



Citizen science enabled planning for species conservation in urban landscapes: the case of Barn Swallows *Hirundo rustica* in southern China

Sihao Chen · Yu Liu · Peisong Li · Samantha C. Patrick · Eben Goodale · Rebecca J. Safran · Xinru Zhao · Xiaoli Zhuo · Jianping Fu · Christiane M. Herr · Emilio Pagani-Núñez

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Abstract

Context Urbanization has detrimental effects on biodiversity, yet how species respond to urban planning zoning outcomes and environmental changes at different spatial scales when selecting urban breeding habitats remains understudied. Mitigating such impacts on wildlife is instrumental to create

biodiversity-friendly cities while accommodating urban development.

Objectives We used Barn Swallow nesting site data (2017–2023) collected from a citizen science program to help identify the most influential factors affecting the presence of Barn Swallow nests at site and landscape scales.

Methods We analyzed the relationship between Barn Swallow nest site selection in urbanized areas of southern China and land use data, including built-up

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S. Chen · E. Goodale
Department of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou 215123, China

S. Chen · S. C. Patrick
Department of Earth, Ocean and Ecological Sciences, School of Environmental Sciences, University of Liverpool, Liverpool L69 3BX, UK

S. Chen · C. M. Herr
School of Design, Southern University of Science and Technology, Shenzhen 518055, China

Y. Liu (✉)
State Key Laboratory of Environmental Criteria and Risk Assessment, Chinese Research Academy of Environmental Sciences, Beijing 100107, China
e-mail: liuyu.qmul@gmail.com

Y. Liu · X. Zhao
Key Laboratory for Biodiversity Sciences and Ecological Engineering, Ministry of Education, College of Life Sciences, Beijing Normal University, Beijing 100875, China

P. Li
Hangzhou Institute of Technology, Xidian University, Hangzhou 311200, China

R. J. Safran
Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80302, USA

X. Zhao · J. Fu
China Bird Watching Society, Beijing 100097, China

X. Zhuo
Beijing No.4 High School, Beijing 100034, China

E. Pagani-Núñez
School of Applied Sciences, Edinburgh Napier University, Edinburgh EH11 4BN, UK
e-mail: e.pagani-nunez@napier.ac.uk

E. Pagani-Núñez
Centre for Conservation and Restoration Science, Edinburgh Napier University, Edinburgh EH11 4BN, UK

percentages, cropland and waterbodies, as well as environmental factors such as heat-island effect (land surface temperature), noise pollution (road density and road simplicity), artificial light at night (ALAN) and nesting building attributes (year constructed, height and surroundings).

Results Our findings revealed a positive association between Barn Swallow nest abundance and several anthropogenic factors, including land surface temperature at the site scale, and ALAN and road simplicity at the landscape scale. Our findings indicated the building year also had a negative impact on the Barn Swallow nests.

Conclusions These results suggest that urban design and revitalization efforts can consider mitigating negative effects by implementing measures to regulate noise pollution and nighttime lighting schemes. Furthermore, urban planning could carefully consider the requirements for biodiversity-friendly architectural elements in new constructions and rezoning process of existing urban districts, such as old residential neighborhoods and urban fringes, to minimize impacts on declining nesting sites in urban areas.

Keywords Urban planning · Land use zoning · Road · Artificial light at night · Building · Barn Swallow *Hirundo rustica*

Introduction

Urbanization drives significant habitat losses and environmental changes, affecting species persistence and distributions (McKinney 2002; Aronson et al. 2014; Plummer et al. 2015; Santos et al. 2025). To persist in urbanized environments, species must respond to the spatial distribution of potential microhabitats and macrohabitats, and their associated resources (Block and Brennan 1993; Donnelly and Marzluff 2006). For instance, habitat requirements for birds of prey or small passerine birds are different in terms of habitat composition and food requirements, and the spatial extent of these landscape elements (Hostetler and Holling 2000). This means that the ability of these bird species to successfully occupy urban environments is strongly determined by the outcome of urban planning at different scales (Johnson 1980; Plummer et al. 2020). Urban planning decisions, particularly through zoning regulations in

North America, or centralized planning regulations in many European and Asian countries, control the spatial distribution of diverse land use types (e.g., residential, commercial, road networks and green spaces) and buildings attributes (e.g., heights) within each land use type (Newman and Thornley 1996; Shatkin 2008; Cullingworth and Caves 2014; Liu and Zhou 2021). These regulations often affect different areas of the city unevenly and across multiple spatial scales (e.g., lots, neighborhoods, districts, and entire urban regions), leading to a concentration of green spaces and specific types of buildings in certain neighborhoods, while others (e.g., industrial areas) may be deprived of these resources (Forman 2008; Levy 2017). Therefore, to prevent further species losses and support biodiversity in urban areas, urban planning practice also needs to focus on creating and enhancing suitable habitats based on a thorough understanding of species' biological needs (Hostetler and Holling 2000; Apfelbeck et al. 2020; Plummer et al. 2020). Despite the advocacy for integrating biodiversity conservation into urban planning and design (Garrard et al. 2018), the mechanistic pathways by which land use zones and building attributes affect species occurrence and nest site selection at different spatial scales remains understudied (Wiens 1989; Levin 1992; Humphrey et al. 2023).

There are two important scales (macrohabitat vs. microhabitat or landscape vs. site) for species survival and reproduction according to habitat selection theory, which correspond to species' habitat choices and foraging activities in certain landscapes (e.g., neighborhoods, districts and beyond) and to nesting at site scales (Johnson 1980; Block and Brennan 1993). Previous studies have documented detrimental effects of a diverse array of environmental factors including land cover types, the urban heat-island effect (high land surface temperature), noise pollution and artificial light at night (ALAN) on breeding fitness of birds in urban areas (as reviewed by Dominoni et al. 2020; Chen et al. 2023). These factors, which are directly shaped by urban planning decisions, can influence species' breeding fitness in varied directions and magnitudes, and can interact. Understanding their effects is essential for planning and designing of urban spaces aiming to support biodiversity across a broad range of taxa (Garrard et al. 2018; Apfelbeck et al. 2020).

Regarding land use changes, alteration of urban land cover at site scales (e.g., building several residential buildings in a specific lot within a community) may not affect urban dwellers such as Chimney Swifts *Chaetura pelagica*, Common Swifts *Apus apus*, House Finches *Haemorhous mexicanus*, House Martins *Delichon urbica*, or Barn Swallows, because buildings of similar age, height and structure in surrounding neighborhoods or districts can provide complementary nesting opportunities and changing the height of buildings, or retaining old buildings might help retain these species (Hoppenbrouwer and Louw 2005). For example, mean spring temperature, nest location, wall surface materials and soffit types, as well as building height (one storey vs. more storeys), and age (new vs. old) were essential factors determining House Martin nesting preferences at the site scale (Murgui 2002; Kettel et al. 2021). However, at the landscape scale, more extensive land cover changes for urban revitalization projects may lead to a significant loss of habitats for foraging and nesting opportunities for habitat specialists such as ground foragers (Aronson et al. 2014; Marzluff 2014; Villaseñor et al. 2020).

