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Nest site and nesting substrate selection by House Sparrows along an urban gradient in Nuwara Eliya, Sri Lanka

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Abstract The House Sparrow *(Passer domesticus)* is an obligate synanthrope experiencing significant population declines across its global range, yet remains locally abundant in certain urban centers. Understanding the drivers of these robust populations is critical for urban avian conservation. We assessed the abundance and nest site selection of House Sparrows across an urban-to-exurban gradient in Nuwara Eliya, Sri Lanka. Data was collected from 20 plots, each representing one of four habitat types. We employed a Negative Binomial Generalized Linear Model to account for overdispersion of data and used Pearson's Chi-square tests to analyze the associations between nest substrate selection, habitat, and building architecture. A total of 185 active nests were recorded. Nest abundance did not vary significantly across habitat types (X^2 = 3.49, p = 0.32) or along building cover (Z = 0.72, p = 0.47) and green cover (Z = -1.78, p = 0.08) gradients, indicating a ubiquitous distribution. However, nest substrate selection was highly non-random and was more strongly associated with building architecture (X^2 = 178.3, p < 0.001) than with broad habitat categories (X^2= 47.34, p < 0.001). Nest boxes were the primary substrate on residential houses (n=45), while commercial buildings and shops provided diverse opportunistic sites such as roofing sheets and wall crevices. The House Sparrow population in Nuwara Eliya is stable and resilient, likely sustained by a combination of traditional human provisioning (nest boxes) and the species' plasticity in exploiting modern architectural features. Our findings suggest that for this species, immediate structural characteristics of the built environment are more significant drivers of occupancy than macro-habitat urbanization labels. This study provides a vital baseline for avian conservation in Sri Lanka and highlights the role of anthropogenic micro-habitats in maintaining urban biodiversity.

Keywords: ecology, nesting, urban, tropical, birds

Összefoglalás A házi veréb *(Passer domesticus)* obligát szinantróp faj, amely globális elterjedési területén jelentős állománycsökkenést mutat, ugyanakkor egyes városi területeken továbbra is nagy egyedszámban fordulhatnak elő. Az ilyen populációk fennmaradását meghatározó tényezők megértése kulcsfontosságú a városok madarainak védelme szempontjából. Vizsgálatunkban a házi veréb abundanciáját és fészkelőhely-választását elemeztük egy városi–városkörnyéki gradiens mentén, Srí Lanka Nuwara Eliya térségében. Az adatgyűjtés 20 mintaterületen történt, amelyek négy különböző élőhelytípust fedtek le. Az adatok elemzésére negatív binomiális általánosított lineáris modellt alkalmaztunk, míg a fészket tartó felület választása, az élőhely és az épületek tulajdonsága közötti összefüggéseket Pearson-féle khi-négyzet próbákkal elemeztük. Összesen 185 aktív fészket találtunk a vizsgálati időszakban. A fészkek abundanciája nem különbözött szignifikánsan az élőhelytípusok között (X^2 = 3,49; p = 0,32), sem az épületborítottság (Z = 0,72; p = 0,47), sem a zöldfelületi borítottság (Z = -1,78; p = 0,08) gradiens mentén, ami az elterjedés általános jellegére utal. Ezzel szemben a fészket tartó felület kiválasztása erős mintázatot mutatott, és szorosabban kapcsolódott az épületek architektúrájához (X^2 = 178,3; p < 0,001), mint a tágabb élőhely-kategóriákhoz (X^2 = 47,34; p < 0,001). Lakóházakon a mesterséges odúk voltak az elsődleges fészkelőhelyek (n = 45), míg a kereskedelmi épületek és üzletek változatos, alkalmi fészkelőhelyeket kínáltak, úgy mint tetőlemezek és falak repedései. A vizsgált házi veréb állomány stabil, fennmaradását valószínűleg együttesen biztosítja a hagyományos emberi gondoskodás (odúk kihelyezése) és a faj nagyfokú plaszticitása a modern építészeti elemek kihasználásában. Eredményeink arra utalnak, hogy e faj esetében a városiasodásra utaló, tágabb élőhelyi kategóriákkal szemben, az épített környezet közvetlen, szerkezeti jellemzői fontosabb meghatározói a megtelepedésnek. A tanulmány alapvető kiindulópontot nyújt a Srí Lanka-i madárvédelmi kutatások számára, és rámutat az antropogén mikroélőhelyek szerepére a városi biodiverzitás fenntartásában.

