

Factors influencing nest site selection of the Laughing Dove (*Spilopelia senegalensis*) in an urban area in Karaj, Iran

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Abstract Urban habitats are rapidly changing, making the conservation and management of species adapted to these environments challenging. Nest site selection is a pivotal point in the process of habitat selection and breeding for bird species. We measured 10 structural and spatial characteristics at 32 nest presence sites and 64 randomly selected nest absence sites of Laughing Doves (*Spilopelia senegalensis*) in an urban environment in Karaj, Iran. To model the nest site selection, we performed spline binary logistic regression. Two variables significantly influenced the nest site selection of Laughing Doves: nest height above ground, with an optimal range of ~286–347 cm, and nest concealment, favoring invisible places from the front and sides. Distance to opposite building, with an optimal range of ~16–34 m, was marginally significant. Additionally, we surveyed the feasibility of occupying artificial nestboxes (n = 17) by Laughing Doves between February and September 2019. The occupancy rate of the artificial nestboxes was ~35%. Overall, these results suggest that despite the relatively high structural heterogeneity of our urban environment, Laughing Doves exhibit distinct preferences for certain nest site characteristics, which may reflect a dependence on close proximity to humans for safety and access to food and water.

Keywords: human-animal interaction, nestbox, nest site preferences, spline, urban bird behavior

Összefoglalás A városi élőhelyek gyorsan változnak, ami miatt nagy kihívás az ilyen környezethez alkalmazkodott fajok megőrzése és kezelése. A fészkelőhely kiválasztása a madárfajok élőhelyválasztási és költési folyamatának egyik sarkalatos pontja. Vizsgálatunkban 10 strukturális és környezeti jellemzőt mértünk meg a pálmagerle (*Spilopelia senegalensis*) esetében 32 fészkes és 64 véletlenszerűen kiválasztott fészkek nélküli helyen az iráni Karajban. A fészkelőhely-választás modellezésére spline bináris logisztikus regressziót alkalmaztunk. Két változó befolyásolta szignifikánsan a pálmagerlek fészkelőhely-választását: a fészkek földtől számított magassága (optimális tartománya ~286–347 cm volt), és a fészkek rejtettsége (a szemből és oldalról láthatatlan helyeket részesítette előnyben). A szemközti épülettől való távolság, amelynek optimális tartománya ~16–34 m volt, csak kis mértékben volt rá hatással. Emellett megnéztük a mesterséges fészkelőládák (n = 17) pálmagerlek általi elfoglalásának valószínűségét is 2019 februárja és szeptembere között. A mesterséges fészkelő ládák elfoglalási aránya ~35% volt. Összességében ezek az eredmények arra utalnak, hogy a városi környezet viszonylag nagy szerkezeti heterogenitása ellenére a pálmagerlek bizonyos fészkelőhelyi jellemzőkkel szemben határozott preferenciákat mutatnak, ami azt tükrözheti, hogy a biztonság, valamint a táplálékhoz és vízhez való hozzáférés szempontjából függnek az emberek közelségétől.

Kulcsszavak: ember-állat interakció, fészkelő láda, fészkelőhely preferencia, spline, városi madarak viselkedése

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Introduction

Comprehending the determinants of nest site selection is essential for advancing avian conservation and management strategies. Nest site selection is an important step in the process of habitat selection and territory establishment in bird species (Suvorov *et al.* 2014). The availability of suitable nesting sites directly impacts reproductive success, making it a critical component of habitat selection (Li & Martin 1991, Jara *et al.* 2020). Identifying the factors that drive nest site selection can enhance our understanding of species' ecological requirements and improve habitat management practices (Clark & Shutler 1999).

The urban space is a permanently changing ecosystem, suffering from decreasing biodiversity, but also providing new anthropogenic habitats for some adaptable species (Sumasgutner *et al.* 2014). The availability of nest sites in native and non-native vegetation, residential houses, uninhabited buildings, and various anthropogenic structures such as metal pipes and bridges significantly influences birds' nesting behaviors in cities (Reynolds *et al.* 2019). Additionally, the provision of nestboxes has been shown to support certain bird species in urban areas (Reynolds *et al.* 2019, Dulisz *et al.* 2022).

The Laughing Dove (*Spilopelia senegalensis*) is one such species that has successfully adapted to urban habitats. Native to most parts of Africa, the Middle East, and South and Central Asia, it has also been introduced to parts of Western Australia (Frith *et al.* 1976, Baptista *et al.* 1997) and Europe (e.g. Rocha 2013, Zannetos *et al.* 2023). This species is commonly found in cultivated areas, trees (but not forests), and human habitations (BirdLife International 2019). The nest is a frail, thin platform of roots, twigs and petioles placed in bushes or trees up to 15 m above the ground (Baptista *et al.* 1997), on buildings under the eaves, on drainpipes or in cracks in walls (Snow & Perrins 1998), and is ~15 cm in diameter (Schodde *et al.* 1986). This species predominantly forages on the ground but sometimes searches for food in small trees and shrubs (Gibbs *et al.* 2010). Its diet mainly consists of fallen seeds from grasses, along with vegetable debris, fruits, nectar, succulent shoots, some insects, and even human food waste (Satheesan *et al.* 1990, Adang *et al.* 2008, Gibbs *et al.* 2010, Hanane 2015).

The presence of Laughing Doves in urban landscapes can be both beneficial and challenging. While these birds contribute to the aesthetic appeal of parks and green spaces, they also may pose health risks and create disturbances in residential areas. A study conducted on the effect of wild bird droppings as a source of *Campylobacter jejuni* in children's playgrounds showed that the presence of wild birds, including Laughing Doves, can cause acute gastroenteritis in humans, especially in children (Abdollahpour *et al.* 2015). In addition, Laughing Doves may infect humans and other animal species by transmitting Newcastle disease virus (Okpanachi *et al.* 2020, Hirschinger *et al.* 2021), West Nile virus, and Usutu virus (Ayadi *et al.* 2017). Therefore, armed with a deeper understanding of the characteristics of Laughing Dove nest sites, we can strategically modify certain locations to discourage their nesting.

Birds in urban areas consider various structural and environmental factors when selecting nest sites, such as building structure, nest tree height, proximity to green spaces, tree coverage, and distance from water sources (e.g. Jokimäki *et al.* 2017, Bressler *et al.* 2020, Ding *et al.* 2023). However, previous studies on the nest site selection of Laughing Doves have primarily focused on their tree nesting habits, particularly in agricultural areas of

Northern Africa (e.g. Boukhriss & Selmi 2009, 2019, Brahmia *et al.* 2015, Hanane 2015), leaving a gap in our understanding of their nest site selection in urban environments.

