.196	Rd		
East orientation	0.69 (0.19)	-1.36	0.175	Rd		
South orientation	0.68 (0.23)	-1.13	0.259	Rd		
Scaled heigth [m]	1.07 (0.10)	0.76	0.449	Rd		
Scaled altitude	1.10 (0.12)	0.92	0.358	Rd		
Nb of nest boxes at the site	0.79 (0.17)	-1.13	0.258	Rd		
Occupied previous year	0.75 (0.12)	-1.82	0.069	0.74 (0.12)	-1.92	0.054
Scaled number of extreme days	0.98 (0.08)	-0.23	0.822	Rd		
Scaled mean precipitations	0.82 (0.07)	-2.23	0.026	0.82 (0.07)	-2.29	0.022
Scaled laying date	0.86 (0.07)	-1.94	0.053	0.90 (0.06)	-1.53	0.127
Random Effects						
	σ^2		3.29	σ^2		3.29
	$\tau_{00\ F\_ring}$		1.03	$\tau_{00\ F\_ring}$		1.05
	$\tau_{00\ M\_ring}$		0.30	$\tau_{00\ M\_ring}$		0.34
	$\tau_{00\ nestid}$		0.00	$\tau_{00\ nestid}$		0.00
	$\tau_{00\ year}$		0.09	$\tau_{00\ year}$		0.08
Model fit						
	Observations		406	Observations		406
	Marginal R^2		0.031	Marginal R^2		0.024
	AIC		1432.6	AIC		1424.0

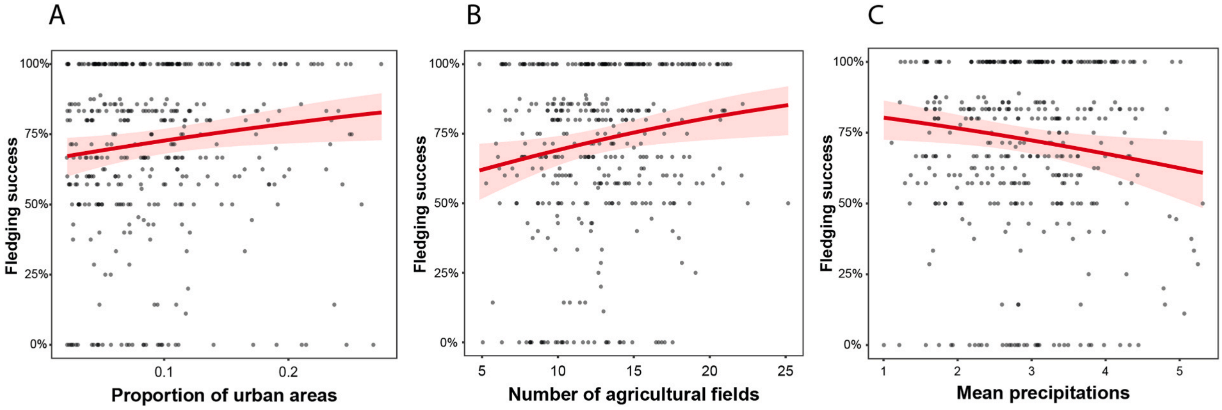

Fig. 4. Factors influencing fledging success: the correlation between fledging success and (A) the proportion of urban areas; (B) the number of agricultural fields; and (C) the mean precipitations. The red shaded area represents the 95% confidence interval around the estimated means in solid red line, while the data are shown in black. The graphs present unscaled relationships for interpretative clarity, despite models utilizing scaled predictors.

laid after late April (*scaled laying date: Est=0.83, SE=0.05, t=-3.04, p=0.002)*. This result was not significant when accounting for all clutches, failed one included (Table 2). We found no evidence of an effect of the other variables tested, namely the density of surrounding breeding sites, the nest box characteristics, and the temperature on fledging success.

