Population size and factors influencing the distribution of the urban pigeon *Columba livia* f. *domestica* in Pamplona

Juan Arizaga[1*], Xabier Esparza[1] & Luis M. Carrascal[2]

The environmental and trophic conditions of cities often give rise to very large populations of urban pigeons *Columba livia* f. *domestica*, which can cause local health and heritage problems due to accumulations of their droppings. Estimating the size of pigeon populations and defining their spatial patterns of abundance are therefore crucial for effective pigeon management in built-up areas. This article estimates the abundance of pigeons in Pamplona and the factors that explain the variability of pigeon abundance at local level. The Random Forest model of abundance at a local scale of 0.25 km^2 cells had very high explanatory power, although its predictive power decreased due to this species' gregariousness. Abundance decreased with increasing distance from the city centre, and from historic buildings and large parks, but increased as the proportion of the area covered by parks and built-up areas increased. The rock pigeon population in Pamplona was estimated at 8,030 individuals (95% CI: 6,483–9,860). The estimated density of urban pigeons for Pamplona as a whole was, on average, 218 birds/km^2, although this figure varied considerably between habitats and areas: the highest values were measured in urban areas with historic buildings (exceeding 600 individuals/km^2; in 35.8% of the 0.25 km^2 cells, more than 200 individuals were estimated). Pigeon densities fell to ca. 250 birds/km^2 in urban areas lacking large parks or green spaces whether near or far from historic buildings. In the peri-urban areas (i.e. arable fields, scrub and woodland), densities decreased to around 10–50 individuals/km^2. In the city of Pamplona, although the population density of urban pigeons did not reach the numbers observed in other northern Spanish cities such as Barcelona, the habitat preference patterns in urban gradients are consistent with those documented in other European regions. We identify specific urban areas for population control and recommend measures such as feeding bans and waste and facade management to make it difficult for urban pigeons to access roosting and breeding sites in buildings.

Key words: bird counts, historical buildings, Navarre, rock pigeon, urban birds, urban parks.

[1]Departamento de Ornitología, Sociedad de Ciencias Aranzadi, Zorroagagaina 11, 20014 Donostia.
[2]Museo Nacional de Ciencias Naturales-CSIC, 28006 Madrid.

*Correspondencia: jarizaga@aranzadi.eus

Received: 26.09.23; Accepted: 11.12.23 / Edited by Carles Barriocanal

Fine-scale knowledge of the distribution and abundance of avifauna in cities is essential for understanding how bird species adapt to the urbanisation process (Clergeau *et al.* 2002, Leveau 2013) and for effectively addressing management and control measures from both conservation and pest control perspectives (Senar *et al.* 2016, Anton *et al.* 2017, Arizaga *et al.* 2021).

Current urban pigeon populations are the result of the colonisation of cities by feral descendants of the free-ranging rock or domestic pigeon (*Columba livia* f. *domestica*), which in turn resulted from the domestication of its wild ancestor, the rock pigeon (*C. livia*) (Johnston & Janiga 1995). The rock pigeon was the first bird to be domesticated, some 5,000–10,000 years ago in the Middle East (Johnston & Janiga 1995). Rock pigeons breed on cliffs and rocks in both coastal and inland areas (Keller *et al.* 2020), while the domestic variety nests on human buildings, mainly in towns and cities. Both forms can interbreed, which means that the existence of 'pure' rock pigeon populations is limited to the most remote mountain and coastal regions. Urban pigeons have individual foraging strategies and are flexible enough to adapt to different urban environments (Rose *et al.* 2006).

The overfeeding of urban pigeons and the environmental conditions offered by cities (e.g. higher temperatures in winter) often mean that very large populations build up, which can cause local health problems including the transmission of microorganisms pathogenic to humans (Dautel *et al.* 1999, Haag-Wackernagel & Moch 2004), psychological problems (Wormuth 1994) and heritage conservation problems due to their droppings (e.g. soiling of facades of historical monuments and chemical deterioration of limestone rock; Dell'Omo 1996). For this reason, urban pigeons are often the target of culling and management actions aimed at reducing their numbers, with highly variable rates of success (Jacob *et al.* 2014, Rivera-Milán *et al.* 2014, Harris *et al.* 2016).