Kulcsszavak: ökológia, fészkelés, városi, trópusi madarak

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Introduction

The House Sparrow (*Passer domesticus* Linnaeus, 1758) is one of the most widespread bird species globally (Anderson 2006, Liebl *et al*. 2015), having established populations across various continents through both natural range expansion (Ravinet *et al*. 2018, Hanson *et al*. 2020) and human-mediated introductions (Lima *et al*. 2012, Andrews & Griffith 2016). As a classic "urban exploiter," House Sparrows have developed a commensal relationship with humans, relying heavily on anthropogenic resources for survival (Sætre *et al*. 2012, Ravinet *et al*. 2018). Their adaptability has historically enabled them to thrive in human settlements worldwide (Anderson 2006, Liebl *et al*. 2015).

Despite their apparent adaptability, House Sparrow populations have experienced significant declines across much of their global range since the late 20th century (Seress *et al*. 2012, Singh *et al*. 2013, Berigan *et al*. 2020, Mohring *et al.* 2021). These widespread declines have raised concerns among conservationists and ornithologists about the long-term viability of urban House Sparrow populations.

Multiple factors have been associated with the decline of House Sparrows in urban environments. These include changes in urban architecture that reduce suitable nesting sites (Newton 2004, Shaw *et al*. 2008), decreased food availability due to intensified agricultural practices (Robinson *et al*. 2005, Summers-Smith 2005), increased predation pressure (MacLeod *et al*. 2006, Bell *et al*. 2010), and various aspects of urbanization such as pollution, infections (Bichet *et al*. 2013, Herrera-Duenas *et al*. 2014), and reduced availability of high-quality food for nestlings (Seress *et al.* 2012). Among all these proposed factors, some authors have also suggested electromagnetic radiation from telecommunication towers to be a potential reason linked to the House Sparrow decline (Balmori & Hallberg 2007, Everaert & Bauwens 2007, Balmori 2021). Therefore, the decline in House Sparrow populations across the globe appears to be a complex phenomenon with multiple contributing factors.

In Sri Lanka, House Sparrows were historically common throughout the country, particularly in areas with human settlements. While comprehensive and quantitative data on House Sparrow population trends across Sri Lanka are lacking, anecdotal reports and localized observations suggest a general pattern of decline or local extinctions in many parts of the country over the recent decades. In stark contrast to these reported local trends, Nuwara Eliya, a city in Sri Lanka's central highlands, appears to sustain a robust House

Sparrow population, presenting a unique context for studying the factors contributing to their persistence.

Despite the global research interests and both local and global population declines, there has been no research specifically examining the population trends or ecology of House Sparrows in Sri Lanka. This represents a significant gap in understanding the species' distribution, population trends, habitat requirements and also causes of widespread local extinctions in this tropical island. The present study aims to address this research gap by investigating the trends in nest site and nest substrate selection of House Sparrows in Nuwara Eliya, Sri Lanka in a previously unstudied context, providing insights into local factors that may support House Sparrow persistence despite global and local declining trends.

Materials and Methods

Study site

Nuwara Eliya (6°58′N 80°46′E), situated in Sri Lanka's Central Highlands at 1,868 m elevation above mean sea level, represents a tropical montane climate characterized by distinct seasonal patterns (De Costa 2008, Nissanka *et al*. 2023). This area experiences bimodal rainfall with annual precipitation averaging 1,900 mm (Amarasinghe & Basnayake 2022, Nissanka *et al*. 2023). The average annual temperature ranges between 11–20 °C and the average annual relative humidity is around 65–93% (Thilakarathne *et al*. 2024). The landscape is dominated by montane rainforests, tea plantations, and anthropogenic settlements. Much of its once prominent natural montane forests have been converted to tea plantations since the middle 19th century (Wickramagamage 1998, Thilakarathne *et al*. 2024). The colonial-era urban design features including gabled roofs, timber-framed structures, and veranda-lined buildings can still be seen within the city limits. Human population density of the Nuwara Eliya District is estimated to be around 427 individuals/km^2 as of 2024 and has been steadily increasing since the past few decades (DCSSL 2025).

Habitat selection and survey design

A 10-hectare (100 × 100 m) square grid was laid over the study area, and a total of 20 grid squares (hereafter plots) were selected by random stratified selection using QGIS (QGIS Development Team 2024) across the 4 habitat types; 1) urban, 2) suburban, 3) periurban, and 4) exurban, identified within the study area *(Figure 1)*. The habitat types were determined through preliminary in-field observations and were defined by characteristic features such as commercial infrastructure, residential properties, private and public green spaces, and agricultural land use following De Laet *et al.* (2011) *(Table 1)*. We ensured not to select adjacent plots in order to minimize spatial autocorrelation. In each of the plots, we determined the building cover percentage and the green cover percentage of each plot using QGIS spatial analysis (version 3.34.5; QGIS Development Team 2024).

