Check for updates

Received: 23 April 2024 | Revised: 2 September 2024 | Accepted: 6 September 2024

DOI: 10.1002/jwmg.22678

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

RESEARCH ARTICLE

Barn owl site occupancy and breeding success in relation to land use and nest box characteristics

Estelle Milliet[1] | **Kim Schalcher**[1] | **Anna Grangier-Bijou**[1] | **Bettina Almasi**[2] | **Fabrizio Butera**[3] | **Alexandre Roulin**[1]

[1]Department of Ecology and Evolution, University of Lausanne, Lausanne, CH 1015, Switzerland

[2]Swiss Ornithological Institute, Seerose 1, Sempach, CH 6204, Switzerland

[3]Institute of Psychology, University of Lausanne, Lausanne, CH 1015, Switzerland

Correspondence
Estelle Milliet, Department of Ecology and Evolution, Biophore Building, Quartier UNIL-Sorge, CH – 1015 Lausanne, Switzerland.
Email: estelle.milliet@unil.ch

Funding information
Schweizerischer Nationalfonds zur Förderung der Wissenschaftlichen Forschung, Grant/Award Number: 310030_200321

Abstract

Agricultural landscapes play a crucial role in enhancing biodiversity because of their widespread presence over the Earth and their ability to encompass diverse ecosystems. Recognizing this, numerous governments are incentivizing farmers through direct payments to adopt sustainable practices, such as managing extensive pastures and meadows, planting wildflowers, or establishing hedgerows. However, the benefit of such sustainable practices on vertebrate species is not well understood. From 2018 to 2020, we investigated nest occupancy, fledging success, and clutch size of a Swiss population of barn owls (*Tyto alba*) with respect to nest box characteristics and the presence of extensive agriculture and urbanization in areas surrounding nest boxes. Our results revealed that extensively used pastures were positively associated with site occupancy but negatively associated with clutch size. The proportion of urban areas was negatively related to both site occupancy and clutch size. The altitude of the nest box location was negatively correlated with occupancy, and the number of nest boxes placed at the same site (either 1 or 2) was positively correlated with site occupancy. Moreover, clutch size, but not fledging success, was larger in nest boxes placed outside barns than in nest boxes placed

Fabrizio Butera and Alexandre Roulin jointly supervised the work.

inside barns. Based on these findings, we recommend installing nest boxes at locations <700 m in altitude and in pairs on the same barn, incorporating biodiversity promotion areas into agricultural landscapes, and avoiding dense urban areas in favor of rural zones with lower urban density. Understanding the nuanced relationships between nest box characteristics, environmental factors, and breeding success provides valuable insights for optimizing artificial nesting sites and enhancing the overall reproductive success of barn owls.

KEYWORDS

artificial nesting site, barn owl fitness, Biodiversity Promotion Areas, nest box installation, *Tyto alba*, urbanization

Agricultural fields dominate landscapes throughout the world (Tilman et al. 2001). While intensive agricultural practices cause several adverse effects on the environment, including increased agrochemical use and soil degradation leading to a strong decline in biodiversity (Stoate et al. 2009), extensive agricultural fields also offer notable positive contributions and ecosystem services. Extensively managed fields can enhance soil fertility, regulate water, or increase carbon sequestration (Swinton et al. 2007, Wittwer et al. 2021) and have high potential for conservation measures (Tscharntke et al. 2005). Farmers thus play an essential role as practitioners and key actors in biodiversity conservation when adopting sustainable agriculture techniques. In addition to financial incentives from subsidies to implement such measures, farmers have an intrinsic motivation that is grounded in their reliance on natural resources and climatic conditions for agricultural production (Wilson and Hart 2000, Burton and Wilson 2006, Lastra-Bravo et al. 2015, McGuire et al. 2015). This makes them uniquely situated to appreciate the benefits of biodiversity conservation and they are often willing to invest in long-term sustainable practices. As we confront the pressing challenges of climate change and biodiversity loss, the role of farmers in safeguarding our ecosystems becomes increasingly vital.

To prevent loss of biodiversity linked to intensive farming practices, governments, conservationists, and agricultural experts have implemented several solutions. Some techniques are highly efficient, such as agroforestry, crop rotation, cover cropping, and integrated pest management (Altieri 1999, Tscharntke et al. 2011, Elhakeem et al. 2019, Martin et al. 2020). In Europe, agri-environmental schemes implemented in 1985 (European Union Regulation 797/85) consist of paying subsidies to farmers committed to environmentally friendly practices. These practices include planting wildflowers and hedgerows and extensively managing meadows and pastures. Their effectiveness on the populations of plants, insects, and small mammals is well documented (Kleijn et al. 2006, Knop et al. 2006, Zingg et al. 2019), with increased biodiversity for such taxa in those areas. However, the impact on larger vertebrates remains understudied despite these taxa having a strong impact on biodiversity and serving as keystone, umbrella, sentinel, flagship, or indicator species (Sergio et al. 2008). Some prior work has explored the responses of songbirds to these areas (Princé and Jiguet 2013, McHugh et al. 2017, Redhead et al. 2018), but further research is needed on larger species such as raptors. Understanding the efficacy of such measures is essential for informing farmers about the practices that best support wildlife conservation in agricultural landscapes.

In addition to general practices aimed at improving conditions for all biodiversity, farmers can also implement targeted conservation measures. One of the main causes of the decrease in farmland bird population is the loss of structural resources for nesting due to agriculture intensification (Newton 2004). Nest boxes provide a great targeted conservation measure, providing nesting locations to combat the loss of tall structures in farmlands. Nest boxes are particularly beneficial to birds that use hollows, including owls (Marti et al. 1979, Meyrom et al. 2009, Gottschalk et al. 2011), kestrels (Hamerstrom et al. 1973), or other raptors (Gehlbach 1994, Johnson 1994, Eschenbauch et al. 2009, Arlettaz et al. 2010, Gottschalk et al. 2011), especially those that rely on agricultural fields as hunting grounds (Perrins and Snow 1998, Roulin 2020). Raptors can help maintain biodiversity in agroecosystems, as they serve as biological pest-control agents (Meyrom et al. 2009, Donázar et al. 2016, Paz-Luna et al. 2020, Montoya et al. 2021). However, nest boxes should be placed with care to maximize their benefit. The surrounding landscape, such as roads (Mulholland et al. 2018) and buildings (Partecke et al. 2006, Almasi et al. 2015), can affect species survival and reproduction rates. Nest box density can also increase inter- and intra-specific competition (Serrano-Davies et al. 2017). Finally, nest box placement (i.e., location, height, and orientation) is essential, as it can affect site occupancy frequency (Goodenough et al. 2008, Wendt and Johnson 2017). It is therefore important to evaluate the factors that could potentially influence the nest box selection process, occupancy, and the subsequent breeding performances of birds to optimize their installation in the best habitat meeting the birds' requirements.

For raptors in agricultural lands, farm buildings are often the most adequate locations for nest box installation because of their proximity to suitable hunting grounds. The barn owl (*Tyto alba*) is a perfect case study because it breeds on agricultural lands where natural nesting cavities are usually scarce, and they nest in artificial nest boxes without problems. Barn owls are efficient predators (Schalcher et al. 2023) that hunt small mammals in open and semi-open areas (Perrins and Snow 1998) and can influence small-mammal populations (Donàzar et al. 2016, Paz-Luna et al. 2020, Montoya et al. 2021), making them a valuable tool for biological pest control. On the Swiss Plateau, more than 300 nest boxes have been installed since the 1990s on local farms by scientists, with the agreement and collaboration of farmers. This scientific project has helped to stabilize the local population of this species (Knaus et al. 2018), a notable achievement given its classification as nearly threatened in Switzerland according to the Swiss Red List (Knaus et al. 2021).