Different forms of anthropogenic disturbance may have varying affects at different scales. Regarding noise pollution, at the site scale, reproductive success and choice of nesting sites of Great Tits *Parus major*

were found not to be affected by noise (ca 62.90–65 dB) inside their nest boxes due to physiological tolerance to noise (Halfwerk et al. 2016; Sprau et al. 2017). Conversely, at the landscape scale, traffic noise from motorways (ca 65–45 dB measured from nest boxes) has been found to reduce clutch size, number of fledglings and fledging mass most likely due to ineffective foraging in noisy breeding territories (Halfwerk et al. 2011; Klett-Mingo et al. 2016). Also, higher levels of ALAN at the landscape scale (e.g., several street blocks) have been found to positively increase foraging time and fledging success of Barn Swallow (Wang et al. 2021), while ALAN measured at the site scale has been reported to have negligible effects on breeding fitness (Zhao et al. 2022). Therefore, it is important to disentangle the scales at which these environmental factors produce the strongest effects on fitness and nesting choice to inform urban planning and biodiversity conservation in cities accordingly.

Based on a multidimensional framework (Chen et al. 2023), our main objectives were to model the relative importance of environmental factors on Barn Swallow nest site selection at the site and landscape scales to provide specific urban planning guidelines for urban regeneration (Fig. 1). We focused on Barn Swallows because as aerial insectivores and human commensals they provide essential ecosystem

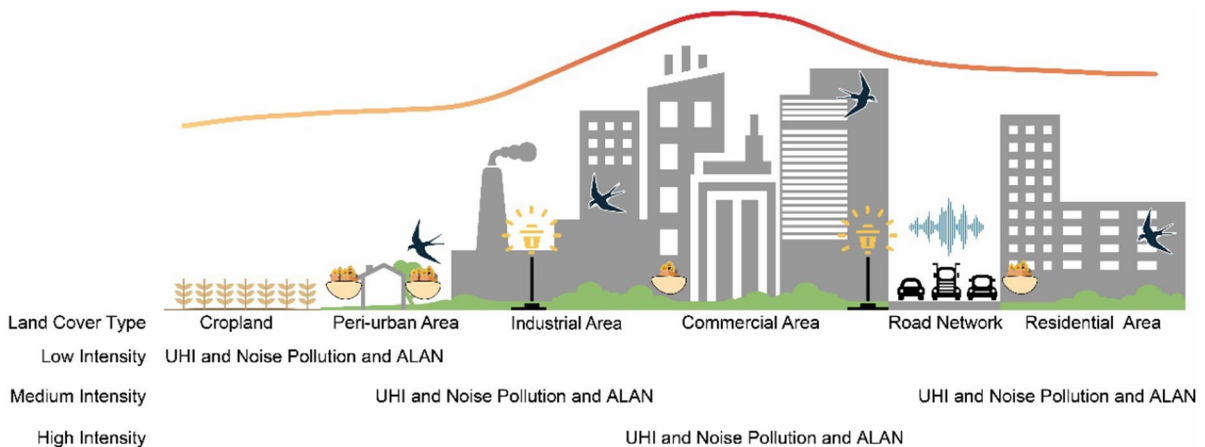


Fig. 1 Concept diagram illustrating potential environmental factors of varied magnitudes affecting the habitat choice of Barn Swallows across urbanized areas. Environmental factors include urban heat-island effect (UHI) caused by impervious surface areas, noise pollution caused by traffic and industrial activities, and artificial light at night (ALAN) near human set-

tlements. In addition, different building typologies and structures may also limit the choice of preferable nesting sites. These icons were adapted from NounProject.com and the Barn Swallow nest icons was created by Boyu Bao (CC BY 3.0; Appendix 1: Table S3)

services in urban areas such as insect population control (Turner 2010; Gaston 2022). Unfortunately, they are experiencing widespread population declines due to the loss of nesting structures and foraging grounds (Bowler et al. 2019; Spiller and Dettmers 2019). If population declines are linked to the disappearance of nesting sites and foraging grounds, it is crucial to consider maintaining or increasing these habitats during planning and design at the site scale. Alternatively, if certain environmental factors discourage species establishment at the landscape scale, zoning and land-use regulations can thus issue special amendments to balance urban development with conservation efforts (Cullingworth and Caves 2014; Levy 2017). Thus, we hypothesized that:

H1 At the site scale, urban land cover, land surface temperature and the suitable building types, rather than noise pollution or ALAN, are the key factors for the occurrence of Barn Swallow nests (Ambrosini and Saino 2010; Gruebler et al. 2010). We expected that Barn Swallow nests would more likely be detected in relatively old and low-rise buildings (Aronson et al. 2014; Newbold et al. 2015). In addition, increased land surface temperature in the early spring can benefit breeding parents by lowering energy expenditure to maintain body condition and by facilitating incubation (Lehikoinen et al. 2006; Rockwell et al. 2012). Therefore, we expected higher land surface temperature would also be linked to a higher density of Barn Swallow nests (Saino et al. 2004). As increased physiological tolerance has been found in insectivorous bird species in urban areas, we expected that noise pollution or ALAN would have limited impact on Barn Swallow nest site selection (Sol et al. 2014; Injaian et al. 2018; Zhao et al. 2022).

H2 At the landscape scale, noise pollution and ALAN, rather than urban land cover and land use zones, can determine Barn Swallow nest site selection (Tuomainen and Candolin 2011; Sol et al. 2014). Barn Swallows usually forage over larger urban areas, often several kilometers from their nesting sites, and noise pollution and ALAN can influence the availability and abundance of prey (e.g., insects) across these broader areas, indicating the overall habitat quality (Madden et al. 2022). In addition, brighter nighttime levels can extend foraging time (Wang et al. 2021) while quieter environments reduce vigilance

time during the offspring rearing stage (Klett-Mingo et al. 2016). Therefore, we expected that Barn Swallows would prefer nesting in certain urban areas with brighter nighttime light levels and lower noise levels.