In the present study, we measured 10 structural and spatial characteristics that we hypothesized could influence Laughing Dove nest site selection. We then modeled the nest site selection to identify statistically significant factors. In addition, we examined the feasibility of Laughing Doves occupying artificial nestboxes as another objective of this study.

Methods

Study area

A portion of Karaj, situated in the Alborz province of Iran, was selected for this study (35°49'36N", 50°58'6"E; 239 ha) (*Figure 1*). Karaj is a densely populated city nestled at the foot of the Alborz mountain range, within the Palearctic realm. It has a metro area population of ~1.59 million inhabitants and a population density of ~9,815 people/km² (Macrotrends 2023). The study area, located in the central part of Karaj, encompassed main streets, side streets, and alleys. Most of the buildings were multi-story apartments, typically three or four stories high. Pedestrian traffic was more pronounced on the main streets and side streets compared to the alleys. Approximately 11% of this area was designed as green space, and the altitude varied from ~1,297–1,355 m above sea level, resulting in a gentle slope (Google 2020).

The prevailing climate in Karaj is known as a local steppe climate, with a mean annual temperature of 14.2 °C (maximum mean temperature of 32.8 °C in summer and minimum mean temperature of –4.6 °C in winter) and precipitation of ~283 mm per year. Although it varied greatly throughout each season, the driest season was summer (4 mm), whereas the rainiest season was winter (127 mm) (Climate Data 2022).

The prominent animal species observed in the study area included Laughing Doves, Rock Doves (*Columba livia*), House Sparrows (*Passer domesticus*), White-eared Bulbuls (*Pycnonotus leucotis*), White Wagtails (*Motacilla alba*), free-ranging dogs (*Canis lupus familiaris*), Eurasian Magpies (*Pica pica*), Hooded Crows (*Corvus cornix*), rats (*Rattus* spp.), and stray cats (*Felis catus*). The last four species are known as potential nest predators (e.g. Shoham *et al.* 1997, Jokimäki & Huhta 2000, Vincze *et al.* 2017, Boukhriss & Selmi 2019). Common tree species included narrow-leafed ash (*Fraxinus angustifolia*), oriental plane (*Platanus orientalis*), Arizona cypress (*Cupressus arizonica*), black locust (*Robinia pseudoacacia*), and Afghan pine (*Pinus eldarica*) (all based on our observations).

Data collection

While the breeding season of Laughing Doves varies across different regions (Baptista *et al.* 1997, Gibbs *et al.* 2010, BirdLife International 2019), our prior observations and existing studies (e.g. Boukhriss & Selmi 2009, Brahmia *et al.* 2015) led us to assume late February as the onset of the breeding season in our study area. From 25 February to 3 April 2019,

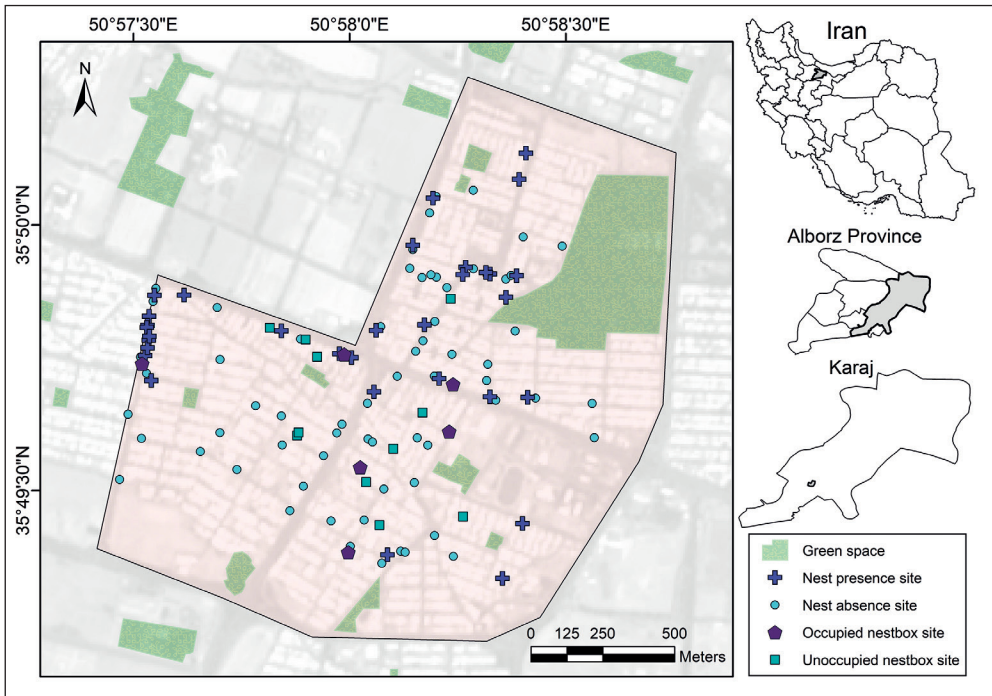


Figure 1. Study area in Karaj, Alborz province, Iran, encompassing 239 ha. Green spaces (green polygons), Laughing Dove nest presence sites (purple crosses, $n = 32$), nest absence sites (cyan circles, $n = 64$), occupied nestbox sites (dark purple pentagons, $n = 6$), and unoccupied nestbox sites (teal squares, $n = 11$) are highlighted. Contains modified Copernicus Sentinel data processed by Sentinel Hub (2022)

1. ábra A vizsgálati terület (239 ha) térképe Karajban, Alborz tartomány, Irán. Zöld területek (zöld poligonok), pálmagerle fészkelő-helyek (lila keresztek), fészeklésre nem használt helyek (kék körök), fészeklésre használt költőládák (sötétlila ötszögek) és üres költőládák (kékes-zöld négyzetek) jelölve vannak

we searched both sides of the streets and alleys, alternating between going and returning on foot from morning to afternoon, ensuring each side was searched once. Moreover, from 29 February to 15 March 2019, we directly approached 82 local residents from our own neighborhood, familiar to us, asking them to report any Laughing Dove nests they observed in the study area. Additionally, we requested that they encourage others to do the same. As a result, we believe that even more individuals indirectly contributed to our study. Based on the assumption that the abandoned nests were built in favorable places by this bird, we also recorded and accounted for them as nest presence sites. The tools and devices used in sampling included a tape measure, a Global Positioning System (GPS) device from Garmin® (USA), a sliding ladder, a compass, and a closed-circuit television (CCTV). Until 3 April 2019, we recorded 32 nest presence sites, 10 of which (31.2%) were found by local residents, and 64 randomly selected nest absence sites (Figure 1).