In a previous study (Milliet et al. 2024), we explored the breeding success and site occupancy of barn owls for 3 decades, from 1993 to 2020, focusing on the number of agricultural fields and the proportion of urban areas surrounding the nest boxes. While this long-term analysis provided valuable insights into general trends and patterns, it highlighted the need for a more nuanced examination of the environmental factors influencing barn owl breeding success. Consequently, we aimed to deepen this analysis with the use of more precise and detailed environmental data available from 2018 onwards. Using data from 2018–2020, we investigated factors affecting nest occupancy, fledging success, and clutch size of barn owls in Switzerland. Building on our foundational work, we specifically focused on factors that farmers can consider when installing a nest box, which are categorized into 3 main domains: the surrounding agricultural and urban environment, the nest box characteristics, and the surrounding breeding site density. We expected barn owls to select nest boxes with a higher proportion of low-intensity agricultural practices in the surroundings, such as extensively used pastures, meadows, or wildflower strips, as such areas are known to provide higher prey densities (Arlettaz et al. 2010). Regarding urban areas, the effects in the literature do not reach a clear consensus. Frey et al. (2011) reported no association between barn owl breeding success and urban areas, while Almasi et al. (2015) observed a negative effect on nestling physiology and body condition but a positive effect on the number of fledglings. Given barn owls are highly adaptable to human-influenced landscapes (Hindmarch and Elliott 2015), we did not have clear expectations about the effect of urban areas on barn owl breeding success. Instead, we further investigated these relationships. Finally, regarding surrounding breeding site density, we expected barn owls to select nest boxes with fewer breeding sites in their surroundings, as found by Meyrom et al. (2009).

STUDY AREA

The present study was carried out from 2018 to 2020 and focused on a wild population of barn owls residing in nest boxes on the Swiss Plateau. This region is characterized by 2 ancient marshy plains, the Broye and Orbe plains, which are now dominated by agricultural fields and urban areas, representing the preferred habitat of the barn owl

(Bunn et al. 1982, Séchaud et al. 2021). The topography of the area is predominantly flat, situated between the Jura Mountains and the Alps. The region experiences a temperate climate with cool winters and mild summers. Average temperatures range from 0°C in winter to approximately 19°C in summer. The area receives an average annual precipitation of around 1,000 mm, with most rainfall occurring during the warmer months. Vegetation in the region is primarily composed of agricultural fields interspersed with hedgerows and forests.

METHODS

Since the 1990s, 379 nest boxes have been installed that are regularly monitored between March and August every year. When discovering a clutch, a standardized protocol of nest visits was systematically executed to record various breeding parameters (Frey et al. 2011), in particular laying date, clutch size, and number of fledglings, and the identification of the parents by their unique ring numbers. Barn owls can produce several clutches per breeding season. During the winter, barn owl pairs select their nest box for their first clutch. In case of failure or abandonment of this first clutch, a replacement clutch may be produced. Following the completion of the first clutch, barn owl pairs can produce a second clutch.

Nest boxes are placed on barn walls, either inside with the entrance hole facing the outside or directly on an outside wall. Depending on the barn, they can be placed in different orientations at different heights, and sometimes 2 nest boxes are placed on the same barn. Each barn with 1 or 2 nest boxes is considered a breeding site in the present study. To account for these differences, we included as covariates in the models the following characteristics of each nest box, specifically the orientation (direction in which the nest box entrance faced, specifically categorized as north, east, south, west), the height above the ground in meters, the location (inside or outside barns), the altitude above sea level where the nest box was located, the number of nest boxes present in or on the same barn (either 1 or 2), and the nest box age in years.

Our sampling protocol was designed to ensure a high probability of detecting barn owl occupancy and breeding success. We monitored all nest boxes monthly from February to September each year, making it nearly impossible to miss a clutch in a nest box. This intensive and consistent monitoring schedule allowed us to achieve near-perfect detection.

Habitat characteristics

The goal of this study was to estimate the influence of the surrounding environment on barn owl breeding success and site occupancy. Therefore, we focused on 3 main habitat factors, namely urban areas, agricultural landscapes, and surrounding breeding site density within the barn owl's home range (Almasi et al. 2015, Séchaud et al. 2021). We extracted all variables within a 1.5-km radius around each breeding site (7 km^2) for each year between 2018 and 2020. This corresponds to the mean home range size of barn owls (Almasi et al. 2015, Séchaud et al. 2021).

To characterize urban areas, we used the Swiss Topographic Landscape Model (TLM3D) catalog of the Swiss Federal Office of Topography (2023). For each breeding site, we extracted 3 variables: the proportion of roads, the proportion of urban areas, and the density of urban areas. To quantify the proportion of roads around each site, we extracted all roads in the 1.5-km radius. To account for different road types, we applied type-specific buffers to each road segment (Table S1, available in Supporting Information). We then calculated the resulting area of roads and divided it by the area of the 1.5-km radius (7 km^2) to get the proportion of roads. For the proportion of urban areas, we extracted each building within the 1.5-km radius around each site and applied a buffer of 50 m around each building. We then merged the buffered areas to form a combined urban area. We calculated the area of this combined urban area and then divided it by the area of the 1.5-km radius (7 km^2) to determine the proportion of urban areas. Finally, to estimate the density of urban area, we summed the area of each building without the 50-m buffer and divided it by the urban area. This calculation yielded the density of urbanized space, providing a metric to understand the concentration of built structures within the defined urban areas surrounding each breeding site.

For agricultural landscapes, we used data provided by the Direction Générale de l'Agriculture, de la Viticulture et des Affaires Vétérinaires of the states of Vaud and Fribourg, which provided the field type of each parcel owned by a farmer. We focused particularly on extensive areas, which are agricultural fields for which farmers receive direct payments from the Swiss Confederation. These fields were selected specifically because their implementation ensures they would be managed as biodiversity promotion areas (AGRIDEA 2018). For each breeding site, we extracted the area of all agricultural fields around each breeding site in the 1.5-km radius, including both cultivated fields and permanent fields. Then, based on this area, we calculated the proportion of biodiversity promotion areas according to 4 categories: extensively used pastures, extensively used meadows, wildflower areas, and hedgerows (see Table S2, available in Supporting Information, for a detailed list of fields per category).

To assess the relationship between surrounding breeding sites and barn owl breeding success, we calculated a density metric for each focal breeding site by summing the reciprocals of the distances to surrounding sites:

$$Density = \sum_{i=1}^{n} \frac{1}{d_i},$$

where n is the number of surrounding sites, and d_i represents the straight distance from the focal site to each surrounding site. We used this metric to assess the potential competition for resources and the overall quality of the breeding environment.

Our analysis differentiated among 4 specific categories of site density to provide a nuanced understanding of the different environmental and competitive pressures. First, barn owl breeding site density was the overall density of barn owl breeding sites surrounding each focal site without regard to their occupancy status. This measurement provides insight into the availability of potential breeding sites for barn owls. Second, occupied barn owl breeding site density was the density of barn owl breeding sites that were occupied either before the laying date or simultaneously depending on the analysis. This measure focuses on the direct competition barn owls face for nest sites with conspecifics. Third, kestrel breeding site density was the overall density of kestrel breeding sites irrespective of occupancy. Because common kestrels (*Falco tinnunculus*) are potential competitors, we used this measurement to help assess the level of potential inter-specific competition. Lastly, the density of occupied kestrel sites was the density of breeding sites occupied by kestrels either before the laying date or simultaneously depending on the analysis. As kestrels can use both types of nest boxes, the ones designed for barn owls and the ones designed for kestrels (those boxes are never occupied by barn owls), both types were included in the kestrel site densities. The kestrel nest box data were obtained through a collaboration with various amateur ornithological groups from the Swiss Plateau. By calculating densities based on both the overall availability and actual occupancy of breeding sites, we aimed to distinguish between the effects of potential versus direct competition and the broader environmental breeding site characteristics influencing barn owl breeding success.