Methods

Citizen science and Barn Swallow nesting sites

Barn Swallow nesting sites were obtained from a nationwide survey program in China (i.e., The China National Swallow and Swift Survey and Conservation—CNSSSC). This program was initiated in 2017 with the aim to document the nesting sites and monitor the population trends of breeding swallows and swifts in China. Amateur birders and citizen scientists perform the survey every year in the second week of May and September. We focused on Barn Swallow nests because they are highly visible and easily recognizable. Further, training in the identification of this species nest was provided by professional ornithologists. From 2017 to 2023, the survey recorded 355 transects (1–3 km) and involved more than 647 participants. The transects were positioned through an unstratified random sampling design. Although participants could select transects based on their preferences, we assumed the transects to be random in nature, because participants were randomly dispersed across urban areas with the flexibility to traverse various parts of the city. Although the transects may reflect the distribution of participants, this was minimized because the participants met together during annual meetings, and discussed how they could make the sampling cover various urban habitats, avoiding spatial clustering within a single community or district while maximizing spatial coverage in different urban districts. The habitats included city centers and edges, as well as peri-urban areas and “urban villages” (Li et al. 2019); the latter two habitat types sometimes included some agricultural fields. Studies have shown that results from habitat modeling using an unstructured random sampling design can be consistent overall with those from a structured random sampling design (Henckel et al. 2020). Given that our research goal was to explain the influence of different environmental factors on Barn Swallow nest site selection across different scales, the survey design and datasets meet the requirements for answering this

question. We acknowledge potential biases arising from uneven spatial coverage. Additionally, since our primary focus was not on predicting occupancy probabilities over the entire study area but understanding the relative importance of different environmental factors in explaining occupancy, the impact from uneven spatial sampling efforts and coverage would not strongly influence the patterns we were most interested in. To ensure a more robust assessment, potential spatial biases were also mitigated by incorporating spatial covariates in our analyses.

During the survey, participants walking at a 2 km/h pace recorded date and weather, transect number and name, GPS locations, number of individuals and nests, and species behaviors (e.g., feeding, foraging, nest-building, and flying-through) in urbanized districts within Guangdong Province (Figs. 2 and 3). The surveyed urbanized areas share

similar characteristics including building attributes, road construction standards and urban planning zoning characteristics, with mean built-up percentages of 58.70 and 73.52%, and standard deviations of 20.62 and 20.80 for radii of 1.26 and 5 km, respectively. On the other hand, as these urbanized areas vary in the scale of urbanization, they differ in how these features are distributed spatially and in their composition in certain areas, such as variations in building types, ages, heights, and the density and simplicity of road networks. The common characteristics provide a consistent basis for examining the scale at which urban environmental factors influence Barn Swallow nest site selection, which can be used for broader cross-regional comparison with Barn Swallow nesting selections identified in other urban environments at similar latitudes. Since we only had data on where Barn Swallow nests

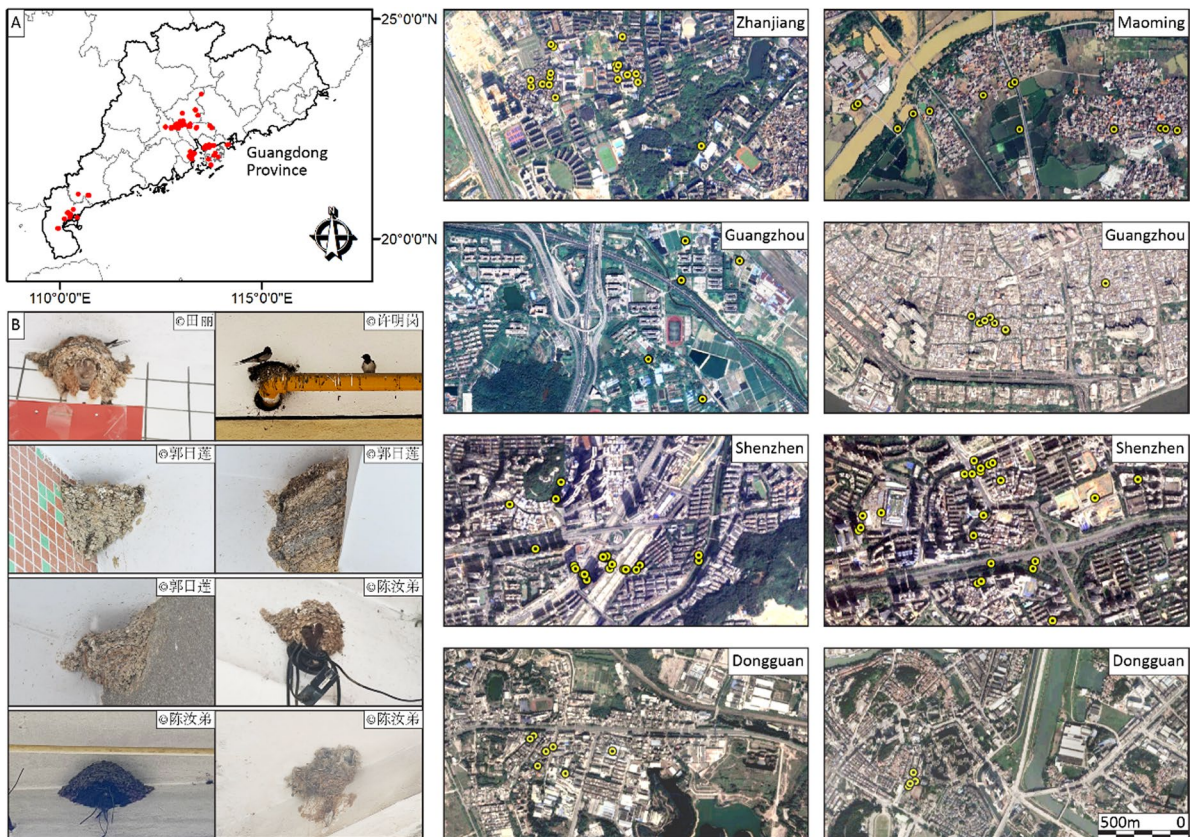


Fig. 2 Barn Swallow *Hirundo rustica* nesting sites found in urbanized areas (Zhanjiang, Maoming, Guangzhou, Shenzhen and Dongguan) of Guangdong Province during citizen science

surveys. Satellite photos were selected to show a range of habitats with varying built-up percentages