Ten structural and spatial variables were measured in this study (Table 1). The vertical distance from the ground to the base of the nest (HEIGHT) was measured using a measuring

Table 1. Variables measured to model the nest site selection of Laughing Dove in 2019.^aDiameter at breast height. ^bA: invisible from the front and sides; B: invisible from the front but visible from one side; C: visible from the front but invisible from the sides

1. táblázat A pálmagerle fészkelőhely-választásának modellezéséhez felmért változók. ^aMellmagasságban mért átmérő. ^bA: sem szemből, sem oldalról nem látható, B: egyik oldalról látható, de szemből nem, C: csak szemből látható

Variable	Unit	Abbreviation	Description
Nest height above ground	cm	HEIGHT	The vertical distance from the ground to the base of the nest
Nest to ceiling height	cm	CEILING	The vertical distance from the ceiling to the base of the nest
Nest horizontal distance to ceiling edge	cm	H_CEILING	The horizontal distance from the edge of the nest to the edge of the ceiling
Distance to nearest tree	m	TREE_DIST	The horizontal distance from the nest to the nearest tree > 10 cm dbh ^a
Distance to opposite building	m	BUILD_DIST	The horizontal distance from the nest to the opposite building
Distance to green space	m	GREEN_DIST	The distance from the nest to the edge of the nearest green space (area > 2 km ²)
Distance to nearest counterpart nest	m	NEST_DIST	The distance from the nest to the nearest counterpart nest
Nest concealment	#	CONCEAL	Visibility of the nest from a distance of 4 m along its horizontal plane; categorized as A, B, or C ^b
Base structure	#	B_STRUCT	A: shop boards, B: building frontispieces, C: building balconies
Base aspect	#	B_ASPECT	A: North, B: East, C: South, D: West

tape positioned directly below the nest. Similarly, the vertical distance from the ceiling to the base of the nest (CEILING) was measured with a measuring tape, with one end placed at the base of the nest and the other at the ceiling. The horizontal distance from the edge of the nest to the edge of the ceiling (H_CEILING) was also measured using a measuring tape held horizontally. The horizontal distances from the nest to the nearest tree with a diameter at breast height (DBH) greater than 10 cm (TREE_DIST) and to the nearest opposite building (BUILD_DIST) were both measured by counting steps to estimate the distances. The distances from the nest to the edge of the nearest green space (area > 2 km²; GREEN_DIST) and to the nearest counterpart nest (NEST_DIST) were both measured using a combination of GPS coordinates and mapping software. The nest concealment (CONCEAL) was assessed visually by us. We imagined our eyes were ~4 m horizontally away from the nest, in the opposite and side directions of the base structure, because it was often not possible to physically reach those viewpoints, especially when they were at a high height or when placing our sliding ladder on the street was required. The nest concealment was then categorized as A (invisible from the front and sides), B (invisible from the front but visible from one side), or C (visible from the front but invisible from the sides). The base structure of the nest (B_STRUCT) was categorized as A (shop boards), B (building

frontispieces), or C (balconies) through visual inspection. Finally, the aspect of the base structure where the nest was located (B_ASPECT) was determined using a compass and categorized as A (North), B (East), C (South), or D (West).

Artificial nestboxes

Because we had not yet developed the nest site selection model, we designed the artificial nestbox (*Figure 2*) and chose its erection locations exclusively considering our previous observations and descriptive statistics of the nest presence sites ($n = 32$). Seventeen artificial nestboxes were erected from 15 to 22 April 2019 (*Figure 1*), with seven placed near shops, two on the frontispieces of buildings, and eight on building balconies. Subsequently, all 10 structural and spatial variables were recorded for these nestboxes in a separate dataset (see following sections for its use in validating the nest site selection model). The erection of artificial nestboxes did not coincide with the assumed onset of the Laughing Dove's breeding season, because we had not yet decided to test the feasibility of their occupancy in the artificial nestboxes.

Artificial nestboxes were made using raw 8-mm MDF sheets. In our observations, we noticed that Laughing Doves did not nest on relatively wide flat surfaces but rather involved their nesting materials. Therefore, we placed a piece of wood inside each artificial nestbox (*Figure 2*).

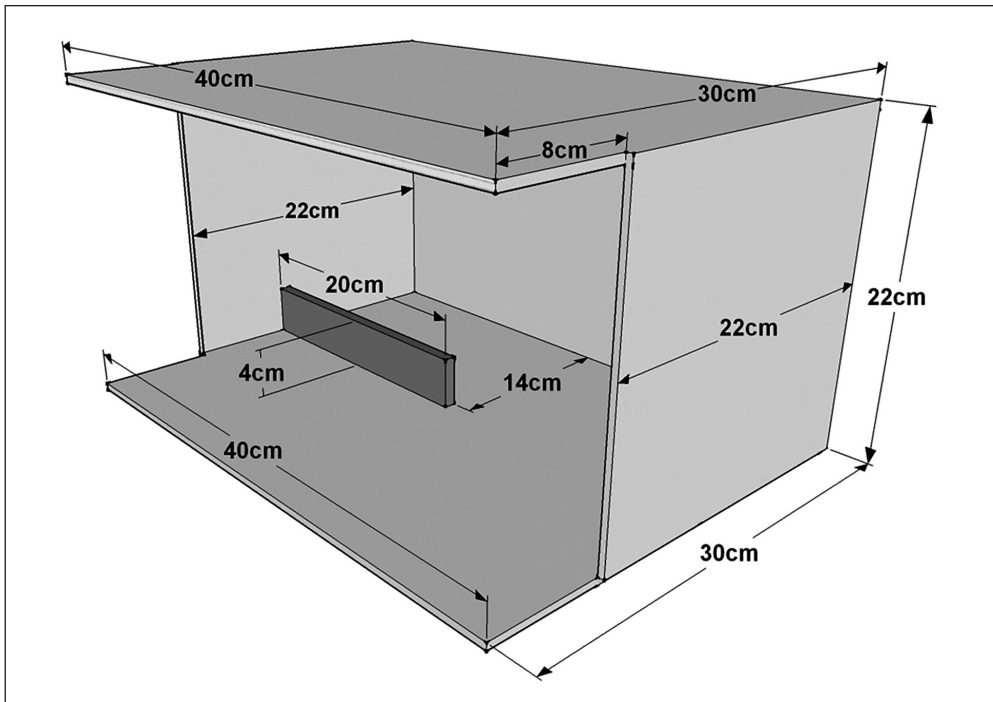


Figure 2. Dimensions of the artificial nestbox designed for the Laughing Dove
 2. ábra A pálmagerle fészkelésére kialakított mesterséges költőládák méretei

Statistical methods

Given that the influence of a continuous predictor variable on the probability of the occurrence of the binary response variable can be nonlinear, we employed the spline binary logistic regression method, specifically using linear splines, to model the nest site selection of the Laughing Dove. In this approach, the continuous predictor variable is divided into bins using knots. Consequently, we can assess any nonlinear effects of the continuous predictor variable (Harrell 2015). By utilizing the spline method, we address the issue of loss of information that arises when categorizing continuous variables (Weinberg 1995, Schuster *et al.* 2022).