3.2. *Annual breeding site occupancy*

On average, the annual breeding site occupancy was 25% (*SD=43%*). Our GLMM reveals that the proportion of urban areas is essential, exceeding 50% of occupancy in sites surrounded by more than 20% of urban area (Fig. 5A). Moreover, the number of agricultural fields tended to positively impact the annual occupancy, with breeding sites surrounded by 20 fields on average being occupied more than 50% of the years (Fig. 5B). Conversely, an increase in the density of surrounding breeding sites was associated with a 28% decrease in the odds of occupancy (Fig. 5C). This was not the case when accounting for the density of occupied breeding sites (*scaled breeding barn owl density: Est=-0.21, SE=0.15, t=-1.35*). Nest box height above ground was positively associated with occupancy, with a 21% increase in odds of occupancy per meter increase in height. Finally, sites occupied the previous year showed nearly four times the likelihood of being occupied again compared to sites not occupied the previous year. We did not find any evidence for an effect of other variables tested, namely the orientation, the altitude, and the climatic data (Table 3).

4. Discussion

By analyzing more than 30 years of barn owl population monitoring data, we assessed how changes in land use through 30 years

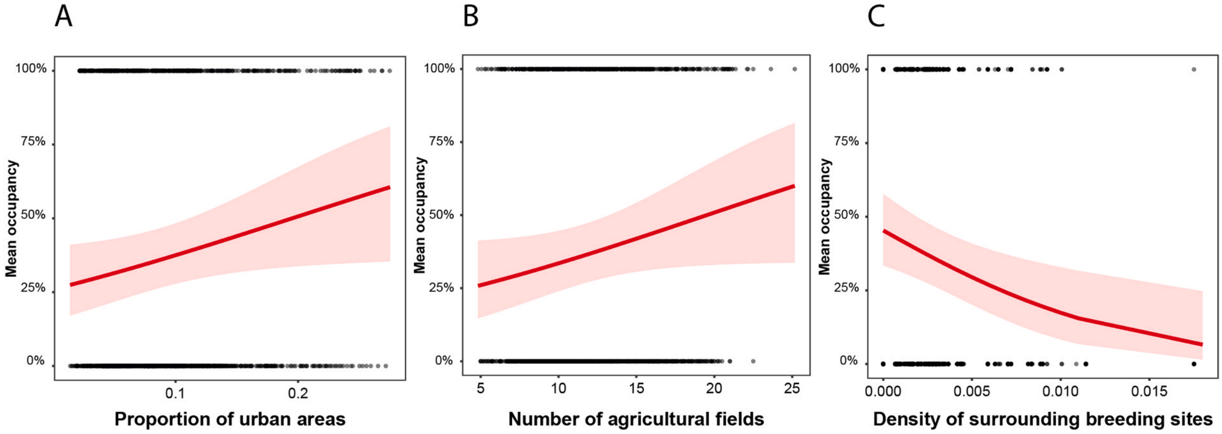

Fig. 5. Factors influencing the annual site occupancy: the correlations between annual site occupancy and (A) the proportion of urban area, (B) the number of agricultural fields, and (C) the density of surrounding breeding sites. Red shaded area represents the 95% confidence interval around the estimated means in solid red line, while the data are shown in black. The graphs present unscaled relationships for interpretative clarity, despite models utilizing scaled predictors.

influenced barn owl site occupancy and reproductive success. Overall, our findings highlight the important role of agricultural landscapes in supporting barn owls' reproductive success, emphasizing the need to maintain the complexity and diversity of agricultural fields. Moreover, various nest box characteristics as well as the density of surrounding breeding sites appear as important and should be considered when installing new nest boxes.