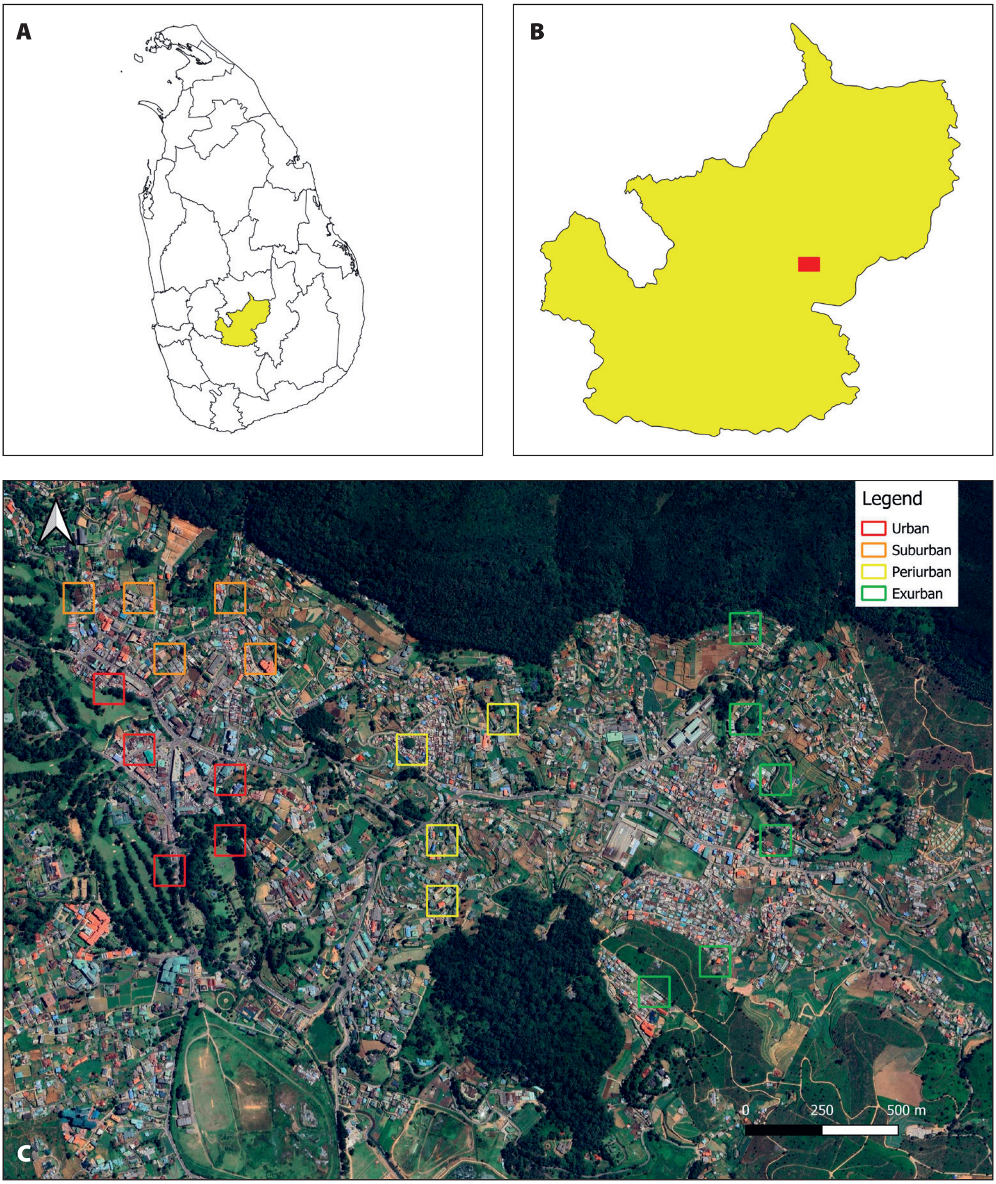

Figure 1. (A) Nuwara Eliya District (marked in yellow) within the island of Sri Lanka. (B) Location of the study site (marked in red) within the Nuwara Eliya District. (C) Spatial distribution of the twenty 10-hectare sampling plots within the study area in Nuwara Eliya (urban in red, suburban in orange, periurban in yellow, and exurban in green)

1. ábra (A) Nuwara Eliya körzet (sárgával jelölve) Srí Lanka szigetén. (B) A vizsgálati terület elhelyezkedése (pirossal jelölve) a körzeten belül. (C) A 20, egyenként 10 hektáros mintaterület térbeli eloszlása a vizsgálati területen (városi: piros, elővárosi: narancssárga, városperemi: sárga, városon kívüli: zöld)

Table 1. The types of habitats, number of 10-ha plots sampled within each habitat type and the characteristic features of each habitat type selected for the study

1. táblázat A vizsgált élőhelytípusok és főbb jellemzőik, valamint az egyes élőhelytípusokon mintázott 10 hektáros mintaterületek száma