We performed a knots-placing procedure based on different numbers of quantiles (2–5 quantiles; 2 quantiles = 1 knot, 5 quantiles = 4 knots) for all continuous predictor variables, using the dataset of nest presence sites ($n = 32$). To determine the most appropriate number of knots (or even no knots) for each continuous predictor variable, we conducted univariate logistic regressions for each predictor, varying the number of knots (up to four knots and no knots). Subsequently, we selected the number of knots that provided the equation with the lowest Akaike Information Criterion (AIC) value to enter into a model selection process (Harrell 2015). Since stepwise selection methods can lead to biased estimates and unreliable p-values due to their tendency to overfit models and fail to account for model uncertainty (Thayer 2002, Whittingham *et al.* 2006, Flom & Cassell 2007), we instead employed an ‘all subsets’ approach to systematically evaluate all subsets of predictor variables (Berk 1978), selecting the best model based on the lowest AIC (Akaike 1974). This method involves generating and comparing all possible combinations of predictor variables to find the model that best balances goodness-of-fit and complexity. The first level of each categorical predictor variable (A) was set as the reference level.

To identify potential correlations between/among variables and separate them into clusters that could be interpreted as single variables, we performed hierarchical variable clustering (cutoff distance value = 0.3) (Chavent *et al.* 2012). We then employed density ridgeline visualization to depict the distribution of a correlated continuous variable, nest height above ground, across various categories of a corresponding categorical variable, base structure (Wilke 2019), to interpret the relationship between different base structures and the heights.

The accuracy of the selected model (the nest site selection model) was evaluated using the area under the curve (AUC) of the receiver operating characteristic (ROC) curve (Swets 1988, Fielding & Bell 1997). The AUC was calculated based on the fitted probabilities from the model, which utilized the combined dataset of nest presence and absence points. This approach measures the model’s ability to distinguish between presence and absence data, with AUC values ranging from 0 to 1 (Phillips & Dudík 2008). A model whose predictions are 100% wrong has an AUC of 0, while a model with perfect predictions has an AUC of 1.

Due to our small sample size ($n = 96$), we used all observations from the combined nest presence and nest absence data to develop the nest site selection model. To validate the model, we employed an ‘external validation’ approach (Terrin *et al.* 2003). We used the dataset of nestbox sites ($n = 17$) as the test dataset, inputting this dataset into the nest site selection model, which generated predictions. These predictions were then

summarized and compared to the actual observed outcomes using a classification table. To determine the optimal threshold value for classification, we calculated the ROC curve for the dataset of nestbox sites using the predicted probabilities and actual outcomes. The optimal threshold was identified by maximizing Youden's J statistic, which balances sensitivity and specificity (Youden 1950, Perkins & Schisterman 2006). We assessed global spatial autocorrelation in the nest site selection model by calculating Moran's I test on the residuals, utilizing a spatial weights matrix derived from inverse distance weighting (IDW) that was based on Euclidean distance (Moran 1950, Legendre & Fortin 1989, Panigrahi 2021, Milliet *et al.* 2024).

All analyses were conducted in R v4.4.0 (R Core Team 2024). The rms R package (Harrell 2024) was used to perform spline binary logistic regression analysis. Receiver operating characteristic (ROC) analyses, along with the calculation of the optimal threshold for classification, were performed using the pROC R package (Robin *et al.* 2011). Visualization of descriptive statistics and comparisons of occupied versus unoccupied artificial nestboxes was conducted using the ggplot2 R package (Wickham 2016). Hierarchical variable clustering was performed using the ClustOfVar R package (Chavent *et al.* 2017). Additionally, the density ridgeline visualization was created using the ggridges R package (Wilke 2024). Spatial autocorrelation was assessed using the spdep R package (Bivand 2022). We utilized ArcGIS v10.2 (ESRI 2013) for map-related processes, including calculating the distance to the nearest counterpart nest and the distance to the nearest green space. Furthermore, we employed SketchUp Pro v15.2 (Trimble Navigation Limited 2014) to design the nestboxes.

Results

For the nest presence sites ($n = 32$), the median nest height above ground (HEIGHT) was 323.5 cm, ranging from 273–1,230 cm. The median nest to ceiling height (CEILING) was 29.5 cm, ranging from 16–138 cm. Nest horizontal distance to ceiling edge (H_CEILING) had a median of 104.0 cm, ranging from 18–197 cm. Distance to nearest tree (TREE_DIST) had a median of 8.0 m, ranging from 4–31 m. The median distance to opposite building (BUILD_DIST) was 19.0 m, ranging from 9–50 m. Distance to green space (GREEN_DIST) had a median of 177.75 m, ranging from 19.3–312.6 m. Distance to the nearest counterpart nest (NEST_DIST) had a median of 86.45 m, ranging from 7.9–408.8 m. Nest concealment (CONCEAL) was predominantly in category A (invisible from the front and sides, $n = 24$), followed by categories B (invisible from the front but visible from one side, $n = 4$) and C (visible from the front but invisible from the sides, $n = 4$). Base structure (B_STRUCTURE) was mostly in category A (shop boards, $n = 26$), with fewer nests in category B (building frontispieces, $n = 2$) and C (balconies, $n = 4$). Base aspect (B_ASPECT) was evenly distributed among categories A (North, $n = 10$) and D (West, $n = 10$), with fewer nests in categories B (East, $n = 7$) and C (South, $n = 5$) (*Appendices 1, 2a–j*).

Following the knots-placing procedure and univariate logistic regressions, the most appropriate number of knots was determined to be two for three variables: nest height above

Table 2. Summary of the nest site selection model for the Laughing Dove. The table presents the estimated coefficients (β), standard errors (SE), Wald z values, and p-values ($\text{Pr} > |z|$) for each predictor variable, including their spline terms or categories. The overall effect of each variable is assessed using the Wald statistics (χ^2), degrees of freedom (df), and p-values

2. táblázat A pálmagerle fészkelőhely-választásának modell eredményei. A táblázat tartalmazza a becsült modell paramétereket (β), azok sztenderd hibáját (SE), Wald z-értékeket és p-értékeket minden magyarázó változóhoz. Az egyes változók hatását Wald-féle statisztikával (χ^2) határoztuk meg, feltüntetve a szabadsági fokokat és p-értékeket