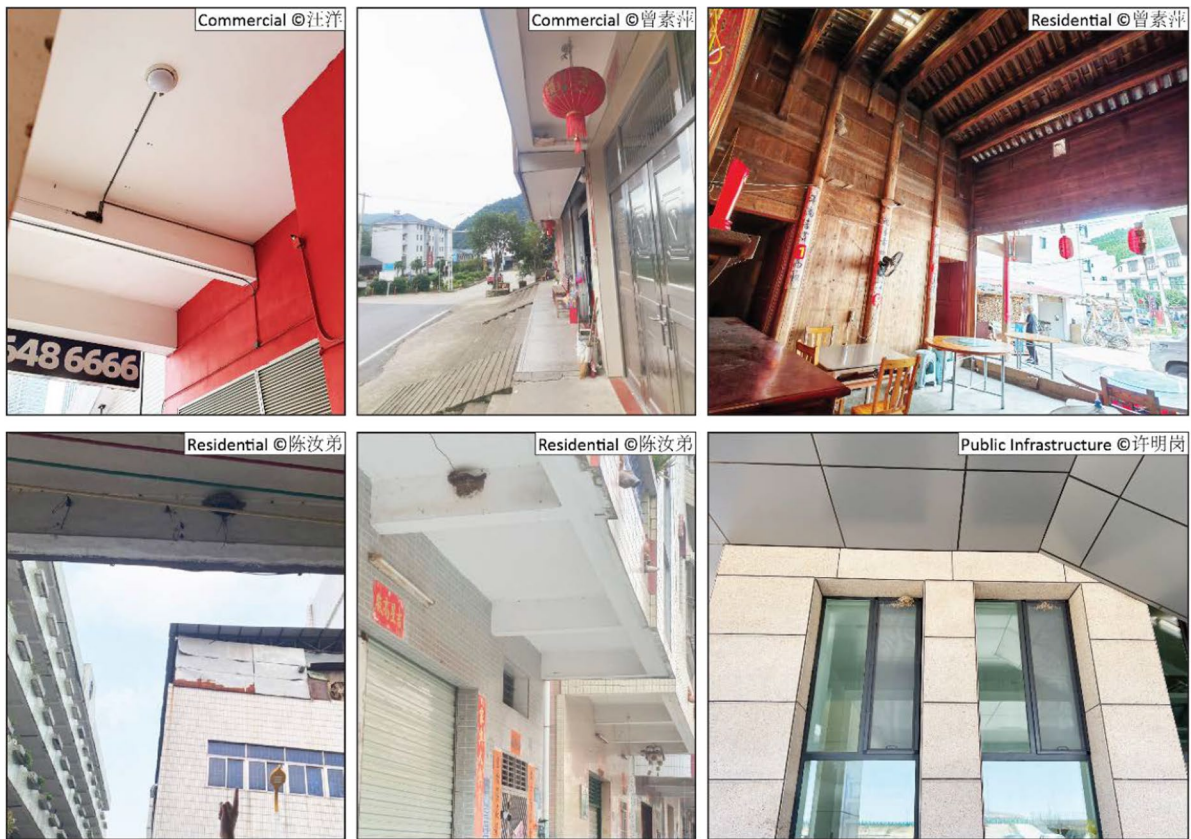


Fig. 3 Typical nest sites of Barn Swallows in our study locations. In southern China, Barn Swallows usually build their nests outside the first floor of buildings with vertically hang-

ing structures, which are common in old buildings designed for residential and commercial uses. These hanging structures can facilitate the nesting building and provide better shading

were present, we used records from the same survey where Barn Swallow nests were not recorded during the transect survey or in transects where Barn Swallow's behaviors were recorded as 'flying high up in the sky at a fast speed' to represent locations where nests were absent. We acknowledge that the absence of nests in urban areas may arise from other factors such as detection limitations due to inaccessibility to indoor spaces or deliberate destruction of nests inside houses. These biases may have been minimized because participants usually asked local people about the presence of nests when there were signs of Barn Swallows. While some people may deter birds to breed in their properties, based on our extensive years of fieldwork experience on this species in China, the relative rarity of such events

suggests that their overall impact on the evaluated environmental factors is negligible.

The effects of environmental factors at multiple spatial scales

To study nesting site preferences of Barn Swallows, we took a multi-scale approach and considered multiple spatial scales (0.5, 1.26, 2.5 and 5 km) (Store and Jokimäki 2003). These distances account for foraging distances and home ranges of common urban birds (Johnson 1980; Newson et al. 2014; Plummer et al. 2020; Madden et al. 2022). The larger distances (2.5 and 5 km) are also commonly used in landscape ecology studies and closely related to urban planning (Wu 2004; Newson et al. 2014). For Barn Swallows, breeding pairs in urban areas have a mean

maximum foraging distance of 1.26 km ranging from 0.11 to 11.26 km, based on a GPS tagging study on Barn Swallow foraging behaviors (Madden et al. 2022). These distances highlight the Barn Swallow's remarkable variability in flight ranges, demonstrating their ability to forage across both relatively short and extended distances within urban environments. In addition, we found a strong correlation of landscape composition between 0.5 km and 1.26 km (Pearson $r=0.83$) as well as 2.5 km and 5 km (Pearson $r=0.91$). To minimize spatial correlation between these scales and avoid multiple testing, we worked at 1.26 km radius as the site scale and 5 km radius as the landscape scale (for further details see also Appendix 1).

Quantification of environmental factors

Land-use change

We acquired land-use data from Dynamic World global datasets in Google Earth Engine (<https://developers.google.com/earth-engine/datasets>). The available datasets contained nine categories (i.e., water, trees, grass, flooded vegetation, crops, shrub and scrub, built areas, bare, snow and ice) at a 10-m pixel resolution from 2015 to 2023 based on Sentinel-2 satellite imagery (Karra et al. 2021; Brown et al. 2022). We reclassified these nine categories into (1) built areas, (2) cropland, (3) green areas, including all vegetated areas, (4) water and (5) bare grounds. These five categories, excluding the 'other' category, have been suggested to be closely associated with the presence of Barn Swallows (Ambrosini and Saino 2010; Gruebler et al. 2010).

Urban heat island effect

We extracted land surface temperature to measure urban heat-island effect. Land surface temperature was calculated from images of the Landsat 8 Operational Land Imager (OLI) satellite, equipped with a 30-m resolution thermal infrared sensor, which started operation in 2013. Satellite imageries were first resampled using the bilinear method in Google Earth Engine to the 10-m resolution with a projection of WGS 1984, in order to match spatial resolution across environmental factors (Gorelick et al. 2017). We computed the vegetation fraction for each nest

based on Normalized Difference Vegetation Index (NDVI) (Choudhury et al. 1994), surface emissivity (Sobrino et al. 2004) and then land surface temperature for the corresponding years (Alemu 2019). We used average temperature from February and March because these are the times of the year with the lowest cloud cover and also correspond to the onset of breeding activities for Barn Swallow in southern China (Zhao et al. 2022). For years with missing or abnormal values due to cloudy imagery for February or March, the best available data computed in the preceding year was used (Hall et al. 2010; Zhong et al. 2014).