In particular, the number of agricultural fields surrounding barn owl nest boxes appears to influence both fledging success and, to a smaller extent, annual site occupancy. This increase in breeding success with increasing number of agricultural fields could be attributed to more diverse and heterogeneous landscapes, with a lot of field margin structures, where prey availability was found to be high (Bühler et al., 2023). Enhanced breeding success in such environments not only benefits the barn owl population but also might help limit small mammal populations in these agricultural areas, as barn owls are a tool in biological pest control (Labuschagne et al., 2016, George and Johnson, 2021). This highlights the importance of habitat diversity within barn owl home ranges. This was shown in our population in a previous study where we looked at a shorter period (5 years) (Almasi et al., 2015) and found that breeding performances were higher in structurally more diverse landscapes. These results thus should encourage farmers to consider practices that promote landscape heterogeneity, such as maintaining or increasing the number of smaller fields, to help the conservation of barn owl populations. It is important to acknowledge that the measure of field numbers as a proxy for agricultural intensity assumes that the total area under cultivation remains relatively stable. However, this may not always be the case. An increase in the number of fields could also result from urban expansion or the subdivision of larger fields, which might have differing ecological impacts. It should be noted that our study did not measure the total agricultural area within the observed landscapes for methodological constraints. This represents a limitation in interpreting the effects of agricultural field number changes on barn owl habitat quality and use. Future research could benefit from incorporating detailed land cover data to assess not only the number but also the total area of agricultural fields. This would allow for a more precise assessment of how changes in agricultural practices influence barn owl populations and other aspects of biodiversity.

The influence of urban areas on barn owl breeding success and nest box occupancy appears to be negligible in our study area, and even positive for the fledging success and the mean occupancy. Given barn owls' ability to adapt to and exploit human settlement for nesting, those results are not surprising and are in line with those from Frey et al. (2011), who reported no significant influence of environmental features on barn owl's breeding parameters from 1987 to 2009. However, Frey and colleagues assumed that the habitat did not change throughout those years. Our analysis shows that, even when accounting for the change, the results are consistent. Hindmarch et al. (2012) also found no significant impact of urban cover on nest box occupancy in Canada, though their study did not explore how urban cover might affect breeding success. However, the negligible effects of urban areas on barn owl breeding success observed in the present study should not be interpreted as an endorsement for the expansion of urban areas. Almasi et al. (2015) demonstrated that nestlings raised in intensively cultivated areas or frequently disturbed areas have higher baseline corticosterone levels, leading to a negative effect on nestling fitness. This suggests that while urban areas may correlate positively with fledging success and site occupancy, anthropogenic effects overall may not be beneficial to barn owl populations in the long-term. Additionally, the characteristics of urban areas must be considered. Larger cities with limited green areas likely exert more negative effects, whereas

Table 3
Analyses for annual site occupancy: Results of fitting generalized linear models with binomial family to the mean site occupancy. Nest box ID nested in the site ID, and year were added as random intercepts. Significant terms ($p<0.05$) are written in bold. The model is based on 1406 occupancy data in 72 different nest boxes at 48 distinct sites between 1993 and 2020.

Parameter	Global model			Final model		
Variable	Estimates (SE)	t	p	Estimates (SE)	t	p
Odds ratio of mean occupancy						
(Intercept)	0.17 (0.09)	-3.31	0.001	0.28 (0.06)	-5.60	<0.001
Scaled proportion of urban areas	1.28 (0.20)	1.55	0.122	1.34 (0.18)	2.09	0.036
Scaled number of agri. fields	1.28 (0.19)	1.61	0.106	1.28 (0.18)	1.76	0.079
Scaled density of surr. breeding sites	0.72 (0.08)	-2.81	0.005	0.72 (0.09)	-2.78	0.005
East orientation	1.28 (0.60)	0.52	0.603	Rd		
South orientation	1.23 (0.72)	0.36	0.722	Rd		
Scaled heigth [m]	1.31 (0.21)	1.71	0.088	1.43 (0.22)	2.36	0.018
Scaled altitude	0.98 (0.16)	-0.13	0.895	Rd		
Number of nest boxes at the site	1.59 (0.51)	1.43	0.154	Rd		
Occupied year before	4.45 (0.76)	8.74	<0.001	4.37 (0.74)	8.67	<0.001
Scaled mean minimal T°	0.62 (0.24)	-1.26	0.208	Rd		
Scaled mean maximal T°	1.51 (0.54)	1.16	0.247	Rd		
Scaled mean precipitations	1.59 (0.45)	1.62	0.106	Rd		
Random Effects						
	σ^2		3.29	σ^2		3.29
	$\tau_{00\ \text{nest\_letter:siteid}}$		0.15	$\tau_{00\ \text{nest\_letter:siteid}}$		0.16
	$\tau_{00\ \text{siteid}}$		0.60	$\tau_{00\ \text{siteid}}$		0.66
	$\tau_{00\ \text{year}}$		0.69	$\tau_{00\ \text{year}}$		0.78
Model fit						
	Observations		1406	Observations		1406
	Marginal R^2		0.178	Marginal R^2		0.156
	AIC		1473.8	AIC		1464.6

smaller villages rich in green areas may have positive effects, such as increasing prey availability. In our study, the maximum urban area proportion did not exceed 30%, comprising predominantly villages with many farms and houses with gardens, indicating that barn owls still rely on natural or semi-natural environments for their survival.