Habitat type	Number of plots	Habitat characteristics
Urban	5	Densely built-up areas dominated by commercial infrastructure including shops, banks, offices, and municipal buildings. Includes a mix of colonial-era structures such as terraced roofs, gabled facades and public green spaces such as parks and golf courses. The vegetation is mostly ornamental.
Suburban	5	Primarily modern residential zones characterized by closely packed houses with little to no private green space (gardens). Includes a mix of residential and small-scale commercial buildings (convenience stores), often sharing walls or located adjacently. Typically lacks natural vegetation or large trees.
Periurban	4	Transitional zones between suburban and exurban areas, consisting of detached residential houses, small private gardens, and mixed-use lands (But some areas have shanty style settlements, referred in this paper as terraced buildings with no garden areas). This habitat includes both built structures and patches of low-intensity agriculture or unused open spaces. Vegetation is moderate and patchy, mainly consists of small-scale tea monocultures.
Exurban	6	Low-density settlement areas with widely dispersed houses, often surrounded by medium to large-scale agricultural lands, mainly tea monocultures and patches of small vegetable cultivations. Natural and semi-natural vegetation is more abundant than in other habitats, though found in small patches. Human infrastructure is minimal, and buildings are often isolated or informal.

House Sparrow surveying

Field surveys followed standardized protocols for urban sparrow census by De Laet *et al*. (2011). Surveys were carried out during peak morning activity period of birds and the period with least human interference (06:30–09:30) from February to May 2025, aligning with the warmest season in the study area, which is the most suitable period of the year for breeding.

Whole area searches were conducted in each plot by walking along all accessible roads, pavements and gardens and counted all active nests observed within each plot. Each plot was surveyed only once during the study period. Active nests were identified by the presence of male sparrows chirping at nest sites or adult birds of either sex entering a nest with or without nesting or food material. For each observed nest, we recorded the type of building and the type of substrate the nest was located *(Table 2)*.

Statistical analysis

All statistical analyses were performed using R statistical software (version 4.4.0; R Core Team 2024). We first assessed whether House Sparrow nest abundance varied significantly across the four habitat types or in response to landscape metrics (building cover and green cover percentage). Initial data exploration indicated that the nest count data did not follow normal distribution, hence we employed Generalized Linear Models (GLMs).

We initially fitted a Poisson GLM and to validate the model assumptions, we checked

Table 2. Building types and nesting substrate categories used by House Sparrows in Nuwara Eliya
2. táblázat A házi veréb által használt épülettípusok és a fészkeket tartó felület kategóriák Nuwara Eliyában

Types of buildings	
Shop	Commercial buildings primarily used for retail or trade, often located along main roads or market areas
Office	Administrative or professional service buildings, including banks, public institutions, or business centers
House	Detached or semi-detached residential dwellings with gardens occupied by families or individuals
Terraced	Rows of adjoining residential units sharing side walls, densely packed urban layouts
Flat	Multi-unit and multi-storied residential buildings, generally more modern, with individual apartments
Shed	Small utility or storage buildings, often used for agricultural or mechanical purposes
Wall	Free-standing or boundary walls not part of a building structure but used opportunistically for nesting
Types of substrates	
Nest box	Artificial containers including wooden/cardboard boxes or clay pots placed intentionally by people to attract nesting birds
Sheet	Metal or plastic roofing or wall sheets (such as corrugated iron) used as cover or support
Gutter	Rainwater channels on rooftops, typically at roof edges
Ceiling	The interior overhead surface of a structure, including rafters or false ceilings
Hole	Cavities in walls, roofs, or facades, either naturally occurring or caused by structural wear
Beam	Structural support elements, usually horizontal wooden or metal bars under roofs
Light meter box	Enclosed boxes housing electrical meters or switches, typically mounted on external walls.
Advertisement board	Enclosed display units or signs used for commercial advertisement, occasionally offering nesting cavities.

for overdispersion by calculating the ratio of the residual deviance to the residual degrees of freedom. A dispersion parameter greater than 1.5 indicated significant overdispersion in our dataset. To account for this, we refitted the data using a Negative Binomial Generalized Linear Model (GLM-NB) (Zuur *et al.* 2009) using the glm.nb function from the *MASS* package (Venables & Ripley 2002). To avoid multicollinearity between habitat categories and the landscape metrics, we fitted two separate Negative Binomial GLMs. The first model assessed the effect of Habitat Type on nest abundance, using Analysis of Deviance (Likelihood Ratio Test) to compare the fitted model against the null model. The second model assessed the response to continuous landscape metrics, Building Cover % and Green Cover % as simultaneous predictors, utilizing Z-tests to evaluate significance of individual coefficients. To investigate nest site selection, we examined the associations between nest substrate type and two categorical variables: habitat type and building type. We constructed contingency tables and performed Pearson's Chi-square tests of independence. Due to the presence of zeros in the interaction tables (because certain substrates were never found on specific building types), we interpreted the magnitude of the Chi-square statistic alongside the p-values to determine the strength of these biological associations.