The aim of this paper is to examine the distribution and abundance patterns of the urban pigeon in the city of Pamplona as a step towards possible management measures aimed at avoiding overpopulation and making the presence of pigeons more compatible with urban human society. The more specific aspects to be addressed are as follows: 1) how certain environmental variables such as different types of urban land cover and proximity to the city centre, historic buildings and parks affect the distribution and abundance of pigeons; 2) the variability in pigeon density between different habitat types; and 3) the total population size and spatial variation in pigeon density at 0.25 km^2 scale.

Methodology

Study area and period

The fieldwork was carried out throughout the municipality of Pamplona (Navarra), an area of 25.14 km^2 (Fig. 1). Many pigeons and doves lay several clutches per year in their natural habitat and the urban pigeon is no exception: the characteristics of the urban environment, however, have enabled it to greatly extend its reproductive cycle (higher average temperatures than in non-urban environments, abundant and constant food availability throughout all or most of the annual cycle, more sheltered nesting areas, etc.) so that breeding individuals can be found virtually all year round (Johnston & Janiga 1995).The species is also fertile from six months of age and each pair usually produces several clutches per year (averaging over four), although chick survival can vary considerably (Uribe *et al.* 1985). On the other hand, due to its sedentary nature, it is a species with a low probability of recruiting 'wintering' individuals from elsewhere, so that the birds counted at the end of winter are generally all of local origin and thus constitute the breeding population for the following spring (Sol & Senar 1985). Pigeon sampling was therefore carried out in February and March 2020–2022, a period when only the potential adult breeding population is present. This avoids counting fledglings, juveniles or immature chicks, which represent a fraction of the population and are subject to high mortality and dispersal rates (Newton 2013).

Sampling protocol

The study area was divided into 148 500×500-m UTM cells (0.25 km^2), which provided the framework for the surveys (Fig. 1). We established 126 line transects, each measuring 200 m in length and wholly confined to a single cell. It should be noted that although there were 148 cells, many of them were located in border areas where a large part of the cell is located outside the municipality of Pamplona. A census belt of 150 m on each side of the transect was considered, so that each transect covered 200 m × 2 belts × 150 m = 60 000 m^2 (0.06 km^2, 24% of the area of the 500×500 m cell). The minimum distance between transects was 200 m. For each pigeon sighting, whether an individual or a group, we recorded the exact distance from the transect line using a GIS map layer on a tablet, along with the number of individuals at each location, i.e. in the case of flocks. These distances were measured perpendicular to the trajectory of the observer, in bands of 0–12.5, 12.5–25.0, 25–50, 50–75, 75–100 and 100–150 m. Transect and distance sampling is a viable and efficient alternative method to those traditionally used to estimate pigeon population sizes (Giunchi

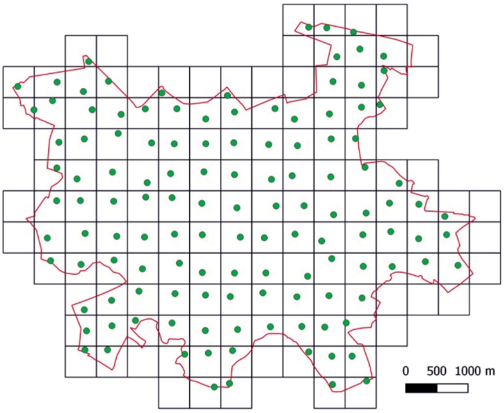


Figure 1. Municipality of Pamplona and grid of 500x50- m UTM cells showing centres of the transects (N = 126) surveyed for feral pigeons in Pamplona (green dots).
Municipi de Pamplona amb la malla de cel·les UTM de 500x500 m utilitzades com a unitat base de mostreig. Centre de cadascun dels transectes (N = 126) recorreguts per censar els coloms a Pamplona (punts verds).

et al. 2007). Census belts were pre-established using GIS mapping and displayed on the tablet employed during transect surveys. Each transect was walked twice on different days to reduce the uncertainty of the estimates (e.g. obtaining extremely high or low values that are unrepresentative of the true abundance of the species in the sampling area). Surveys were carried out during a period of four hours after sunrise or two hours before sunset, coinciding with the periods of maximum bird activity.