The influence of the density of surrounding breeding sites emerges as an important factor, having a negative effect on clutch size and site occupancy. Notably, an increase in the density of surrounding breeding sites goes with a decrease in site occupancy. As this is not linked to whether the surrounding nest boxes are themselves occupied, this could be simply due to a higher number of nesting possibilities, thus decreasing the likelihood of sites to be occupied, and not being linked to territoriality or competition for nesting sites. However, the effect of competition is more evident later within the breeding cycle, at egg laying, as nest boxes with higher density of surrounding sites produced fewer eggs. Barn owls may adjust their breeding strategies to resource constraints due to higher population densities. Furthermore, it could also reflect selective behavior by breeding individuals: high-quality individuals, who are more experienced and better at securing optimal resources, might select the best nest sites with lower density of surrounding sites. Consequently, less experienced individuals are left with poorer-quality breeding sites in denser areas, resulting in smaller clutches, as described in the density limiting hypothesis from Fretwell and Lucas (1969).

We also conducted a comprehensive analysis of various nest box characteristics. The orientation had an effect on the clutch size, with larger clutches being laid in nest boxes facing North. This goes in line with the study of Goodenough and Stallwood (2012), who showed that orientation has an impact on the microbial community, which led to differences in Great Tits (*Parus major*) offspring quality, with nest boxes facing North and North-East having lower fungal loads than those facing South and South-West. However, it goes in contradiction to the findings of Butler et al. (2009), who found that, despite significant differences in temperatures and humidity among orientations, the breeding success of American kestrels (*Falco sparverius*) was not impacted. In our case, the sample may exhibit a bias due to the majority of nest boxes being placed in tobacco barns, which are mainly orientated towards the northeast. For installation purposes, the majority of nest boxes follow this orientation, thus possibly explaining the influence of this specific orientation. The height at which the nest box is placed in the barn also impacted the mean site occupancy, with nest boxes placed higher being more likely to be occupied. This could be explained either by easier access for owls in flight, fewer disturbances from humans, or lower predation risk inside the nest box. It is important to note that the main predator in this context is the beech marten (*Martes foina*), which is known to inhabit barns (Roulin, 2020). Although higher placements of nest boxes are generally recommended to deter such predators, we have not empirically tested the correlation between nest box height and predation risk by beech martens, which is anyway relatively rare in our population (personal observation). Therefore, any assumptions regarding the effectiveness of elevated nest boxes in reducing predation risks remain speculative and warrant further investigation. Additionally, the altitude above sea level at which the nest box is placed had a negative effect on clutch size. This result goes in line with barn owls' preference to avoid high altitudes driven by their vulnerability to cold temperatures (Massemin and Handrich, 1997; Thouzeau et al., 1999; Altwegg et al., 2006). However, as the majority of our nest boxes are placed below 600 m above sea level, there is a potential bias in the dataset that should be kept in mind.

Finally, intrinsic clutches factors appear as important predictors of breeding success. The laying date positively impacted clutch size, with late-season clutches being larger, but with lower fledging success for successful clutches, which was already found in previous studies (Roulin, 2002, Chausson et al., 2014). The observed decline in fledging success may be due to lower prey availability later in the season, deteriorating weather conditions, or higher intra-specific competition as more pairs are simultaneously breeding. It is important to note that the data analyzed focused only first clutches, with the breeding season ending by the end of July for the latest. Whether sites were occupied the year before positively impacts site occupancy, as sites that were occupied in the preceding year exhibit a four times higher likelihood of being occupied again. This effect could suggest either site fidelity by adult barn owls, who will prefer to return to the same site, especially if the same pair stayed together as shown by Dreiss and Roulin (2014), or social cues among adult barn owls, who might perceive previously occupied sites as favorable. However, fledging success was observed to be lower in previously occupied nest boxes. As part of our study protocol, the research team does not intervene or clean the nest boxes between breeding seasons. This may lead to the accumulation of organic debris such as pellets and prey remains, creating suitable conditions for the proliferation of ectoparasites, as well as potentially harmful bacteria and viruses. Studies have shown that nests can serve as major source of microorganisms (Goodenough et al., 2017; van Veelen et al., 2017), which could adversely impact fledglings' microbiota, potentially explaining the observed decrease in fledging success.