Variable	β	SE	Wald z	$\text{Pr}(> z)$	Wald Statistics (Overall Effect)		
Intercept	-36.567	11.160	-3.28	0.001	χ^2	df	p
HEIGHT' (<313cm)	0.099	0.031	3.21	0.001	11.53	3	0.009
HEIGHT' (313–367cm)	-0.172	0.052	-3.34	0.001			
HEIGHT'' (>367cm)	0.074	0.025	2.93	0.003			
CONCEAL = B	-1.463	0.833	-1.76	0.079	6.87	2	0.032
CONCEAL = C	-1.815	0.787	-2.31	0.021			
BUILD_DIST' (<16m)	0.211	0.207	1.02	0.309	7.09	3	0.069
BUILD_DIST' (16–25m)	-0.111	0.283	-0.39	0.695			
BUILD_DIST'' (>25m)	-0.211	0.143	-1.47	0.141			
CEILING' (<24cm)	0.263	0.167	1.57	0.116	6.07	3	0.109
CEILING' (24–49cm)	-0.397	0.203	-1.96	0.050			
CEILING'' (>49cm)	0.156	0.066	2.36	0.018			
TREE_DIST	0.117	0.078	1.51	0.131	2.28	1	0.131

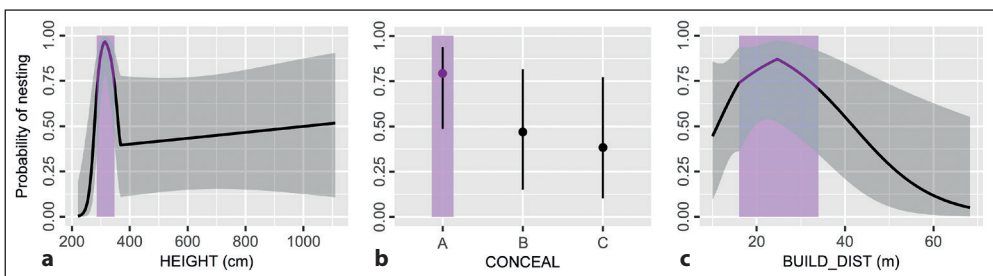


Figure 3. Influence of two significant variables and one marginally significant variable on the probability of Laughing Dove nesting based on the predictions of the nest site selection model (adjusted to the median of other predictor variables). Probability values greater than 0.7 are highlighted using purple bands for the following variables: (a) nest height above ground (HEIGHT), (b) nest concealment (CONCEAL), and (c) distance to opposite building (BUILD_DIST)

3. ábra A két szignifikáns és egy közel szignifikáns változó hatása a pálmagerle fészkelési valószínűségére a fészkelőhely-választás modellje alapján. A 0,7-nél nagyobb valószínűség értékek lila sávval vannak jelölve a következő változók esetében: (a) a fészkek talaj feletti magassága (HEIGHT), (b) fészkek rejtettsége (CONCEAL) és (c) a szemközti épület távolsága (BUILD_DIST)

ground, nest to ceiling height, and distance to opposite building. For the other variables, it was zero (no knots). After assessing the AIC for all possible combinations of predictor variables ($n = 1,023$), the selected model was constructed using five predictors: two significant variables, nest height above ground ($\chi^2 = 11.53$, $df = 3$, $p = 0.01$) and nest concealment ($\chi^2 = 6.87$, $df = 2$, $p = 0.03$); a marginally significant variable, distance to opposite building ($\chi^2 = 7.09$, $df = 3$, $p = 0.07$); and two non-significant variables, nest to ceiling height ($\chi^2 = 6.07$, $df = 3$, $p = 0.11$) and distance to nearest tree ($\chi^2 = 2.28$, $df = 1$, $p = 0.13$) (Table 2).

According to the nest site selection model, the optimal range for nest height above ground (with probability values adjusted to the median of other predictor variables > 0.7) was ~286–347 cm (Figure 3a). Regarding nest concealment, Laughing Doves preferred places that were invisible from the front and sides (probability value = 0.79) (Figure 3b). Additionally, the optimal range for distance to opposite building, although marginally significant, was ~16–34 m (Figure 3c).

Following the implementation of hierarchical variable clustering, a strong correlation was observed between the two variables, nest height above ground and base structure, with a distance value of 0.15 (Appendix 3). The density ridgeline plot revealed that the category of shop boards within the base structure variable had a higher density within the optimal range of the nest height above ground variable (Appendix 4).

The nest site selection model demonstrated good performance with an area under the ROC curve (AUC) of 0.91. The optimal threshold for classification was found to be 0.52,



Figure 4. An artificial nestbox erected on a balcony, occupied by Laughing Doves. The picture was captured from CCTV footage on 11 May 2019.

4. ábra Kihelyezett költőláda egy erkélyen, amelyben pálmagerle költ. A kép a CCTV felvételéből készült 2019. május 11-én

with the classification table revealing that the nest site selection model correctly predicted 76.5% of the artificial nestbox site cases (*Appendix 5*). We observed no indication of spatial autocorrelation (Moran's $I = 0.01$, $z = 0.88$, $p = 0.19$).

As of 22 September 2019, six of the 17 artificial nestboxes erected were occupied by Laughing Doves (*Figure 1*). Four nestboxes were occupied in the vicinity of the shops, and two on the balconies of the buildings (*Figure 4, Appendix 6a–j*).

Discussion

Our findings revealed that Laughing Doves prefer nesting at a specific height above the ground. Additionally, nest concealment is a significant factor, with Laughing Doves favoring sites that are invisible from the front and sides. The distance to the opposite building is also marginally significant, with an optimal range identified. These results suggest that despite the structural heterogeneity of our urban study area, Laughing Doves exhibit distinct preferences for certain nest site characteristics. Furthermore, the feasibility of occupying artificial nestboxes has been confirmed.

Given the wide range of Laughing Dove nest heights – spanning from 273–1,230 cm – and the presence of outliers, we believe that considering the optimal range obtained from the nest site selection model is more informative than relying solely on the mean value, with the median being the next best option. The optimal nesting height – which fell within the range of ~286–347 cm – was slightly higher than the mean nest height reported for this species in most studies. Hanane (2015) found a mean height of 2.29 ± 0.05 m in an agricultural area in Tadla, Morocco. Boukhriess and Selmi (2019) observed a mean height of 2.59 ± 0.09 m in a grove in the oasis of Kettana, Tunisia, with a range of 0.80–5.98 m. Almalki (2023) documented a mean height of 2.74 ± 0.10 m, with a range of 1.05–5.20 m, around Taif City, Saudi Arabia. However, it was ~1 m lower than the mean nest height reported by Brahmia *et al.* (2015) in an olive orchard in the Guelma region of Algeria, which was 4.21 ± 0.08 m, with a range of 2.94–5.76 m. According to Jennings (2010), Laughing Dove nests in Saudi Arabia had heights ranging from 30 cm to 12 m, with one nest found at a height of 25 m on a building. Despite the structural variability in urban environments, we infer that Laughing Doves likely exhibit preferences for specific nesting heights.