Statistical analyses

We estimated the factors associated with barn owl site occupancy and reproductive success through 3 different models, each focusing on a specific response variable, namely annual site occupancy, clutch size, and fledging success. First, we focused on annual breeding site occupancy, with a breeding site considered as occupied if at least one egg was laid in a specific year, including first, replacement, and second clutches. We fitted a generalized linear mixed model (GLMM) with a binomial family to annual site occupancy using the function glmer from the package lme4 (Bates et al. 2015). We included predictors related to nest box characteristics, surrounding breeding site densities, and the surrounding environment. Predictors related to nest box characteristics included orientation (north, east, south, west), height in meters, location (inside or outside the barn), altitude above sea level in meters, number of nest boxes at the site (1 or 2), and nest box age in years. Predictors related to the surrounding breeding site densities included the 4 variables of densities of barn owl and kestrel sites or occupied sites described above. Predictors describing the surrounding environment included the proportion of roads, the proportion of urban areas, the density of urban areas, the area of agricultural fields, the proportion of extensive pastures, the proportion of wildflower areas, the proportion of extensive meadows, and the proportion of hedgerows. We included year and site ID as random intercepts in the models. In cases when 2 nest boxes were installed at the same site, we kept only one nest box record per site per year, as their occupancy was mutually exclusive. This means that if one nest box was occupied in a given year, the other was not. We calculated occupancy as follows: if one of the nest boxes was occupied, we kept the record for that nest box; if neither of the nest boxes was occupied, we randomly selected 1 nest box at the site to include in analysis.

To estimate the factors related to clutch size and fledging success, we focused on the first annual clutch of each breeding pair. We chose only first clutches because they are more strongly influenced by environmental factors, which are the primary focus of our analysis. In contrast, the breeding parameters of second clutches depend on many confounding factors, such as the success of the first clutch or the parents' conditions (Béziers and Roulin 2016). We modeled clutch size with a linear mixed model (LMM) using the function lmer from the package lme4 (Bates et al. 2015) and fledging success (i.e., the number of fledglings divided by the clutch size) with a weighted GLMM with a binomial family, with clutch size as weights, using the function glmer of the package lme4 (Bates et al. 2015). We used the same covariates as we used in the annual site occupancy model (nest box characteristics, surrounding breeding site densities, and surrounding environment predictors), adding control predictors specific to the clutch, namely the laying date and the barn owl pair identity classified into 4 categories: the same pair as the previous year, the same female but a different male as the previous year, the same male but a different female as the previous year, or different pair. For the surrounding breeding site densities, we ran 2 separate models to differentiate between the density of available breeding sites and the density of occupied breeding sites. Each run included one of these variables for both barn owls and kestrels, allowing us to isolate and compare their respective effects on the response variables. We included female ID, male ID, nest box ID nested in site ID, and year as random intercepts in the models.

We performed statistical analyses using R 4.2.1, with RStudio as a graphic user interface (R Core Team 2022, RStudio Team 2022). We checked for collinearity among predictors for each model and verified assumptions with the performance package (Lüdecke et al. 2021). Additionally, we visually inspected residual diagnostic plots. We constructed the 3 global models (occupancy, clutch size, and fledging success) with predictors selected for their biological relevance to barn owl ecology and their specific interest in this study. In every model, we z-scaled linear predictors, which allowed direct comparison of effect sizes across variables of different units. We checked for spatial autocorrelation for all models by plotting residuals against the spatial coordinates, and we found no evidence of spatial autocorrelation.

RESULTS

We analyzed data for 300 nest boxes at 232 different sites. The nest boxes were on average 19 years old (SD = 10 years; min. = 3 years, max. = 40 years), placed at an average altitude of 539 m (SD = 81 m, min. = 375 m, max. = 797 m), at a height of 6.4 m (SD = 1.98 m, min. = 2.34 m, max. = 12.52). The majority were placed inside barns (n = 254), orientated towards east (n = 172) or north (n = 92), and were single nest boxes (n = 162).

On average, the area surrounding nest boxes comprised 6.2% roads (SD = 2.2%, min. = 2.9%, max. = 19.3) and 17.7% urban areas (SD = 9.7%, min. = 4%, max. = 72%). Regarding extensive areas, the area surrounding nest boxes comprised 7.2% extensive pastures (SD = 4.4%, min. = 0%, max. = 20.1%), 0.8% wildflower areas (SD = 0.7%, min. = 0%, max. = 4.4%), 18.8% extensive meadows (SD = 7.4%, min. = 0%, max. = 42.7%), and 0.7% hedgerows (SD = 0.4%, min. = 0.02%, max. = 2.7%).

Breeding site occupancy

For the 3 years considered, 23% of breeding sites were occupied in 2018, 26% in 2019, and 36% in 2020, leading to an overall occupancy of 28%. The analysis of site occupancy, conducted using a GLMM, revealed effects from a variety of predictors (Table 1). The model demonstrated a negative correlation between altitude and site

TABLE 1 Odds ratios from generalized linear models with a binomial family of mean site occupancy of barn owls in Switzerland. We constructed a global model of all variables predicted to have a biological significance and added nest box ID nested in the site ID and year as random factors (τ_{00}). The variance of the random effects is represented by σ^2. Significant terms ($P < 0.05$) are indicated with an asterisk (*). The model is based on 232 sites between 2018 and 2020. The estimates are presented as odds ratios, where values > 1 indicate a positive effect on occupancy (increased likelihood of occupancy), and values < 1 indicate a negative effect (decreased likelihood of occupancy).

Parameter variable	Odds ratio (SE)	*t*	*P*
Mean occupancy			
(Intercept)	0.28 (0.13)	−2.76	0.006
Scaled altitude*	0.53 (0.12)	−2.77	0.006
East orientation	1.02 (0.41)	0.05	0.963
South orientation	0.71 (0.39)	−0.62	0.535
West orientation	0.97 (0.59)	−0.05	0.959
Located outside	1.48 (0.68)	0.86	0.389
Scaled height [m]	1.38 (0.30)	1.49	0.135
Scaled nest box age	0.78 (0.14)	−1.41	0.159
Number of nest boxes at the site	1.90 (0.72)	1.68	0.092
Scaled proportion of roads around	1.06 (0.32)	0.19	0.848
Scaled density of urban areas*	0.56 (0.16)	−2.01	0.045
Scaled proportion of urban areas	1.15 (0.35)	0.46	0.649
Scaled area of fields	1.28 (0.30)	1.04	0.300
Scaled proportion of extensive pastures*	0.51 (0.11)	−3.02	0.003
Scaled proportion of wildflowers	1.18 (0.19)	1.04	0.298
Scaled proportion of extensive meadows	0.99 (0.19)	−0.07	0.947
Scaled proportion of hedgerows	1.37 (0.25)	1.68	0.093
Scaled surrounding barn owl site density	0.74 (0.13)	−1.74	0.081
Scaled surrounding kestrel site density	0.92 (0.15)	−0.52	0.606
Random effects			
	σ^2		3.29
	$\tau_{00\ \text{site ID}}$		2.96
	$\tau_{00\ \text{year}}$		0.18
Model fit	Observations		708
	Marginal R^2		0.182