Results

A total of 185 active House Sparrow nests were recorded across the 20 sampled plots. Initial data exploration indicated significant overdispersion in the nest counts (Dispersion parameter = 3.29), with high variance observed within habitat categories *(Figure 2)*. Consequently,

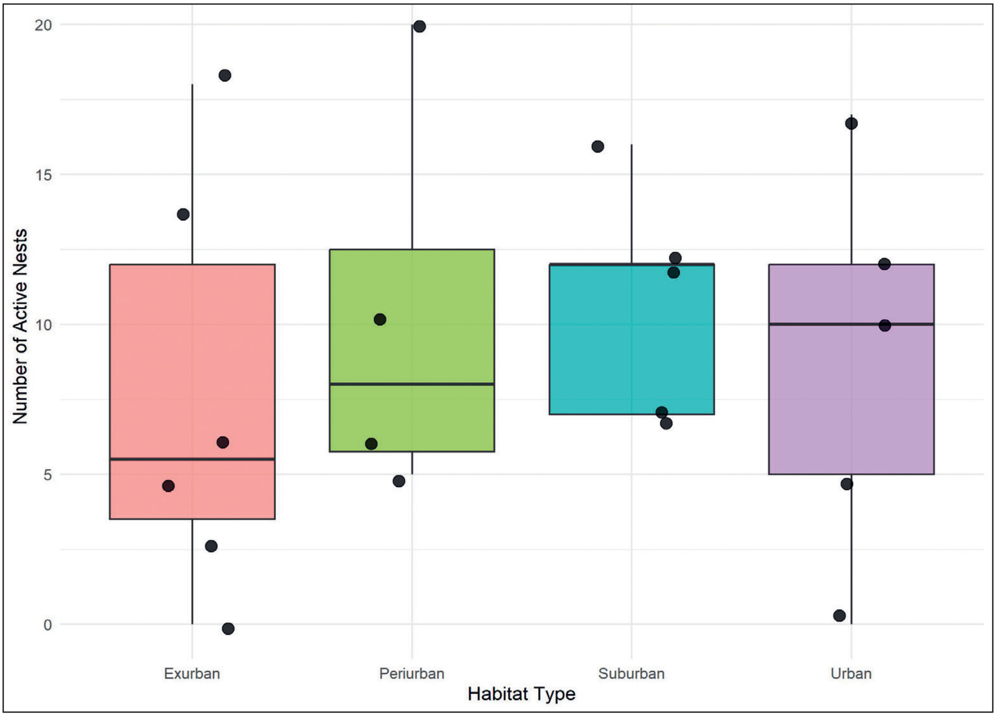

Figure 2. Variation in the number of active House Sparrow nests across the four habitat types (Exurban, Periurban, Suburban, Urban). Box plots show the median (horizontal line) and interquartile range (IQR), while whiskers extend to 1.5 times the IQR. Jittered points represent the raw count data for individual plots

2. ábra Az aktív házi veréb fészkek számának változása a négy élőhelytípusban. A dobozok a mediánt (vízszintes vonal) és az interkvartilis terjedelmet (IQR) mutatják, míg a függőleges vonalak az IQR másfélszereséig terjednek. A szórt pontok az egyes mintaterületek nyers fészekszámlálási adatait jelölik