The strong correlation between the two variables of nest height above ground and base structure, along with the high density of the category of shop boards across the optimal range of nesting height, may indicate the desirability of shop boards for Laughing Dove nesting. Shoham *et al.* (1997) reported that in the busy streets of Tel Aviv, Israel, Laughing Dove nests were often built on ledges above shops, often less than 1 m above people's heads. We speculate that shop boards, in addition to having structural advantages such as suitable height and shelter, may also provide security and food for Laughing Doves because of high pedestrian traffic around them.

Our nest site selection model suggested that nest concealment was a significant factor, and Laughing Doves may have preferred places that were less likely to be easily detected by potential nest predator birds. Similar patterns have been observed in other bird species. For

instance, the Eurasian Collared Dove (*Streptopelia decaocto*) in Spanish dehesas preferred specifically the holm oak evergreen tree (*Quercus ilex*), which provides concealment (Bermúdez-Cavero *et al.* 2021). Additionally, Kövér *et al.* (2015) documented that, although Hooded Crows in an urban environment in Eastern Europe preferred taller trees for nesting, they chose more concealed trees in areas with shorter trees. Concealed nests may reduce nest predation by minimizing the transmission of visual, chemical, and auditory cues to predators (Martin 1993, Burhans & Thompson 1998).

The distance to the opposite building, which itself depended on whether the nests were on main streets, side streets, or alleys, emerged as a marginally significant factor influencing the nest site selection of Laughing Dove. We infer that Laughing Doves may prefer busy main streets with abundant shops and high pedestrian traffic for nesting. This preference is likely influenced by the availability of food scraps left by people, particularly around bakery shops, and the perceived security provided by the constant human presence. In contrast, Bermúdez-Cavero *et al.* (2021) reported a completely opposite behavior for Eurasian Collared Doves in urban and periurban areas of eastern Spain. These doves avoided areas with heavier pedestrian traffic, which coincide with buildings, restaurants, and commercial centers, preferring green spaces instead. Rao and Koli (2017) reported that spatial heterogeneity, less predation, optimal feeding ground, and a higher number of advertising and display boards of shops at roadside buildings might be crucial factors for birds' nesting in the highly disturbed city of Udaipur, Rajasthan, India. Our observations align with these hypotheses, at least for the urban-adapted Laughing Dove population in our study area.

All our observed Laughing Dove nests were situated in close proximity to pedestrian traffic, and remarkably, these birds seemed to make minimal effort to conceal themselves or their nests from human view. To investigate this behavior further, we erected two artificial nestboxes in uninhabited buildings located far away from human activity, yet none of these boxes were occupied. However, we are aware that only two artificial nestboxes are too few to test this hypothesis. Hanane (2015) reported a relatively short distance between Laughing Dove nests and human settlements in the agricultural regions of Central Morocco. The Laughing Dove's reliance on proximity to human settlements, both in urban and agricultural environments, could be attributed to its relatively short wingspan, which may limit its ability to fly long distances in search of water and food (Shoham *et al.* 1997). Furthermore, Sumasgutner *et al.* (2014) indicated a trade-off between higher nest site availability in central Vienna, Austria, and longer distances to larger open green spaces as optimal foraging grounds for the Eurasian Kestrel (*Falco tinnunculus*). In our study area, nest site availability and optimal foraging grounds may co-locationally affect nest site selection in the Laughing Dove.

Some people, especially shopkeepers, were supplementary feeding birds mainly with wheat or millet seeds. We specifically observed Laughing Doves, House Sparrows, and Rock Doves foraging on the sidewalks. In contrast, potential nest predators of the Laughing Dove, such as Eurasian Magpies and Hooded Crows, are typically regarded as ominous and nuisance by humans due to ancient cultural beliefs (Clucas & Marzluff 2012, Król & Hernik 2020). As human behavior directed at birds can affect their behavior (Clucas & Marzluff 2012), this differential treatment of humans may have influenced nest site selection in the Laughing Dove.

Given the potential for Laughing Doves to be perceived as nuisances or carriers of pathogenic agents for both humans and other animal species (Abdollahpour *et al.* 2015, Ayadi *et al.* 2017, Okpanachi *et al.* 2020, Hirschinger *et al.* 2021), understanding the characteristics of their nest sites becomes crucial. By identifying preferred nesting locations, urban planners and conservationists can take targeted measures to manage and mitigate potential damages. Strategies may include discouraging nesting in certain areas or providing alternative nesting sites away from sensitive locations. Balancing the benefits of having these birds in urban spaces with the need to minimize health risks requires a thoughtful approach that considers both human well-being and wildlife conservation (Hedblom *et al.* 2017).

In light of the fact that ~35% of artificial nestboxes were occupied by Laughing Doves, it becomes evident that designing and erecting such nestboxes is a practical approach for managing, researching, or even providing recreational opportunities for this species (Reynolds *et al.* 2019, Dulisz *et al.* 2022). Notably, as small shops give way to shopping malls, the modern infrastructure often lacks suitable nesting sites for Laughing Doves (according to our observations). Unlike their more traditional counterparts, mall shopkeepers may deliberately prevent bird nesting when designing shop boards and facilities. Additionally, Clucas and Marzluff (2012) found an inverse correlation between urbanization gradient (light to heavy urbanization) and bird feeding by humans. This finding suggests that as urban areas become more densely populated, people's indifference or even dissatisfaction toward bird-related activities may increase. Consequently, artificial nestboxes emerge as valuable tools for the management and conservation, especially for future generations of this species (Reynolds *et al.* 2019, Dulisz *et al.* 2022).

Previous studies on the Laughing Dove (e.g. Kluijver 1966, Boukhriss & Selmi 2009, 2019, Brahmia *et al.* 2015, Hanane 2015) and similar columbid species (e.g. Csathó & Bozó 2022, Ramírez-Albores *et al.* 2024) have extensively documented their nesting habits in trees. Csathó and Bozó (2022) even showed a competition for nesting trees between the Eurasian Collared Dove and the Common Wood Pigeon (*Columba palumbus*) in an urban region in Southeast Hungary. When there were trees in the vicinity of almost all observed nests, and there were green spaces in our study area, we observed no Laughing Dove nests or nesting attempts on trees. We speculate that the avoidance of tree nesting by Laughing Doves may stem from factors such as the absence of suitable trees, diminished nest concealment, and consequently, an elevated risk of nest predation by Eurasian Magpies, Hooded Crows, and stray cats. Extending the study area, ideally across an urban-rural gradient, might help address this issue.