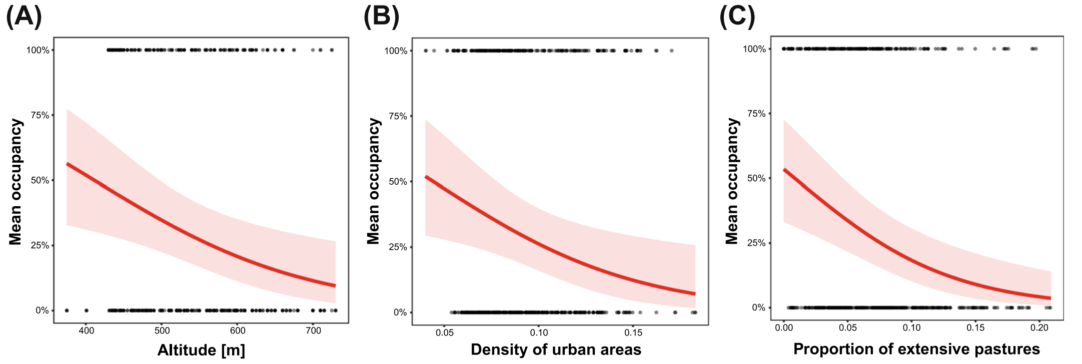

FIGURE 1 Predicted effects (and 95% CI) of environmental factors and nest box characteristics on mean site occupancy of barn owls in Switzerland, 2018–2020, including A) the association between mean site occupancy and the altitude, B) the association between mean site occupancy and the density of urban areas surrounding the nest box, and C) the association between mean site occupancy and the proportion of extensive pastures. The red shaded area represents the 95% confidence interval around the estimated means in solid red line, while the data are shown in black.

occupancy; occupancy diminished sharply with increasing altitude, falling to <12% occupancy at altitudes >700 m (Figure 1A). Additionally, there was weak evidence that number of nest boxes at the site affected occupancy (Table 1); single nest boxes tended to be 36% less likely to be occupied compared to pairs of nest boxes (mean occupancy of single nest boxes = 0.31; mean occupancy of pairs of nest boxes = 0.48). We did not find any evidence that the orientation, height, location, and age of the nest box explained annual occupancy rates. The proportion of surrounding pastures decreased the odds of occupancy (Figure 1C). Finally, the model indicated that urban density was negatively related to site occupancy (Figure 1B).

Breeding parameters

The model focusing on the clutch size (Table 2) showed that, on average, 5.44 eggs were laid per clutch (SD = 1.5 eggs, min. = 1 egg, max. = 9 eggs). The location of the nest box affected clutch size; clutches were larger by 0.56 eggs in nest boxes placed outside the barns (mean inside = 5.24 eggs; mean outside = 5.89 eggs). We did not find any evidence that the orientation, altitude, height, or age of the nest box or the number of nest boxes present at the site explained any variation in clutch size. Regarding the surrounding environment, we found weak evidence that the proportion of extensive pastures correlated positively with clutch size (Table 1). Clutches were smaller when surrounded by a higher proportion of urban areas (Figure 2).

The model focusing on fledging success indicated support for several predictors (Table 3). On average, 63.3% of eggs hatched and survived until fledging (SD = 31.7%). Laying date affected fledging success and had a quadratic effect; fledging success was higher in the middle of the breeding season compared to the early or late parts of the season. The density of surrounding barn owl breeding sites was also associated with fledging success, with higher fledging success observed in nest boxes with higher densities of surrounding barn owl sites (Figure 3). We did not find support for this trend when we included only surrounding sites that were simultaneously occupied (scaled surrounding occupied barn owl site density: $\beta = 1.15$, $SE = 0.13$, $t = 1.24$, $P = 0.214$). The relationship between fledging success and density of surrounding barn owl sites was also apparent when including only successful clutches, i.e., clutches with at least one fledgling (scaled density of surrounding barn owl sites: $\beta = 1.32$, $SE = 0.13$, $t = 2.81$, $P = 0.005$).

TABLE 2 Parameter estimates from linear models of clutch size of barn owls in Switzerland, 2018–2020. We constructed a global model of all variables predicted to have a biological significance and added nest box ID nested in site ID, year, female ID, and male ID as random factors (τ_{00}). The variance of the random effects is represented by σ^2. Significant terms ($P < 0.05$) are indicated with an asterisk (*). The model is based on 188 broods in 118 different nest boxes between 2018 and 2020.

Parameter variable	Estimates (SE)	*t*	*P*
Clutch size			
(Intercept)	5.83 (0.82)	7.1	<0.01
Scaled altitude	0.02 (0.17)	0.13	0.900
East orientation	0.28 (0.31)	0.90	0.372
South orientation	0.07 (0.49)	0.14	0.889
West orientation	−0.41 (0.48)	−0.85	0.397
Located outside*	0.77 (0.34)	2.26	0.026
Scaled height [m]	−0.07 (0.17)	−0.41	0.685
Same female before	−0.89 (0.96)	−0.92	0.359
Same male before	−0.80 (0.77)	−1.04	0.301
Different pair	−0.82 (0.73)	−1.12	0.267
Scaled nest box age	0.01 (0.13)	0.10	0.919
Number of nest boxes at the site	−0.01 (0.28)	−0.03	0.979
Scaled proportion of roads around	0.06 (0.23)	0.26	0.794
Scaled density of urban areas	0.37 (0.23)	1.60	0.114
Scaled proportion of urban areas*	−0.47 (0.22)	−2.17	0.032
Scaled area of fields	−0.03 (0.19)	−0.15	0.884
Scaled proportion of extensive pastures	0.30 (0.18)	1.69	0.094
Scaled proportion of wildflowers	0.08 (0.15)	0.56	0.574
Scaled proportion of extensive meadows	0.06 (0.15)	0.44	0.659
Scaled proportion of hedgerows	−0.14 (0.16)	−0.92	0.359
Scaled surrounding barn owl site density	−0.16 (0.14)	−1.16	0.249
Scaled surrounding kestrel site density	0.09 (0.13)	0.70	0.486
Scaled laying date	1.56 (0.84)	1.84	0.068
Scaled squared laying date	−1.42 (0.83)	−1.71	0.089
Random effects			
	σ^2		1.51
	$\tau_{00\ \text{female ID}}$		0.55
	$\tau_{00\ \text{male ID}}$		0.05
	$\tau_{00\ \text{nest ID: site ID}}$		0.28
	$\tau_{00\ \text{site ID}}$		0.00
	$\tau_{00\ \text{year}}$		0.16
Model fit	Observations		188
	Marginal R^2		0.065

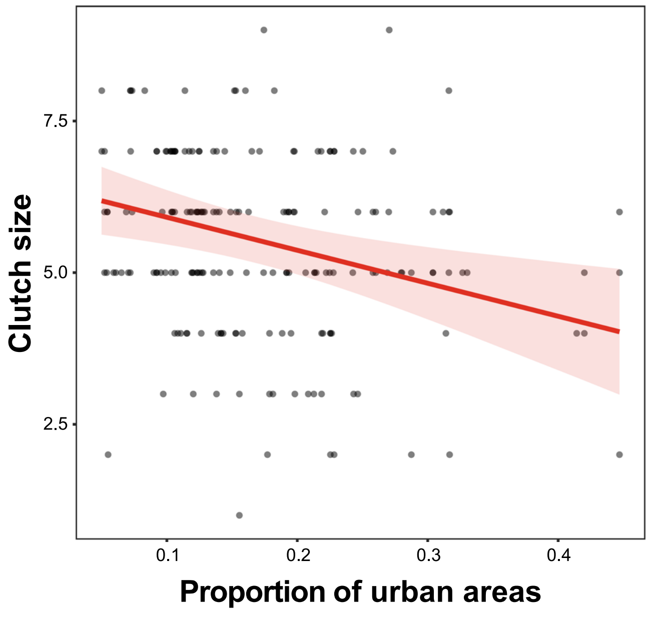

FIGURE 2 The association between barn owl clutch size and the proportion of urban areas in Switzerland, 2018–2020. The red shaded area represents the 95% confidence interval around the estimated mean (solid red line), while the data are shown in black. The graphs present unscaled relationships for interpretative clarity, despite models using scaled predictors.