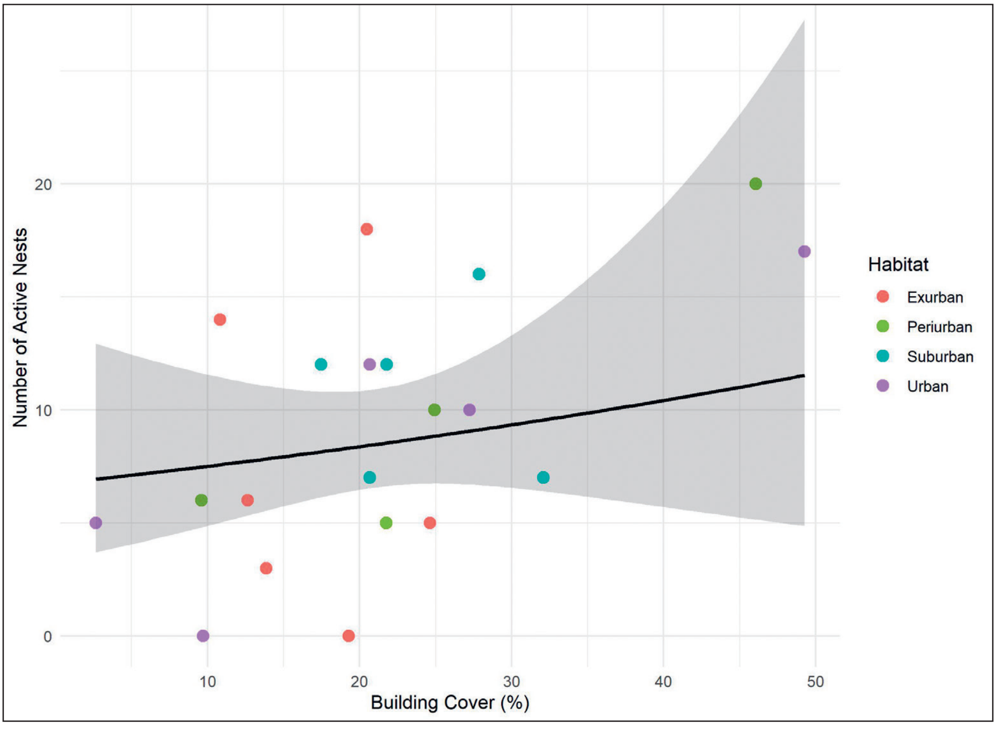

Figure 3. Scatter plot illustrating the relationship between building cover percentage and the total number of active nests per plot. The trend line represents the predicted values from the Negative Binomial Generalized Linear Model, accounting for overdispersion. The shaded area indicates the 95% confidence interval. The wide confidence interval reflects the high variance in the data, consistent with the non-significant statistical result (p = 0.47)

3. ábra Szórásdiagram, amely az épületborítottság százalékos aránya és az egy mintaterületre jutó aktív fészkek teljes száma közötti kapcsolatot szemlélteti. A trendvonal a negatív binomiális általánosított lineáris modell által becsült értékeket mutatja. Az árnyékolt terület a 95%-os konfidenciaintervallumot jelzi. A széles konfidenciaintervallum az adatok nagy varianciáját tükrözi, összhangban a nem szignifikáns statisztikai eredménnyel (p = 0,47)

a Negative Binomial Generalized Linear Model (GLM-NB) was employed to assess the drivers of abundance. In the categorical model, results showed that nest abundance did not differ significantly across the four habitat types (Periurban: Z = 0.64, p = 0.52; Suburban: Z = 0.81, p = 0.42; Urban: Z = 0.32, p = 0.75; LRT: $X^2 = 3.49$, df = 3, p = 0.32). Furthermore, in the continuous gradient model, neither Building Cover % (Z = 0.72, df = 1, p = 0.46) nor Green Cover % (Z = 1.78, df = 1, p = 0.08) were statistically significant predictors of nest abundance at the plot level *(Figure 3)*. In contrast to abundance, nest substrate selection was non-random and highly dependent on structural variables. A statistically significant association was found between nest substrate type and habitat type ($X^2 = 47.34$, df = 21, $p < 0.001$) *(Figure 4)*. Furthermore, a substantially stronger association was observed between nest substrate type and building type as well ($X^2 = 178.3$, df = 42, $p < 0.001$) *(Figure 5)*.

The contingency table further revealed distinct nesting patterns based on building architecture. Houses primarily supported nest boxes (n=45) and nests located on ceilings or beams (n=53).

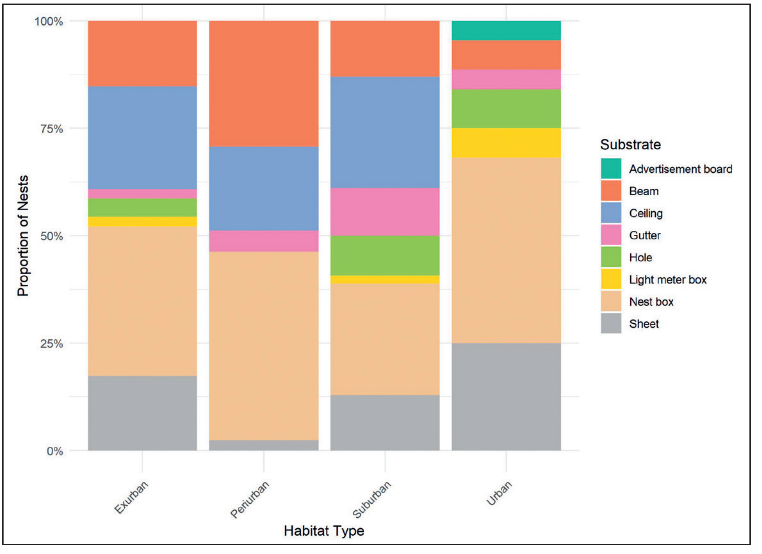

Figure 4. Proportional distribution of House Sparrow nest substrates across the four habitat types (Exurban, Periurban, Suburban, Urban). Stacked bars represent the percentage contribution of each substrate type to the total nests recorded in each habitat category