Noise pollution

Traffic is considered one of the most prominent noise sources in urban areas, with the global network potentially expanding to 70 million lane-kilometers and the number of vehicles reaching 2.8 billion by 2050 (Dulac 2013; WHO 2018; Yang et al. 2020). Urban areas with more complex road networks such as dense road intersections and multiple lanes, experience a higher number of high-speed vehicles, which directly contributes to increased noise (Lu et al. 2019). Consequently, the roads networks and associated noise have been shown to alter bird community composition and drive declines in species populations (Kociolek et al. 2011; Cooke et al. 2020a, b). However, because of the large extent of our study area, we were not able to collect sound measurements, and rather used road density and simplicity as a proxy for noise pollution. We acknowledge the limitation of using these two proxies, as they may not fully capture micro-scale noise levels at the site where Barn Swallows select their nesting sites. Furthermore, it is important to note that actual noise levels can be influenced by additional factors, including traffic volume, vehicle speed, and road surface material (Yang et al. 2020). Road density was defined as the ratio of the total length of the road network to the buffer area and road simplicity as the ratio of the total length of the road network to the number of road segments (Boeing 2017). We accessed OpenStreetMap (OpenStreetMap contributors 2017) via the python package "OSMnx" (Boeing 2017). We retrieved historical OpenStreetMap data from 2017 to 2023 for these calculations. Eight locations returned no data, so we manually checked the satellite imagery to ensure that

no information was missing from the OpenStreetMap database. We found these locations were within small villages, so we thus assigned them a road density and simplicity of 0.

Artificial light at night

Artificial light at night (watt per steradian per square meter) was extracted in Google Earth Engine from the global nighttime lights time series (2012–2022), produced by NASA/NOAA Visible Infrared Imaging Radiometer Suite (VIIRS) with a 464-m resolution (Elvidge et al. 2021). The lack of available VIIRS datasets for the year 2023 was compensated with data from 2022. Bilinear resampling techniques were also used to match spatial resolution of 10 m across environmental factors (Gorelick et al. 2017).

Building characteristics and urban planning land-use categories

The architectural characteristics of buildings are one of the most crucial factors to determine whether Barn Swallows can build their nests in an area. For example, Barn Swallows in Asia are usually observed in older neighborhoods and low-rise residential buildings (Pagani-Núñez et al. 2016; Zhao et al. 2022), because most of these buildings were built several decades ago with prevailing architectural features of that time, such as architectural canopies or cantilevered horizontal structures that can aid Barn Swallows to attach their nests (Marzluff 2001; Zhu 2009). Therefore, we used building years, heights and urban planning land-use categories to represent the characteristics of buildings used by Barn Swallows. First, based on GPS coordinate of Barn Swallow nesting sites, we geolocated each building on Baidu and Google maps. Then, we obtained the construction years of these buildings from their official or real estate websites (Appendix 1: Table S1). For old villages, we coded them as the year of 1984 to distinguish them from other buildings, since the majority of buildings in our study area were built within the last two decades (Wu 2015). Second, we used the best-available building height datasets in 2020 for China at a 10-m spatial resolution to represent the building heights during the period of 2017 to 2023 (Wu et al. 2023). Lastly, we obtained urban planning land-use categories from Sentinel-2A/B, OpenStreetMap

and other geospatial big data with a 10-m resolution (Gong et al. 2020). This dataset contains information about urban planning land uses including residential, commercial, industrial, transportation, and public management and service categories in 2018. To assess the nesting building preference for residential and commercial buildings, we kept the residential and commercial categories as their own categories and grouped industrial, transportation, and public management and service categories as an “other” category. Since these categories are evaluated every five years, we used the data from 2018 to represent urban planning land-use types from 2017 to 2023 (State Council of the People’s Republic of China 2021).

Statistical analyses

To evaluate the relative importance of environmental variables that determine the preference for nesting sites by Barn Swallows, we used generalized additive mixed-effect models (GAMMs) to fit our absence and presence data with a binomial distribution, logit link function and a spatially explicit model structure (Dormann et al. 2007). We used GAMMs because such models allow the addition of latitude and longitude data as smoothing terms to control spatial autocorrelation (Guisan and Zimmermann 2000; Lobo et al. 2010). Prior to building our models, we centered and scaled our study variables to mean 0 and standard deviation 1, which reduces heterogeneity of variance due to different value ranges and measurement units. We constructed two sets of models according to the two scales (1.26 km and 5 km radii).

We ran the two sets of models for the different scales with the absence-presence of Barn Swallow nests as the dependent variable. The explanatory variables included land-use change (percentages of built-up areas within buffers), crop area percentages, land surface temperature ($^{\circ}\text{C}$), road simplicity (the ratio of total length road network to the number of road segments), ALAN ($\text{nW cm}^{-2} \text{sr}^{-1}$), building year, building height and urban planning land-use categories, while the district was used as the random factor. In the preliminary analysis, we estimated spatial autocorrelation for model residuals and computed Moran’s I, but significant spatial correlation ($p < 0.05$) was found. Therefore, we added a Gaussian smooth structure based on latitude and longitude to control for spatial autocorrelation in our mixed-effect

models. Lastly, a correlation matrix of explanatory variables at the site and landscape scale showed that the variables used in models had not strong correlations (>0.6) and is provided in Appendix 1: Figs. S1 and S2.

To select the best models (Appendix 1: Table S2), we implemented a top-down strategy following Zuur et al. (2009). Specifically, we applied model selection on explanatory variables based on Akaike Information Criterion by fitting models with maximum likelihood and computing variation inflation factors (VIF) to examine multicollinearity. VIFs <4 were set as a threshold (O'Brien 2007). Explanatory variables were removed from the models based on collinearity and non-significance until the highest deviance was explained by the model. After the optimal model was identified, we refit the model with REML (Restricted Maximum Likelihood) and obtained the final results. Finally, we implemented model validation following Zuur et al. (2009) by verifying the normality of residuals via histograms and assessing homogeneity between residuals and fitted values and between residuals and each explanatory variable.

All statistical analyses were performed using R language 4.2.3 (R Core Team 2021) in R Studio (RStudio Team 2020). We used packages “ggplot2” v3.4.3 (Wickham 2016), “corrplot” v0.92 (Wei et al. 2021), “mgcv” v1.8–42 (Wood 2011), “DHARMA” v0.4.6 (Hartig 2022), and “performance” v0.11.0 (Lüdtke et al. 2021) to run these analyses.