DISCUSSION

Agricultural lands, which dominate our landscapes (Tilman et al. 2001), play a crucial role in influencing the environment. This is particularly true for species that rely heavily on these areas, such as barn owls. This species depends on agricultural fields to hunt small mammals (Perrins and Snow 1998) and uses artificial nest boxes fixed on barns for nesting. Understanding the influence of agriculture on their breeding parameters is essential for improving conservation strategies and providing information to farmers interested in sustainable practices. Moreover, barn owls are highly efficient predators, consuming up to 800 prey items per breeding attempt during the short 62-day chick-rearing period (St. George and Johnson 2021, Schalcher et al. 2023), thus helping to control small-mammal populations (Labuschagne et al. 2016, Montoya et al. 2021). They are essential for farmers who would like to replace pesticides with biological pest control agents. By monitoring >200 breeding sites over 3 years, we evaluated the relationships between fine-scale landscape structures and site occupancy and barn owl breeding success.

We failed to detect a relationship between biodiversity promotion areas, such as wildflower areas or hedgerows, and barn owl breeding success or site occupancy. This is in line with results from in a previous study within the same barn owl population (Arlettaz et al. 2010), showing that wildflower areas increase small-mammal densities but that barn owls do not forage specifically in such areas. However, this contradicts a recent study performed on the same population by Séchaud et al. (2021), who showed that barn owls preferred wildflower areas for hunting. One potential explanation for our findings could be the homogeneity of the study area and very low proportion of wildflower areas overall. It may be necessary to perform such analysis in a more varying environment with a higher proportion of wildflower areas to deeply understand their impact.

An unexpected result was the dual effect of the proportion of extensively used pastures. While we found weak evidence for a positive correlation between extensive pastures and larger clutch sizes, we also observed a negative relationship between extensive pastures and site occupancy. It is reasonable to assume that barn owls in

TABLE 3 Parameter estimates from a weighted generalized mixed model with a binomial family of fledging success of barn owls in Switzerland with clutch size as weight. We constructed a global model of all variables predicted to have a biological significance and added nest box ID nested in site ID, year, female ID, and male ID as random factors (τ_{00}). The variance of the random effects is represented by σ^2. Significant terms ($P < 0.05$) are indicated with an asterisk (*). The model is based on 188 broods in 118 different nest boxes between 2018 and 2020.

Parameter variable	Estimates (SE)	*t*	*P*
Fledging success			
(Intercept)	3.80 (2.57)	1.97	0.049
Scaled altitude	1.01 (0.14)	0.05	0.958
East orientation	0.66 (0.17)	−1.57	0.117
South orientation	0.92 (0.37)	−0.19	0.847
West orientation	0.62 (0.25)	−1.19	0.233
Located outside	0.66 (0.19)	−1.46	0.146
Scaled height [m]	0.89 (0.13)	−0.80	0.425
Same female before	0.57 (0.47)	−0.69	0.493
Same male before	0.83 (0.53)	0.28	0.777
Different pair	0.62 (0.38)	−0.76	0.445
Scaled nest box age	1.10 (0.12)	0.82	0.411
Number of nest boxes at the site	1.10 (0.27)	0.41	0.682
Scaled proportion of roads around	1.18 (0.23)	0.87	0.386
Scaled density of urban areas	0.76 (0.14)	−1.44	0.149
Scaled proportion of urban areas	1.22 (0.23)	1.06	0.289
Scaled area of fields	1.24 (0.20)	1.33	0.184
Scaled proportion of extensive pastures	0.88 (0.13)	−0.89	0.375
Scaled proportion of wildflowers	0.93 (0.11)	−0.58	0.559
Scaled proportion of extensive meadows	0.99 (0.12)	−0.08	0.940
Scaled proportion of hedgerows	0.87 (0.12)	−1.03	0.301
Scaled surrounding barn owl site density*	1.27 (0.15)	2.03	0.042
Scaled surrounding kestrel site density	0.95 (0.11)	−0.47	0.641
Scale laying date*	4.91 (3.45)	2.26	0.024
Scaled squared laying date*	0.20 (0.14)	−2.35	0.019
Random effects			
	σ^2		3.29
	$\tau_{00\ \text{female ID}}$		0.22
	$\tau_{00\ \text{male ID}}$		0.38
	$\tau_{00\ \text{nest ID: site ID}}$		0.00
	$\tau_{00\ \text{site ID}}$		0.00
	$\tau_{00\ \text{year}}$		0.05
Model fit	Observations		188
	Marginal R^2		0.066

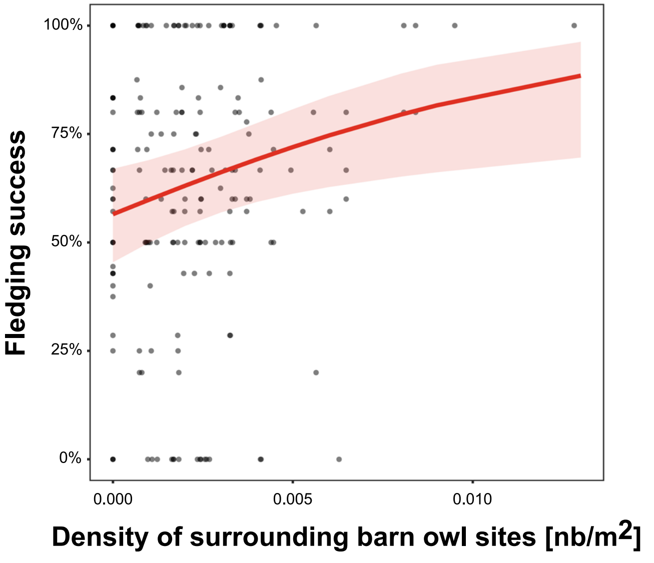

FIGURE 3 The association between the density of surrounding barn owl breeding sites (number [nb] of sites/ m^2) and barn owl fledging success in Switzerland, 2018–2020. The red shaded area represents the 95% confidence interval around the estimated mean (solid red line), while the data are shown in black. The graphs present unscaled relationships for interpretative clarity, despite models using scaled predictors.

pasture-rich areas may be in better condition and can thus increase their clutch size given that pastures are known for high small-mammal densities (French et al. 1976, Aschwanden et al. 2007), thus providing ample food resources for barn owls (Bühler et al. 2023). However, the negative correlation we observed between extensively-used pastures and site occupancy warrants further investigation. One plausible explanation could be that the proportion of pastures correlates with untested variables that adversely affect barn owl site occupancy. These unidentified factors might be environmental, ecological, or anthropogenic. Given this possibility, it would be highly beneficial to replicate this analysis over multiple years and across other species. Additionally, studying the impact of natural or uncultivated land cover types on barn owl site occupancy and breeding success could provide further insights. Such studies could help determine the consistency of the patterns we observed and potentially uncover hidden variables influencing barn owl site occupancy in pasture-rich environments.

The urban areas surrounding nest boxes also appeared important to barn owls' breeding success. Barn owls are highly adapted to human settlements and often use them as nesting grounds (Roulin 2020). In the present study, we found no evidence of a relationship between the proportion of urban areas and site occupancy, highlighting barn owl adaptability to human settlements, in line with results from a previous study in the United States (Busby et al. 2024). However, the density of urban areas was negatively related to site occupancy, showing that even if barn owls exhibit this adaptability, they must still secure suitable hunting grounds nearby, which is possible in sparser urban areas. This is supported by our results showing that a high proportion of urban areas was negatively associated with clutch size. This indicates that barn owls may benefit from environments where smaller urban areas are interspersed with agricultural fields. The proportion of urban area surrounding breeding sites in this study was on average low and consisted mainly of villages with numerous farms and houses with gardens. We did not detect any association between roads and barn owl breeding success, contradicting previous research from the same barn owl population (Frey et al. 2011) and studies from other regions (Charter et al. 2012, Hindmarch et al. 2012, Busby et al. 2024). This indicates a dual role of roads; while they are a major cause of mortality for barn owls (Boves and Belthoff 2012, De Jong et al. 2018), they can also provide perches for hunting, as noted by Schalcher et al. (2023).