4. ábra A házi veréb fészkeket tartó felületek aránya a négy élőhelytípusban. A halmozott oszlopdiagramok az egyes típusok százalékos hozzájárulását mutatják az adott élőhelytípusban regisztrált összes fészeknél

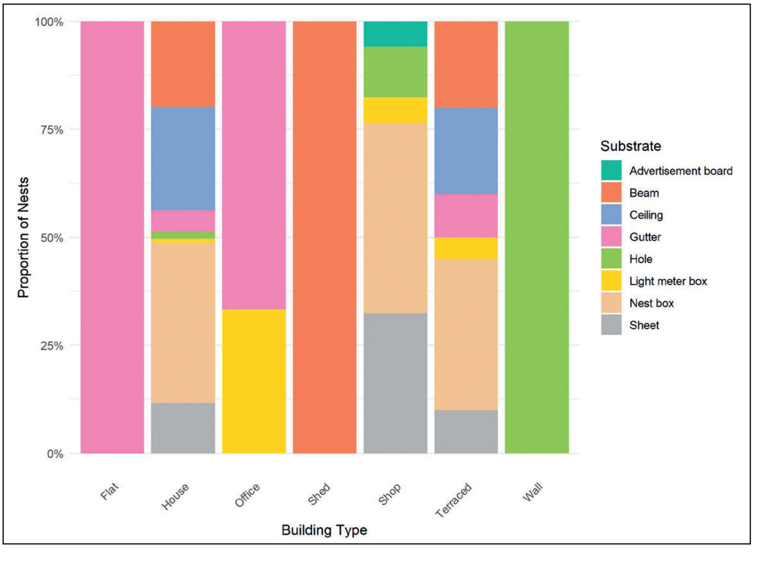

Figure 5. Proportional distribution of House Sparrow nest substrates categorized by building type (flat, house, office, shed, shop, terraced, wall). Stacked bars illustrate the strong association between architectural form and nest site selection ($X^2 = 178.3$, $p < 0.001$)

5. ábra A házi veréb fészkeket tartó felületek aránya épülettípusok szerint (tömbház, lakóház, iroda, gazdasági épület, üzlet, sorház, fal). A halmozott oszlopdiagramok szemléltetik az építészeti forma és a fészkelőhely-választás közötti erős kapcsolatot ($X^2 = 178{,}3$, $p < 0{,}001$)

Shops supported a mix of nest boxes (n=15) and nests situated under roofing sheets (n=11). Opportunistic nesting in holes was largely observed on boundary walls (n=5) and shops (n=4), while gutters and light meter boxes were most frequently utilized on office buildings.

Discussion

Contrary to the urban exploiter paradigm often observed in temperate regions, where House Sparrow densities peak in urban centers and decline in rural or exurban areas (MacGregor-Fors *et al.* 2017), our results indicate that the Nuwara Eliya population is remarkably ubiquitous. The Negative Binomial model revealed no significant difference in nest abundance across the urban-to-exurban gradient, and abundance was not strictly limited by building density. This suggests that the exurban landscape of Nuwara Eliya, characterized by tea plantations interspersed with estate housing and labor lines, provides sufficient nesting resources to support populations, reaching densities comparable to the urban center.

This lack of stratification may be attributed to the specific nature of the green matrix in the study area. Unlike natural forests which sparrows typically avoid, the exurban green cover largely consists of tea monocultures. While previous studies suggest agricultural intensification can reduce food availability (Hole *et al*. 2002), the presence of human settlements within these plantations likely provides anthropogenic food subsidies and nesting structures, buffering the population against resource scarcity. The high overdispersion observed in our data further highlights that sparrow distribution is not continuous but highly clumped; they form dense colonies around specific suitable structures regardless of the broader habitat category.

While sparrows were present across all habitats, their nesting behavior was non-random and strictly governed by the built-up environment. Our results establish that building type is a far stronger predictor of substrate selection than broad habitat categories. This implies that the habitat effects often reported in urban ecology may essentially be proxies for the structural composition of the landscape (Chamberlain *et al*. 2007).

This architectural dependence demonstrates the species' high plasticity. On houses, sparrows exploited traditional structural features (eaves/beams) and human-provided resources (nest boxes). In contrast, on shops and commercial buildings, which often lack garden space and traditional eaves, they opportunistically utilized gaps under roofing sheets and crevices in walls *(Figure 6)*. This adaptive flexibility, a hallmark of synanthropic species (Sheard *et al*. 2024), allows them to persist in the modernizing urban center, exploiting the nooks and crannies of commercial infrastructure where natural nesting sites are absent (Bernat-Ponce *et al.* 2024).