Results

Urban planning land-use category and building characteristics

After data processing, 177 Barn Swallow nests and 114 absent nest locations were retained. The presence of Barn Swallow nests was found mostly in residential areas, commercial areas and public facilities near greenspaces, respectively (34%, 22% and 11%; Fig. 4). Among these buildings, the mean height of buildings was 18.87 ± 5.10 m (six-story buildings), with the lowest height 9.78 m (three-story buildings) and the tallest height 36.75 m

(twelve-story buildings). The oldest buildings were more than thirty years old and usually in villages, whereas the newest building in which Barn Swallow nests were found was constructed in 2019.

Model results at the site scale (1.26 km radius)

After accounting for variation in latitude and longitude, the top model identified that at the site scale higher land surface temperatures and older buildings were significantly related to a higher likelihood of Barn Swallow nesting sites (Table 1 and Fig. 5). Building height and road simplicity did not explain the presence of Barn Swallow nests. Nor did the model show significant differences in Barn Swallow nesting site preferences between urban planning land-use categories (i.e., residential vs. other, commercial vs. other, and residential vs. commercial). To assess the significance of the urban planning land-use categorical factor, we compared the top models with and without the urban planning land-use category and found that this categorical factor was not significant ($df=2$, $F=0.09$, $p=0.91$).

Model results at the landscape scale (5 km radius)

The spatially explicit top model accounting for variation in latitude and longitude at the landscape scale showed that higher mean artificial light at night and road simplicity were positively correlated with Barn Swallow presence (Table 2 and Fig. 5). In contrast, neither land surface temperature, building height nor the year of building construction was correlated with the presence of Barn Swallow nests. Similar to the results at the site scale, the urban planning land-use category did not significantly correlate with the presence of Barn Swallow nests. The top model at the landscape scale indicated that the urban planning land-use category was not a significant predictor of Barn Swallow nest presence ($df=2$, $F=0.57$, $p=0.57$).

Discussion

Although it is known that urban areas filter out a large proportion of regional species (McKinney 2002; Santos et al. 2024), growing evidence has shown that cities have great potential to conserve

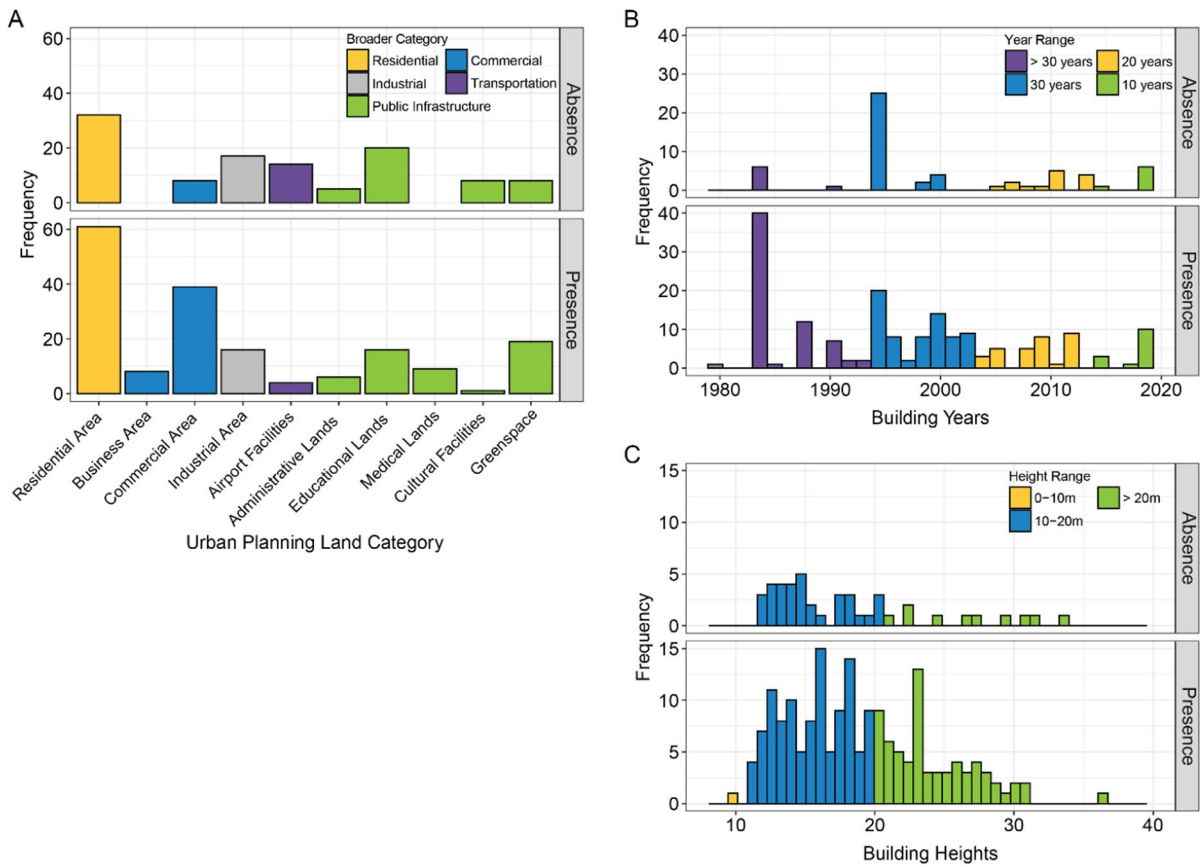


Fig. 4 Barn Swallow nests distributed across different urban planning land-use types (A) and characteristics of building heights and years (B and C)

Table 1 Results of selected, spatially explicit, generalized additive mixed-effect models fit by restricted maximum likelihood at the site scale

Model	Parameters	β	SE	<i>t</i>	<i>p</i>
	Intercept	1.36	0.84	1.62	0.11
	Mean February and March land surface temperature	2.82	0.47	5.95	< 0.01
	Building height	- 0.50	0.33	- 1.50	0.14
	Building year	- 0.94	0.36	- 2.59	0.01
	Residential planning category	- 0.01	0.83	- 0.02	0.99
	Commercial planning category	0.34	0.89	0.38	0.70
	Road simplicity	0.21	0.42	0.49	0.62

The response variable was the presence/absence of Barn Swallow nests, while explanatory variables included mean February and March land surface temperature, artificial light at night, building height, building year, urban planning category (residential, commercial and other), and road simplicity; city, latitude and longitude were random factors. Explanatory variables were scaled and centered accordingly