Regarding nest box characteristics, several factors stand out as having a significant association with site occupancy and breeding success. Altitude was important, as nest boxes at higher altitudes were less likely to be occupied. This is likely context-dependent, as barn owls may show a quadratic relationship with altitude (Van Horne 1983). However, over the range of altitudes explored in this study (375–730 m), the relationship appears to be generally negative. This is probably because barn owls avoid high-altitude locations driven by their difficulties coping with harsh winters, as observed in the same population (Altwegg et al. 2006). Moreover, nest boxes placed in pairs within the same barn tended to be more likely to be occupied. This could be explained by the increased nest box availability when 2 nest boxes are placed together, decreasing inter-specific competition, especially with common kestrels. In addition, barn owls can use the second nest box as a roosting site during the day, as found by Séchaud et al. (2021), or for the second annual clutch (Béziers and Roulin 2016).

Location on the barn also appeared to be important, with barn owls producing larger clutches in nest boxes placed outside barns. This may be attributed to the environmental conditions prevalent outside barns, such as enhanced ventilation or cooler temperatures, which potentially offer more optimal conditions for the females incubating eggs. Alternatively, outside conditions might be more challenging, prompting an increase in clutch size as a compensatory response to anticipated higher offspring mortality. An in-depth investigation into the microclimate within nest boxes, comparing those situated inside versus outside, would help understand whether and how the environmental conditions inside the nest box differ and affect barn owl breeding strategies. Our findings did not reveal any notable correlation between nest box location and fledging success, indicating that the variations in clutch size do not translate to differences in offspring survival to fledging. This lack of correlation indicates that while external placement may favor larger initial clutch sizes, it does not necessarily affect the overall breeding success.

Nest box orientation was not associated with barn owls' breeding parameters in the present study. This finding diverges from the results presented by Butler et al. (2009), who reported an effect of nest box orientation on internal temperature and humidity levels in kestrel nest boxes. Specifically, they found that boxes facing west had significantly cooler average temperature and lower humidity levels than those facing south or east, leading to variations in breeding successes. Differences among studies may be attributed to differences in nest box design. Kestrel nest boxes typically feature a large opening and are placed externally, making them more susceptible to environmental conditions. Conversely, barn owl nest boxes used in our study were designed with only a small entry hole and were more enclosed, offering greater protection from external temperature and humidity fluctuations. Additionally, the distribution of nest box orientations in our study was predominantly towards the north and east, primarily because of installation constraints. This uneven distribution could further contribute to the absence of observable effects related to orientation in our findings.

The density of surrounding barn owl breeding sites correlated positively with fledging success. We observed an increase in fledging success in environments with a higher density of surrounding barn owl sites. This finding could indicate that such environments are of higher quality, attracting numerous pairs to breed in the most favorable areas. However, we did not detect any effect of the density of surrounding kestrel sites. This suggests that despite kestrels being competitors for nesting sites and, to a lesser extent, for hunting resources (Charter et al. 2010, Montoya et al. 2021), both species are capable of coexisting within the same environment.

A comparison between the previous long-term study (Milliet et al. 2024) and our current short-term study revealed intriguing patterns in barn owl breeding behavior and habitat preferences. While some predictors were consistently associated with barn owl breeding success across studies, others were highlighted only in one. Both studies highlighted the effects of nest box characteristics, though with different focal parameters. A consistent predictor in both studies was altitude above sea level, which was negatively associated with occupancy in the short term and with clutch size in the long term. Notably, while the long-term data suggested a positive relationship between urban areas and barn owl fledging success and site occupancy, the present study revealed dual effects of both the density and proportion of urban areas. This finding indicates that more precise urban data can reveal previously unnoticed trends. Both studies also demonstrated an overall positive association with agricultural landscapes, emphasizing the importance of biodiversity promotion areas for barn owl breeding success. As for the density of surrounding nest boxes, the 2 studies reported contradictory trends, with a negative association with clutch size and site occupancy in the long term but a positive association with fledging success in the short term. This discrepancy might suggest that the 3 years analyzed in the current study had good conditions, leading to a decrease in intra-specific competition.

CONSERVATION IMPLICATIONS

This study analyzed the extent to which the interplay between various environmental landscapes and nest box characteristics associated with barn owl breeding success. Overall, urbanization seems to pose some challenges to the barn owl, especially site occupancy and clutch size, while biodiversity promotion areas provide favorable conditions. These findings offer valuable insights for people interested in installing barn owl nest boxes. Our study area is the Swiss Plateau, a region characterized by its rolling plains and diverse landscapes, including small cities, villages, and a mix of agricultural fields. Overall, the following key recommendations emerged from our analysis. We recommend installing a pair of nest boxes on the same barn at sites <700 m in elevation. We encourage the incorporation of biodiversity promotion areas within the agricultural landscape to increase barn owl presence and breeding success. Within the context of areas predominantly consisting of small cities and villages (no large metropolitan areas), we recommend avoiding the installation of nest boxes in dense urban areas (areas where up to 15% of the area is occupied by buildings). This study provides practical advice for those interested in helping barn owl populations and contributes to the broader understanding of factors associated with barn owl breeding success. These recommendations have the potential to increase barn owl presence, the implementation of which might further contribute to the promotion of biodiversity within agricultural landscapes.

ACKNOWLEDGMENTS

This study was financially supported by the Swiss National Science Foundation (grant number 310030_200321). We thank all the people that worked in the field for collecting the data, and all members of the Barn Owl Research Group for their help and feedback on this study. Many thanks to J. Lesser for providing part of the kestrel data and R. Bühler for his help with the biodiversity promotion areas data extraction, especially the hedgerows. Open access funding provided by Universite de Lausanne.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

ETHICS STATEMENT

This study has been conducted in accordance with the legal requirements for the capture and handling of barn owls in Switzerland. The relevant legal authorizations have been obtained from the Department of the Consumer and Veterinary Affairs (VD, FR and BE 3213 and 3571) and the Federal Office for the Environment (capture and ringing permissions).

DATA AVAILABILITY STATEMENT

Data available on request from the authors.

ORCID

Estelle Milliet http://orcid.org/0000-0001-9196-5446

REFERENCES

AGRIDEA. 2018. Vue d'ensemble des surfaces de promotion de la biodiversité et des contributions. AGRIDEA, Lausanne, Switzerland. http://www.bff-spb.ch/fileadmin/pdfs/FR/Contributions_SPB.pdf

Almasi, B., P. Béziers, A. Roulin, and L. Jenni. 2015. Agricultural land use and human presence around breeding sites increase stress-hormone levels and decrease body mass in barn owl nestlings. Oecologia 179:89-101. https://doi.org/10.1007/s00442-015-3318-2

Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. Page 19–31 *in* M. G. Paoletti, editor. Invertebrate biodiversity as bioindicators of sustainable landscapes. Elsevier, Amsterdam, The Netherlands. https://doi.org/10.1016/B978-0-444-50019-9.50005-4

Altwegg, R., A. Roulin, M. Kestenholz, and L. Jenni. 2006. Demographic effects of extreme winter weather in the barn owl. Oecologia 149:44-51. https://doi.org/10.1007/s00442-006-0430-3

Arlettaz, R., M. Krähenbühl, B. Almasi, A. Roulin, and M. Schaub. 2010. Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding barn owls. Journal of Ornithology 151:553-564. https://doi.org/10.1007/s10336-009-0485-0

Aschwanden, J., O. Holzgang, and L. Jenni. 2007. Importance of ecological compensation areas for small mammals in intensively farmed areas. Wildlife Biology 13:150-158. https://doi.org/10.2981/0909-6396(2007)13[150:IOECAF]2.0.CO;2

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67(1):1-48. https://doi.org/10.48550/arXiv.1406.5823

Béziers, P., and A. Roulin. 2016. Double brooding and offspring desertion in the barn owl *Tyto alba*. Journal of Avian Biology 47:235-244. https://doi.org/10.1111/jav.00800

Boves, T. J., and J. R. Belthoff. 2012. Roadway mortality of barn owls in Idaho, USA. Journal of Wildlife Management 76: 1381-1392. https://doi.org/10.1002/jwmg.378

Bühler, R., K. Schalcher, R. Séchaud, S. Michler, N. Apolloni, A. Roulin, and B. Almasi. 2023. Influence of prey availability on habitat selection during the non-breeding period in a resident bird of prey. Movement Ecology 11:1-17. https://doi.org/10.1186/s40462-023-00376-3

Bunn, D. S., A. B. Warburton, and R. D. Wilson. 1982. The barn owl. Buteo Books, Vermillion, South Dakota, USA.