A defining feature of the Nuwara Eliya population is its heavy reliance on anthropogenic provisioning *(Figure 7)*. Nest boxes were the most utilized substrate, particularly in residential houses (n=45) and shops (n=15). This widespread use suggests that active tolerance and provisioning by residents play a pivotal role in sustaining this population. In many global contexts, modern architecture excludes sparrows by removing cavities (Shaw *et al.* 2008). However, in Nuwara Eliya, the cultural practice of placing nest boxes appears to be compensating for the loss of natural cavities or architectural changes. This synanthropic

Figure 6. Different nesting substrates used by House Sparrows (A) Holes on walls (B) Light meter box (C) Gutters (see the edges of the roof)

6. ábra A házi veréb által használt különböző fészkelőhelyek: (A) falakon található üregek, (B) villanyóra-szekrény, (C) ereszcsatornák (a tető szélein)

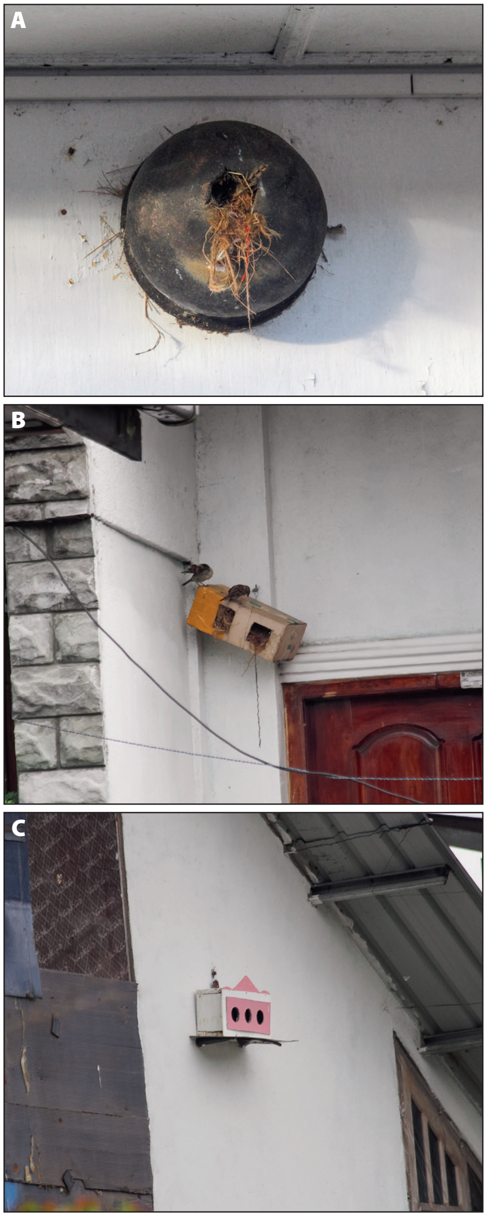

Figure 7. Different structures provided by humans as nest boxes for House Sparrows (A) Clay pots (B) Cardboard boxes (C) Artificial bird nests

7. ábra Az emberek által biztosított, házi veréb számára kialakított különböző mesterséges fészkelőhelyek: (A) agyagcserepek, (B) kartondobozok, (C) mesterséges madárodúk subsidy may explain why this population remains robust while many others in South Asia face declines (Bhattacharya *et al.* 2011, Choudhary *et al.* 2020).

Although this study did not investigate factors such as predation or electromagnetic radiation, existing research suggests that these stressors may influence House Sparrow populations, particularly in urban settings (Balmori & Hallberg 2007, Bell *et al*. 2010). While our findings indicate that House Sparrows currently maintain a visibly healthy breeding population in built-up areas of Nuwara Eliya, ongoing urban development and the expansion of telecommunication infrastructure may pose emerging threats that warrant close monitoring.

While our study offers valuable insights, it was limited to a single breeding season and relied on observational nest counts, which may be influenced by detection bias (e.g. nests hidden in inaccessible structures may have been unnoticed, compared to more visible nest boxes or nests on exterior structures). Future work should incorporate multi-seasonal monitoring and explore reproductive outcomes to better understand nest success. Longitudinal studies tracking marked individuals or populations over several breeding seasons would provide critical insights into nest fidelity, changes in site selection patterns, and the long-term viability of this population in the face of ongoing urban developments.

Our findings suggest that conservation strategies for House Sparrows in tropical highland cities should focus on microsite availability rather than macro-habitat preservation. Since the population is not strictly limited by urbanization intensity, urban planning need to view development and sparrow conservation as mutually exclusive. Instead, maintaining architectural diversity, specifically retaining structures with eaves or retrofitting modern buildings with nest boxes, can effectively sustain populations. The marginally non-significant negative trend with green cover suggests that while sparrows prefer built-up areas, they can tolerate greener landscapes provided that suitable nesting structures (like estate housing) are present. Future conservation efforts should encourage the continued installation of nest boxes, particularly in rapidly urbanizing zones where traditional nesting sites are being replaced by modern, sealed facades.

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