Significant effects are shown in bold

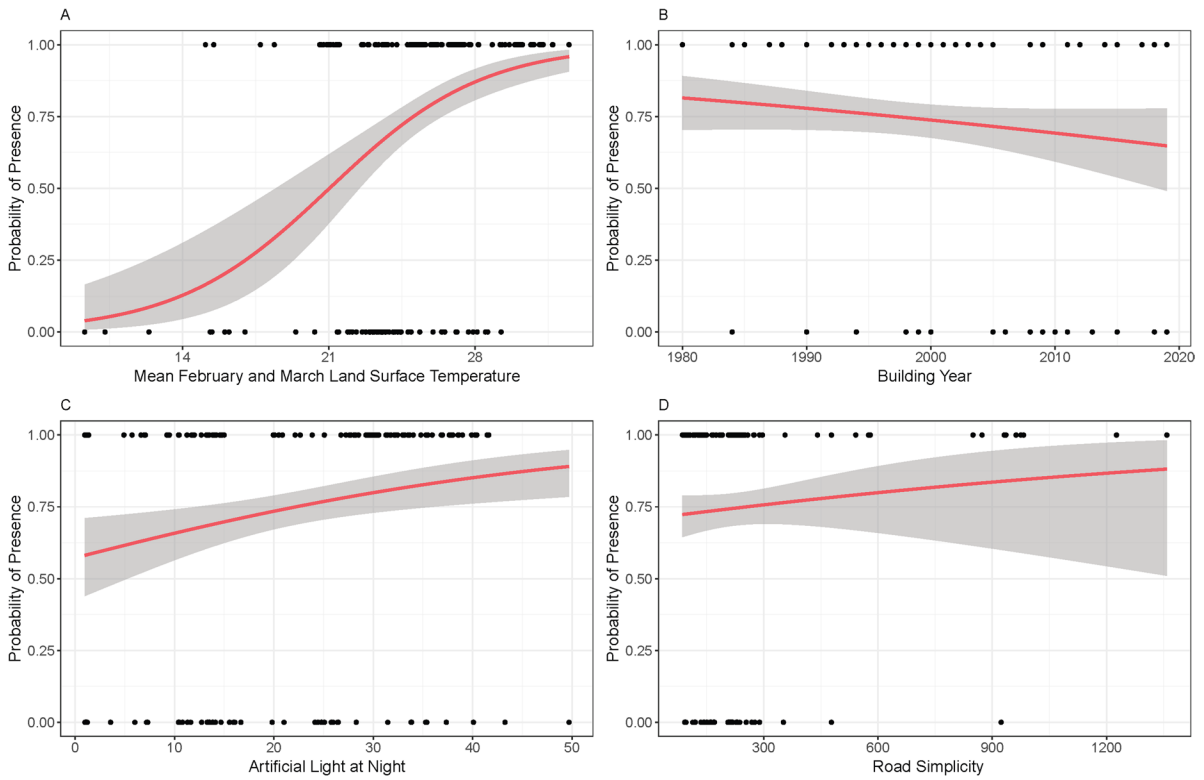


Fig. 5 Diagrams showing relations between mean February and March land surface temperature (A) and building year (B) at the site scale, as well as artificial light at night (C) and road

simplicity (D) at the landscape scale, and presence of Barn Swallow nests with 95% confidence intervals

Table 2 Results of selected, spatially explicit, generalized additive mixed-effect models fit by restricted maximum likelihood at the landscape scale

Model	Parameters	β	SE	t	p
	Intercept	0.83	0.56	1.49	0.14
	Mean February and March land surface temperature	0.23	0.35	0.65	0.52
	Mean artificial light at night	0.73	0.35	2.10	0.04
	Residential planning category	0.28	0.56	0.50	0.62
	Commercial planning category	0.77	0.72	1.07	0.29
	Road simplicity	1.87	0.60	3.10	<0.01

The response variable was the presence/absence of Barn Swallow nests, while explanatory variables included mean February and March land surface temperature, artificial light at night, urban planning category (residential, commercial and other), and road simplicity; city, latitude and longitude were random factors. Explanatory variables were scaled and centered accordingly

Significant effects are shown in bold

not only common species but also threatened species (Ives et al. 2016; Jokimäki et al. 2018; Li et al. 2024). However, studies rarely consider the implications of different land use zones, building attributes, and urbanization-associated environmental factors to investigate species habitat selection at the site and landscape scales in urban areas (Humphrey et al. 2023). Understanding how species respond to these environmental changes can aid species-targeted conservation approaches in urban planning, which must be planned at the optimal scale to make efficient use of limited conservation resources. Using publicly accessible satellite imagery and citizen science data for Barn Swallow nests, we recorded strong scale effects on the factors determining presence of an aerial insectivore in one of the most densely urbanized regions of the world. We found support for our hypotheses that building year and land surface temperature strongly determine the presence of Barn Swallow nests at the site scale, whereas road network complexity and

artificial light at night are positively associated with Barn Swallow nests at the landscape scale, suggesting complex interactions between Barn Swallow nest site selection and the environment at multiple spatial scales.

Land surface temperature and building year at the site scale (1.26 km)

We found that increased land surface temperature exerted a positive impact on the presence of Barn Swallow nests. This result is consistent with previous research suggesting increased temperature in livestock farms was associated with more Barn Swallow nests and breeding activities (Saino et al. 2004; Ambrosini et al. 2006; Ambrosini and Saino 2010; Grübler et al. 2010; Roseo et al. 2024). Warmer temperatures can contribute to the success of Barn Swallow reproduction for several reasons, although it is important to note that there is likely an upper thermal limit beyond which reproduction may be hindered. Warm temperatures could extend the window of favorable thermal conditions for Barn Swallows to initiate breeding and build nests (Crick and Sparks 1999; Møller 2007). To a point, warmer temperatures could lower the physiological stress of egg production and reduce the cost of incubation, thus contributing to enhanced female body condition and nest attendance (Englert Duursma et al. 2019; Saino et al. 2004). Studies have found that warm temperatures were more important to explain fitness at the micro-scale habitat than the macro-scale habitat, especially with regards to enhancing egg quality (Ambrosini and Saino 2010). Furthermore, studies show that increased ambient temperatures may be an indicator of higher food abundance—for example, warm temperatures can increase the presence of flies (Diptera)—suggesting that places with warm thermal conditions may lead to better offspring quality (Ambrosini et al. 2006; Roseo et al. 2024). Our result provides new evidence that Barn Swallows in urban areas also preferred locations with higher ambient temperature, suggesting Barn Swallow may have adapted to an urban lifestyle by selecting urban microhabitats for their nests where warmer thermal conditions may shelter advanced laying behaviors against marked temperature fluctuation in the early spring (Crick and Sparks 1999; Zhao et al. 2022).