Burton, R. J., and G. A. Wilson. 2006. Injecting social psychology theory into conceptualisations of agricultural agency: towards a post-productivist farmer self-identity? Journal of Rural Studies 22:95-115. https://doi.org/10.1016/j.jrurstud.2005.07.004

Busby, B. T., M. P. Gordon, and J. Belthoff. 2024. Roads reduce breeding occupancy and productivity in barn owls. Journal of Wildlife Management 88:e22597. https://doi.org/10.1002/jwmg.22597

Butler, M. W., B. A. Whitman, and A. M. Dufty. 2009. Nest box temperature and hatching success of American kestrels varies with nest box orientation. Wilson Journal of Ornithology 121:778-782. https://doi.org/10.1676/08-124.1

Charter, M., I. Izhaki, and Y. Leshem. 2010. Effects of the risk of competition and predation on large secondary cavity breeders. Journal of Ornithology 151:791-795. https://doi.org/10.1007/s10336-010-0514-z

Charter, M., Y. Leshem, K. Meyrom, O. Peleg, and A. Roulin. 2012. The importance of micro-habitat in the breeding of barn owls *Tyto alba*. Bird Study 59:368-371. https://doi.org/10.1080/00063657.2012.669360

Donázar, J. A., A. Cortés-Avizanda, J. A. Fargallo, A. Margalida, M. Moleón, Z. Morales-Reyes, R. Moreno-Opo, J. M. Pérez-García, J. A. Sánchez-Zapata, I. Zuberogoitia, and D. Serrano. 2016. Roles of raptors in a changing world: from flagships to providers of key ecosystem services. Ardeola 63:181-234. https://doi.org/10.13157/arla.63.1.2016.rp8

Elhakeem, A., W. van der Werf, J. Ajal, D. Lucà, S. Claus, R. A. Vico, and L. Bastiaans. 2019. Cover crop mixtures result in a positive net biodiversity effect irrespective of seeding configuration. Agriculture, Ecosystems & Environment 285:106627. https://doi.org/10.1016/j.agee.2019.106627

Eschenbauch, J. E., E. A. Jacobs, and R. N. Rosenfield. 2009. Nest-box occupancy and reproductive performance of kestrels in central Wisconsin. Journal of Raptor Research 43:365-369. https://doi.org/10.3356/JRR-08-79.1

French, N. R., W. E. Grant, W. Grodzinski, and D. M. Swift. 1976. Small mammal energetics in grassland ecosystems. Ecological Monographs 46:201-220. https://doi.org/10.2307/1942251

Frey, C., C. Sonnay, A. Dreiss, and A. Roulin. 2011. Habitat, breeding performance, diet and individual age in Swiss barn owls (*Tyto alba*). Journal of Ornithology 152:279-290. https://doi.org/10.1007/s10336-010-0579-8

Gehlbach, F. R. 1994. Nest-box versus natural-cavity nests of the eastern screech-owl: an exploratory study. Journal of Raptor Research 28:154-157.

George, D. A. S., and M. D. Johnson. 2021. Effects of habitat on prey delivery rate and prey species composition of breeding barn owls in winegrape vineyards. Agriculture, Ecosystems & Environment 312:107322. https://doi.org/10.1016/j.agee.2021.107322

Goodenough, A. E., D. P. Maitland, A. G. Hart, and S. L. Elliot. 2008. Nestbox orientation: a species-specific influence on occupation and breeding success in woodland passerines. Bird Study 55:222-232. https://doi.org/10.1080/00063650809461526

Gottschalk, T. K., K. Ekschmitt, and V. Wolters. 2011. Efficient placement of nest boxes for the little owl (*Athene noctua*). Journal of Raptor Research 45:1-14. https://doi.org/10.3356/JRR-09-11.1

Hamerstrom, F., F. N. Hamerstrom, and J. Hart. 1973. Nest boxes: an effective management tool for kestrels. Journal of Wildlife Management 37:400-403. https://doi.org/10.2307/3800132

Hindmarch, S., and J. E. Elliott. 2015. A specialist in the city: the diet of barn owls along a rural to urban gradient. Urban Ecosystems 18:477-488. https://doi.org/10.1007/s11252-014-0411-y

Hindmarch, S., E. A. Krebs, J. E. Elliott, and D. J. Green. 2012. Do landscape features predict the presence of barn owls in a changing agricultural landscape? Landscape and Urban Planning 107:255-262. https://doi.org/10.1016/j.landurbplan.2012.06.010

Johnson, P. N. 1994. Barn owls in Norfolk, England. Journal of Raptor Research 28:149-153.

de Jong, J., A. B. van den Burg, and A. Liosi. 2018. Determinants of traffic mortality of barn owls (*Tyto alba*) in Friesland, the Netherlands. Avian Conservation and Ecology 13:2. https://doi.org/10.5751/ACE-01201-130202

Kleijn, D., R. A. Baquero, Y. Clough, M. Díaz, J. De Esteban, F. Fernández, D. Gabriel, F. Herzog, A. Holzschuh, R. Jöhl, et al. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology Letters 9: 243-254. https://doi.org/10.1111/j.1461-0248.2005.00869.x

Knaus, P., S. Antoniazza, V. Keller, T. Sattler, H. Schmid, and N. Strebel. 2021. Liste rouge des oiseaux nicheurs. Espèces menacées en Suisse. Office fédérale de l'environnement (OFEV) et la Station ornithologique suisse, Berne, Switzerland.

Knaus, P., S. Antoniazza, S. Wechsler, J. Guélat, M. Kéry, N. Strebel, and T. Sattler. 2018. Atlas des oiseaux nicheurs de Suisse 2013-2016: distribution et évolution des effectifs des oiseaux en Suisse et au Liechtenstein. Station ornithologique suisse, Sempach, Switzerland.

Knop, E. V. A., D. Kleijn, F. Herzog, and B. Schmid. 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. Journal of Applied Ecology 43:120-127. https://doi.org/10.1111/j.1365-2664.2005.01113.x

Labuschagne, L., L. H. Swanepoel, P. J. Taylor, S. R. Belmain, and M. Keith. 2016. Are avian predators effective biological control agents for rodent pest management in agricultural systems? Biological Control 101:94-102. https://doi.org/10.1016/j.biocontrol.2016.07.003

Lastra-Bravo, X. B., C. Hubbard, G. Garrod, and A. Tolón-Becerra. 2015. What drives farmers' participation in EU agri-environmental schemes? Results from a qualitative meta-analysis. Environmental Science & Policy 54:1-9. https://doi.org/10.1016/j.envsci.2015.06.002

Lüdecke, D., M. S. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. performance: an R Package for assessment, comparison and testing of statistical models. Journal of Open Source Software 6(60):3139. https://doi.org/10.21105/joss.03139

Marti, C. D., P. W. Wagner, and K. W. Denne. 1979. Nest boxes for the management of barn owls. Wildlife Society Bulletin 7:145-148. https://www.jstor.org/stable/3781754

Martin, A. E., S. J. Collins, S. Crowe, J. Girard, I. Naujokaitis-Lewis, A. C. Smith, K. Lindsay, S. Mitchell, and L. Fahrig. 2020. Effects of farmland heterogeneity on biodiversity are similar to—or even larger than—the effects of farming practices. Agriculture, Ecosystems & Environment 288:106698. https://doi.org/10.1016/j.agee.2019.106698