Boukhriss and Selmi (2019) found that the presence of palm trees near Laughing Dove nest trees increased the risk of predation by nest predators, particularly Black Rats (*Rattus rattus*), which used palm trees as refuges. Shoham *et al.* (1997) also considered nest predation by various species, including Hooded Crows, to be the main cause of Laughing Dove nesting failure. In our study, despite the usual nesting of potential nest predators such as Eurasian Magpies and Hooded Crows in urban green spaces (Dupak & Telizhenko 2023), the distance to the green spaces did not significantly influence the Laughing Dove's nest site preferences. This leads us to question: Does the distance of Laughing Doves' nests from their potential nest predators affect their reproductive success? And if so, does their reproductive success impact their nest site selection?

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Data availability

The data supporting the findings of this study are available in Dryad at <https://doi.org/10.5061/dryad.gxd2547rk>.

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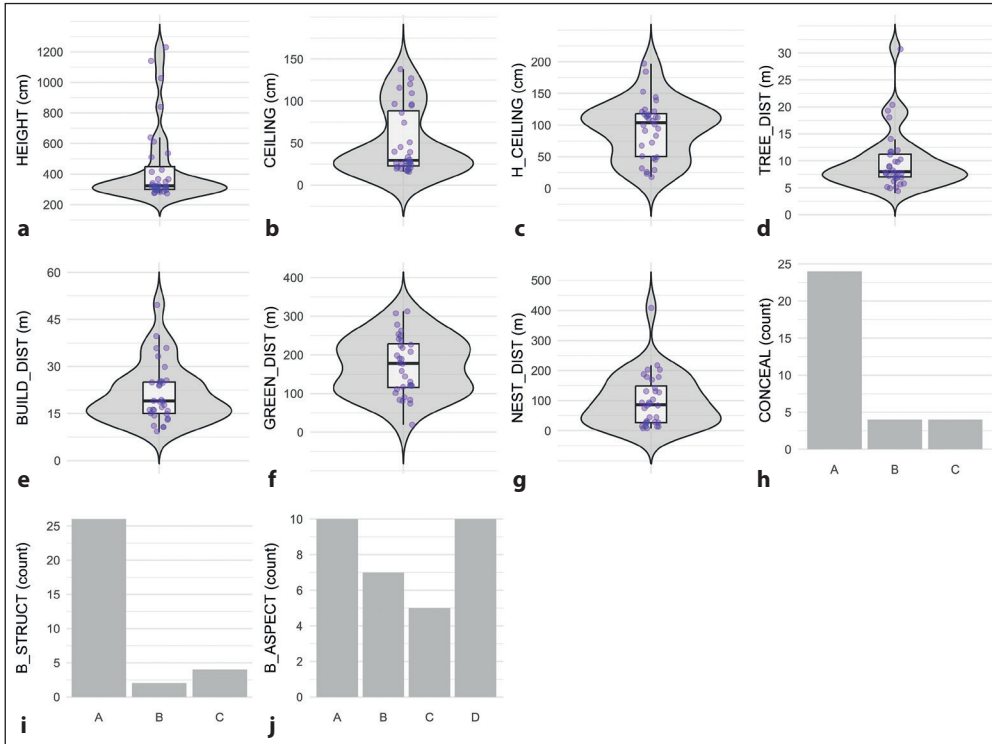
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Appendix 1. Descriptive statistics table of the Laughing Dove nest presence sites in 2019 (n = 32). For continuous variables, the table includes mean, standard deviation (SD) of the mean, median, minimum (Min), and maximum (Max) values. For categorical variables, the table shows the count (n) for each category: nest concealment (A: invisible from the front and sides, B: invisible from the front but visible from one side, C: visible from the front but invisible from the sides), base structure (A: shop boards, B: building frontispieces, C: balconies), and base aspect (A: North, B: East, C: South, D: West)

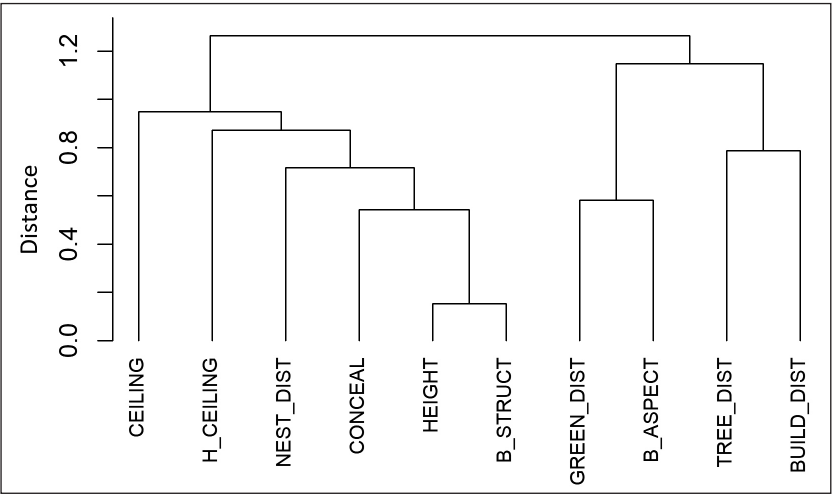
1. melléklet A pálmagerle fészkelőhelyeinek leíró mérőszámai 2019-ből. A folytonos változók esetén az átlag, a medián, a sztenderd hiba, a minimum és a maximum, míg a kategorikus változók esetén a darabszám van feltüntetve

Continuous Variables	Mean	SD	Median	Min	Max
Nest height above ground (cm)	444.91	259.03	323.50	273	1,230
Nest to ceiling height (cm)	51.62	39.37	29.50	16	138
Nest horizontal distance to ceiling edge (cm)	94.31	46.01	104.00	18	197
Distance to nearest tree (m)	9.91	5.52	8.00	4	31
Distance to opposite building (m)	21.44	9.52	19.00	9	50
Distance to green space (m)	172.10	75.28	177.75	19.3	312.6
Distance to nearest counterpart nest (m)	100.14	87.86	86.45	7.9	408.8
Categorical Variables	A (n)	B (n)	C (n)	D (n)	
Nest concealment	24	4	4	N/A	
Base structure	26	2	4	N/A	
Base aspect	10	7	5	10	