Although previous research reported the architecture of rural buildings (traditional stables vs. modern

sheds) could affect the abundance of Barn Swallow nests in Italy (Ambrosini et al. 2002), to our knowledge, no study systematically considered the impact of building attributes (i.e., height and age) on Barn Swallow nests in urban areas. We found that the building year at the site scale was an important factor to predict where Barn Swallows select their nesting sites. One explanation could be that the building year largely reflects the dominant architectural styles, materials and structures of the years when buildings were constructed (Wu 2015). Building types constructed in the surveyed locations in the early 2000s were more likely to be built with suitable features for Barn Swallow nests compared to buildings built in the 2020s (e.g., traditional low or medium concrete buildings vs. glass-walled high-rise buildings). Specifically, the traditional buildings usually have limited heights of up to five to seven floors, with open soffits, small features or signage on walls and potentially open balconies or staircases. Barn Swallow nests are usually found in old neighborhoods and located in the roofs and awnings of the first floor of low-rise buildings in cities, with coarse wall building materials like cement concrete mortar that can support mud pellet nests (Zhao et al. 2022). Therefore, our results highlight the fact that certain building types in old neighborhoods may be important habitats for certain species. Understanding how buildings are related to the presence of species in certain urban areas is necessary when urban regeneration planning becomes the main paradigm for urban development (Li et al. 2019; Hui et al. 2021).

Road simplicity and artificial light at night at the landscape scale (5 km)

Previous research has recorded relationships between the characteristics of road networks and the abundance of many bird species including the Barn Swallow in urban areas (e.g., Palomino and Carrascal 2007; Cooke et al. 2020a, b). We found that Barn Swallow nests were more abundant when road networks were simpler. In other words, more Barn Swallow nests were present in areas with longer road lengths and with fewer road intersections, indicating that the road network of preferred nesting areas is less interconnected and the landscape is less fragmented (Boeing 2017). Therefore, our results suggest Barn Swallow may be able to tolerate and select nesting

sites with a lower number of road segments and with relatively large landscape patches (Ambrosini and Saino 2010; Sol et al. 2014). Furthermore, our result was in line with previous research showing a positive effect of ALAN on Barn Swallow nests. Studies have suggested that species with low-light vision such as Barn Swallow may seize the opportunity to extend their foraging time with the help of ALAN in urban areas, which can lead to more food resources for offspring and higher breeding success (Senzaki et al. 2020; Wang et al. 2021). The ability of Barn Swallows to select areas with certain ALAN may help explain why certain species could thrive in urban areas via flexible foraging behaviors (Tuomainen and Candolin 2011). Overall, these patterns in our study seem to suggest that Barn Swallows can respond to these mixed effects at multiple spatial scales and efficiently adapt to various environmental conditions across the urbanized landscape (Zhao et al. 2022).

Limitations and future research

We must acknowledge certain limitations in our study. For instance, the environmental factors studied here may not reflect all the dimensions of human disturbance in this urban landscape. Barn Swallows have close cultural ties with people, so incorporating human perceptions of Barn Swallow nests may help address this question (Alberti and Wang 2022). Detailed assessment of architectural attributes such as building structures and typologies, building materials and vertical hanging structures could also provide additional understanding regarding this question (Ambrosini et al. 2002). At the site scale, the availability of mud resources may also explain nest site selection. Furthermore, we did not have prey data for Barn Swallow nests, which could be a key factor limiting nesting site choice (Ambrosini and Saino 2010). More generally, since we only focused on a single species, future research understanding habitat selection for multiple species can help provide detailed insights on how to maximize conservation efforts in urban areas.

Implications for urban planning and management

Our study offers important insights for urban planning and management by demonstrating that urban planning outcomes can have direct impacts on

wildlife (Apfelbeck et al. 2020). For instance, the ecological value and importance of older neighborhoods and substitution with equivalent biodiversity-friendly features in newly built sections of the urban fabric should be evaluated thoroughly during the master planning process for urban regeneration projects (Marzluff 2014; Buron et al. 2022). Architectural typologies and building features and materials that are beneficial for Barn Swallows and other urban species can be considered wherever possible during the architectural design of new buildings. For example, integrating nest support structures such as soffits, exterior ledges and cornices in lower storeys systematically to façade design are feasible options to facilitate nest building by the Hirundine family (swallows and martins) (Murgui 2002; Kettel et al. 2021). Natural stone, rough-sawn wood, textured plaster and stucco, and brick and mortar contribute to creating coarse and rough finishes and increasing grip and adhesion for wall surfaces, which are ideal for mud nest building. We can also design animal-friendly building features that direct nest building to locations where maintenance and cleaning can be efficiently conducted, and mutual bird and human activity disruption can be minimized.

Regarding applications at the landscape level, urban transportation planning may incorporate wildlife corridors when updating infrastructure to mitigate the negative impact of complex road networks (Mason et al. 2007). Biodiversity-friendly strategies for urban management such as keeping ALAN within a certain threshold in areas with abundant wildlife should be considered when drafting urban planning and design guidelines (Garrard et al. 2018; Visintin et al. 2024). While our results show that increased ALAN intensity from 0 to 40 nW cm⁻² sr⁻¹ at the landscape scale may be associated with a higher chance of finding Barn Swallow nests, this may not necessarily result in higher reproductive success, and future research is needed on this issue (Injaian et al. 2018; Wang et al. 2021). Implementing urban planning initiatives for lighting schemes can benefit ALAN-sensitive species in urban areas. For example, several planning departments such as the City of Flagstaff in Arizona and the City of Boulder in Colorado in North America have already implemented strict lighting rules through local ordinances by requiring full cutoff (fully shielded) lighting fixtures with color temperature rating less than 3000 Kelvin

for exterior lighting. In addition, the City of Toronto Ontario requires illumination on rooftops and exterior facades be extinguished between the hours of 10 p.m. and 6 a.m. (City of Toronto 2017). These planning and design specifications can be further enhanced by requiring a motion sensor and timer to automatically turn off the lights after a period of inactivation, especially for areas installed with high-illuminance fixtures in sports fields and parking lots (City of Boulder 2009). Considering these findings, local and regional zoning amendments could further enhance the practical applicability of biodiversity-friendly concepts.

Conclusion

Urban planning outcomes are an important factor for urban wildlife as habitat choice can be directly linked to survival and reproduction (Block and Brennan 1993; Ambrosini and Saino 2010; Humphrey et al. 2023; Roseo et al. 2024). Even though species may manage to respond to complex landscape components, environmental factors at different scales can produce mixed effects on habitat choices. Here, we found that Barn Swallows in urban areas of southern China responded to building year, temperature, road network density and ALAN when building their nests in a complex fashion. Our results suggest that although Barn Swallow populations can adapt to increasingly urbanized environments, reducing the availability of older buildings in cities, or constructing new housing without biodiversity-friendly features, can pose considerable threats to this and other urban bird species.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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