McGuire, J. M., L. W. Morton, J. G. Arbuckle Jr., and A. D. Cast. 2015. Farmer identities and responses to the social–biophysical environment. Journal of Rural Studies 39:145-155. https://doi.org/10.1016/j.jrurstud.2015.03.011

McHugh, N. M., M. Prior, P. V. Grice, S. R. Leather, and J. M. Holland. 2017. Agri-environmental measures and the breeding ecology of a declining farmland bird. Biological Conservation 212:230-239. https://doi.org/10.1016/j.biocon.2017.06.023

Meyrom, K., Y. Motro, Y. Leshem, S. Aviel, I. Izhaki, F. Argyle, and M. Charter. 2009. Nest-box use by the barn owl *Tyto alba* in a biological pest control program in the Beit She'an valley, Israel. Ardea 97:463-467. https://doi.org/10.5253/078.097.0410

Milliet, E., K. Schalcher, A. Grangier-Bijou, B. Almasi, F. Butera, and A. Roulin. 2024. The effects of land use changes on site occupancy and breeding success of the barn owl (*Tyto alba*) from 1993 to 2020. Global Ecology and Conservation 52:e02988. https://doi.org/10.1016/j.gecco.2024.e02988

Montoya, A., X. Cabodevilla, J. A. Fargallo, E. Biescas, G. Mentaberre, and D. Villanúa. 2021. Vertebrate diet of the common kestrel (*Falco tinnunculus*) and barn owl (*Tyto alba*) in rain-fed crops: implications to the pest control programs. European Journal of Wildlife Research 67:79. https://doi.org/10.1007/s10344-021-01515-0

Mulholland, T. I., D. M. Ferraro, K. C. Boland, K. N. Ivey, M. L. Le, C. A. LaRiccia, J. M. Vigianelli, and C. D. Francis. 2018. Effects of experimental anthropogenic noise exposure on the reproductive success of secondary cavity nesting birds. Integrative and Comparative Biology 58:967-976. https://doi.org/10.1093/icb/icy079

Newton, I. 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146:579-600. https://doi.org/10.1111/j.1474-919X.2004.00375.x

Partecke, J., I. Schwabl, and E. Gwinner. 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. Ecology 87:1945-1952. https://doi.org/10.1890/0012-9658(2006)87[1945:SATCUA]2.0.CO;2

Paz-Luna, A., H. Bintanel, J. Viñuela, and D. Villanúa. 2020. Nest-boxes for raptors as a biological control system of vole pests: high local success with moderate negative consequences for non-target species. Biological Control 146:104267. https://doi.org/10.1016/j.biocontrol.2020.104267

Perrins, C. M., and D. W. Snow. 1998. The complete birds of the Western Palearctic on CD-ROM. Oxford University Press, Oxford, United Kingdom.

Princé, K., and F. Jiguet. 2013. Ecological effectiveness of French grassland agri-environment schemes for farmland bird communities. Journal of Environmental Management 121:110-116. https://doi.org/10.1016/j.jenvman.2013.02.039

R Core Team. 2022. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RStudio Team. 2022. Rstudio: integrated development for R. RStudio, PBC, Boston, Massachusetts, USA.

Redhead, J. W., S. A. Hinsley, B. C. Beckmann, R. K. Broughton, and R. F. Pywell. 2018. Effects of agri-environmental habitat provision on winter and breeding season abundance of farmland birds. Agriculture, Ecosystems & Environment 251: 114-123. https://doi.org/10.1016/j.agee.2017.09.027

Roulin, A. 2020. Barn owls: evolution and ecology. Cambridge University Press, Cambridge, United Kingdom.

Schalcher, K., E. Milliet, R. Sechaud, R. Buehler, B. Almasi, S. Pottier, P. Becciu, E. L. C. Shepard, and A. Roulin. 2023. Landing force reveals new form of motion-induced sound camouflage in a wild predator. eLife 12:RP87775. https://doi.org/10.7554/eLife.87775.3

Séchaud, R., K. Schalcher, A. P. Machado, B. Almasi, C. Massa, K. Safi, and A. Roulin. 2021. Behaviour-specific habitat selection patterns of breeding barn owls. Movement Ecology 9(1):1-11. https://doi.org/10.1186/s40462-021-00258-6

Sergio, F., T. Caro, D. Brown, B. Clucas, J. Hunter, J. Ketchum, K. McHugh, and F. Hiraldo. 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. Annual Review of Ecology, Evolution, and Systematics 39:1-19. https://doi.org/10.1146/annurev.ecolsys.39.110707.173545

Serrano-Davies, E., R. Barrientos, and J. Sanz. 2017. The role of nest-box density and placement on occupation rates and breeding performance: a case study with Eurasian blue tits. Ornis Fennica 94:21-32. https://doi.org/10.51812/of.133909

Stoate, C., A. Baldi, P. Beja, N. D. Boatman, I. Herzon, A. Van Doorn, G. R. de Snoo, L. Rakosy, and C. Ramwell. 2009. Ecological impacts of early 21st century agricultural change in Europe–a review. Journal of Environmental Management 91:22-46. https://doi.org/10.1016/j.jenvman.2009.07.005

Swinton, S. M., F. Lupi, G. P. Robertson, and S. K. Hamilton. 2007. Ecosystem services and agriculture: cultivating agricultural ecosystems for diverse benefits. Ecological Economics 64:245-252. https://doi.org/10.1016/j.ecolecon.2007.09.020

Swiss Federal Office of Topography. 2023. Swiss Topographic Landscape Model - swissTLM3D. https://www.swisstopo.admin.ch/en/landscape-model-swisstlm3d. Accessed 9 Jun 2023.

Tilman, D., J. Fargione, B. Wolff, C. D'antonio, A. Dobson, R. Howarth, D. Schindler, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science 292(5515):281-284. https://doi.org/10.1126/science.1057544

Tscharntke, T., Y. Clough, S. A. Bhagwat, D. Buchori, H. Faust, D. Hertel, D. Hölscher, J. Juhrbandt, M. Kessler, I. Perfecto, et al. 2011. Multifunctional shade-tree management in tropical agroforestry landscapes–a review. Journal of Applied Ecology 48:619-629. https://doi.org/10.1111/j.1365-2664.2010.01939.x

Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. Ecology Letters 8:857-874. https://doi.org/10.1111/j.1461-0248.2005.00782.x

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:893-901. https://doi.org/10.2307/3808148

Wendt, C. A., and M. D. Johnson. 2017. Multi-scale analysis of barn owl nest box selection on Napa Valley vineyards. Agriculture, Ecosystems & Environment 247:75-83. https://doi.org/10.1016/j.agee.2017.06.023

Wilson, G. A., and K. Hart. 2000. Financial imperative or conservation concern? EU farmers' motivations for participation in voluntary agri-environmental schemes. Environment and Planning A 32:2161-2185. https://doi.org/10.1068/a3311

Wittwer, R. A., S. F. Bender, K. Hartman, S. Hydbom, R. A. Lima, V. Loaiza, T. Nemecek, F. Oehl, P. A. Olsson, O. Petchey, et al. 2021. Organic and conservation agriculture promote ecosystem multifunctionality. Science Advances 7:eabg6995. https://doi.org/10.1126/sciadv.abg6995

Zingg, S., E. Ritschard, R. Arlettaz, and J. Y. Humbert. 2019. Increasing the proportion and quality of land under agri-environment schemes promotes birds and butterflies at the landscape scale. Biological Conservation 231:39-48. https://doi.org/10.1016/j.biocon.2018.12.022

Associate Editor: Jen Cruz.

SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

How to cite this article: Milliet, E., K. Schalcher, A. Grangier-Bijou, B. Almasi, F. Butera, and A. Roulin. 2024. Barn owl site occupancy and breeding success in relation to land use and nest box characteristics. Journal of Wildlife Management e22678. https://doi.org/10.1002/jwmg.22678