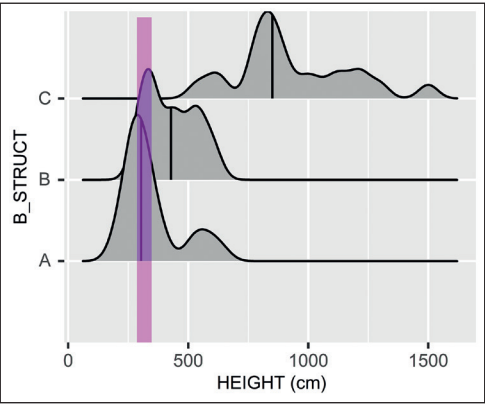
Appendix 2. Distributions of various nest site characteristics, including kernel density estimates, for Laughing Dove nest presence sites in 2019 ($n = 32$). The charts include box plots showing the median, interquartile range, and data points, as well as bar graphs displaying counts of categories. The plots (a) to (j) represent the following variables: (a) nest height above ground (HEIGHT), (b) nest to ceiling height (CEILING), (c) nest horizontal distance to ceiling edge (H_CEILING), (d) distance to nearest tree (TREE_DIST), (e) distance to opposite building (BUILD_DIST), (f) distance to green space (GREEN_DIST), (g) distance to nearest counterpart nest (NEST_DIST), (h) nest concealment categories (CONCEAL: A – invisible from the front and sides, B – invisible from the front but visible from one side, C – visible from the front but invisible from the sides), (i) base structure categories (B_STRUCT: A – shop boards, B – building frontispieces, C – balconies), and (j) base aspect categories (B_ASPECT: A – North, B – East, C – South, D – West)

2. melléklet A pálmagerle fészkelőhelyének az 1. mellékletben felsorolt tulajdonságait leíró értékek eloszlását bemutató ábrák



Appendix 3. Dendrogram of hierarchical variable clustering reveals a strong correlation between nest height above ground (HEIGHT) and base structure (B_STRUCT; distance value = 0.15)

3. melléklet A hierarchikus klaszterezéssel megállapított kapcsolatok a változók között erős összefüggést mutatnak a fészek talaj feletti magassága (HEIGHT) és a tartószerkezet (B_STRUCT) között (távolság = 0,15)



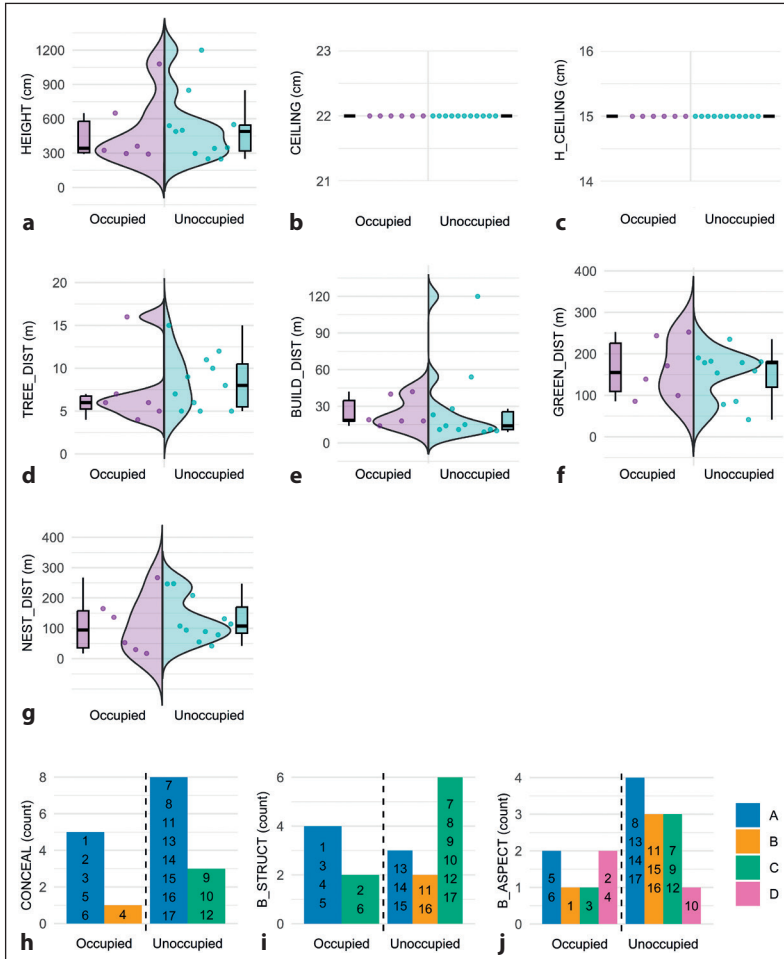
Appendix 4. Density ridgeline plot reveals that the Shop boards category (A) within the base structure (B_STRUCT) variable exhibits a higher density across the optimal range of nest height above ground (HEIGHT; 286–347 cm, as highlighted using a purple band). Vertical black lines indicate the medians

4. melléklet A fészek talaj feletti magassága (HEIGHT) és a tartószerkezet (B_STRUCT) közötti kapcsolat alapján a boltok táblái (A) magasabb denzitást mutatnak az optimális fészek magasságon belül (lila sávval jelölve). A függőleges fekete vonalak a mediánt jelölik az egyes kategóriákban

Appendix 5. The dataset from artificial nestbox sites for Laughing Doves (n = 17) was input into the nest site selection model. The model's analysis resulted in a classification table showing a correct prediction rate of 76.5% (optimal threshold = 0.52)

5. melléklet A kihelyezett költőládák helyeinek értékei a fészkelőhely-választás modellje alapján. A modell 76,5%-ban jól becsült (optimális küszöb = 0,52)

	Predicted Absence	Predicted Presence	Percentage Correct
Observed Absence	8	3	72.7%
Observed Presence	1	5	83.3%
Overall Percentage Correct			76.5%



Appendix 6. Comparisons of occupied versus unoccupied artificial nestboxes: In 2019, a total of 17 artificial nestboxes were erected, of which six were occupied and 11 were unoccupied. The variables include: (a) nest height above ground (HEIGHT), (b) nest to ceiling height (CEILING), (c) nest horizontal distance to ceiling edge (H_CEILING), (d) distance to nearest tree (TREE_DIST), (e) distance to opposite building (BUILD_DIST), (f) distance to green space (GREEN_DIST), (g) distance to nearest counterpart nest (NEST_DIST), (h) nest concealment categories (CONCEAL: A – invisible from the front and sides, B – invisible from the front but visible from one side, C – visible from the front but invisible from the sides), (i) base structure categories (B_STRUCT: A – shop boards, B – building frontispieces, C – balconies), and (j) base aspect categories (B_ASPECT: A – North, B – East, C – South, D – West). The charts include box plots showing the median, interquartile range, and individual data points, which are arranged from left to right in order of IDs (1-17) to track each nestbox across all subplots. They also display kernel density estimates of the data distribution. Bar graphs display counts of categories and, inside bars, the IDs of each nestbox. Category colors in bar graphs: A – blue, B – orange, C – green, and D – purple

6. melléklet A fészkelésre használt és nem használt költőládák összehasonlítása a korábban bemutatott tulajdonságok alapján. A kihelyezett 17 költőládából 6-ot használták a pálmagerlék 2019-ben