Interestingly, we could not find any correlation between temperature data and breeding success. This outcome could be particularly encouraging in the context of global climatic changes and rising temperatures. However, a more thorough investigation specifically focusing on climate change is necessary to accurately determine its impact on barn owl breeding success. Given the species' large geographic distribution range (Roulin, 2020), barn owls may possess a high flexibility to a wide range of temperatures and precipitations. Nevertheless, we found a negative correlation between mean precipitations and fledging success. This goes in line with the results of Chausson et al. (2014), who observed a negative effect of precipitation on fledglings' body mass. Increased precipitations can negatively affect prey activity, potentially diminishing barn owl hunting efficiency (Roulin, 2020; Taylor, 1994), leading to lower feeding rates and consequently reduced fledging success.

The overall findings of this study suggest that barn owls can adapt to a changing environment but are still influenced by the agricultural landscape surrounding their nest boxes, as well as the characteristics of the nest box and densities of surrounding breeding sites. This adaptability suggests that the species possesses remarkable flexibility and resilience, which might explain how *Tytonidae* has become one of the most widespread and cosmopolitan families among birds in the world (Roulin, 2020). The barn owl's ability to thrive in diverse environments contributes to its global distribution and success. However, it is important to highlight that, on the whole, the statistical models exhibited notably low R-squared values despite a good fit to the data, indicating that the predictors selected explain a minimal amount of variance. This observation could highlight some highly influential factors that were disregarded in our selection of predictors. Regarding agricultural landscapes, even though field size is known to be negatively linked to biodiversity (Herzog et al., 2012; Fahrig et al., 2015; Sirami et al., 2019), other factors such as the type of agricultural crops were not included in our analysis but should be considered. It might be possible that the type of fields plays a more significant role in influencing barn owls' hunting behaviors (Séchaud et al., 2021; Bühler et al., 2023) and, consequently, their fitness. It would thus be interesting to investigate the evolution of the types of crops and their impact on barn owl breeding success and nest box occupancy, to estimate their efficiency. Such an analysis was not feasible with the greyscale aerial photography used in this study, but incorporating this dimension would deeply enhance our understanding of environmental influences on barn owl breeding success.

5. Conclusion

In conclusion, our study highlights the important role of agricultural fields in the reproductive success of barn owls in the long term. Moreover, it emphasizes the importance of proper installation of nest boxes, a critical tool in supporting barn owl populations. Finally, this research highlights the adaptive capacity of barn owls, offering a positive perspective on their resilience. By understanding the factors that influence barn owl site occupancy and breeding success, especially in agricultural landscapes, our study makes an important contribution to conservation efforts. This is essential, considering the potential role raptors can play in stabilizing ecological balance in agricultural landscapes, as they act as biological pest control agents, a concept reviewed by Sergio et al. (2008).

CRediT authorship contribution statement

Estelle Milliet: Writing – review & editing, Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kim Schalcher:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Anna Grangier-Bijou:** Writing – review & editing, Data curation, Conceptualization. **Bettina Almasi:** Writing – review & editing, Resources. **Fabrizio Butera:** Writing – review & editing, Supervision, Conceptualization. **Alexandre Roulin:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgment

This study was financially supported by the Swiss National Science Foundation (grants no. 310030_200321). We thank all the people that worked in the field over the last 30 years for collecting the data, and all members of the Barn Owl Research Group for their help and feedback on this study. Finally, many thanks to two anonymous reviewers and the Editor for their time, effort, and constructive comments.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2024.e02988.

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