Statistical analysis

In the models developed to explain and predict urban pigeon abundance, several environmental features were used as predictors describing the characteristics of the urban environment:

1) Land cover. This is the area covered by each type of land use as a percentage of the total area of the spatial unit of analysis. It was obtained by GIS (Corine Land Cover layer) and grouped into 14 categories: GRASS, grassland (meadows, pastures); SCRPAS, scrubland and grassland; MATMED, Mediterranean scrubland; OAK, oak woodland; DECID, deciduous woodland; WOODCUL, woody crops (vines, etc.); CULHER, herbaceous crops (mainly cereals); AGRURB, urban orchards; URBEDI, urban and built-up; GARDEN, gardens, urban parks and, in general, green areas in the city; URBVIA, non-built-up urban areas (streets, squares, etc.); URBOTR, other types of areas in the city (e.g. industrial areas, wasteland, etc.); WATER, water (rivers, ponds).
2) Distances to elements of potential interest for birds (source of GIS layer: Ayuntamiento de Pamplona). Variables: DISPAR, minimum distance to a large urban park; DISEDI, minimum distance to a historical building/monument.
3) Geographical variables. Variables: UTMX, longitude; UTMY, latitude; DISCEN, distance to the geographical barycentre of Pamplona.

This set of variables was measured for each transect (in an area 150 m radius from the centre of each transect, Fig. 1) and for each of the 500×500-m UTM cells.

Random forest (RF) models (Breiman 2001, Cutler *et al.* 2007) were used to explain and predict the distribution and abundance of pigeons in Pamplona. Specifically, RF was used to:

1) Estimate the relative importance of the 19 predictor variables defining habitat preferences and spatial variation in pigeon numbers.
2) Predict pigeon abundance in 500×500-m cells.
3) Quantify what proportion of the variability in counts is predictable and explainable as a function of the 19 environmental variables. Explainability and predictability represent distinct aspects of data modelling: the former corresponds to the extent to which a model can account for the variations observed in the entire dataset it is applied to; the latter relates to the model's ability to accurately explain or anticipate variations in a subset of data based on a model constructed from a different subset of the data.

RF models take into account non-linear relationships based on regression trees when the target variable such as bird transect counts is continuous. RFs require the introduction of randomisation processes to create variability between the regression trees that make up the 'random forest'. The two randomisation procedures relate to (1) the number of samples from which each regression tree is generated and (2) the number of variables used in the modelling.

In the first case, a bootstrapping procedure was used, while in the second case three of the predictor variables were randomly selected to be included in each branch of the regression tree. This strategy makes it possible to avoid possible correlations between the predictor variables and to identify those that are most relevant in predicting the number of birds detected. The number of randomly selected predictors was determined using the *tuneRF* function of the R package {*randomForest*} to obtain the optimal number of variables taking into account the correlation between the predictor variables and the number of samples to be analysed (the procedure was repeated 30 times to obtain an average of 3.2 predictors). The procedure described was repeated 1,000 times to generate a RF model with 1,000 regression trees, which were subsequently averaged.

The probability of detection (PD) of urban pigeons was estimated using the 'distance' method (Buckland *et al.* 2007). This is essential for estimating absolute densities and population sizes, as detection is not perfect during transects (the probability of detecting a bird decreases with greater distance from the observer). Two fitting models referred to as 'half-normal' and 'hazard-rate' with fine cosine and polynomial fits were applied to the distribution of the detection distances for each contact. The four fitted models were averaged according to their Akaike's AIC indices. Estimates were made by removing the most extreme detection distances (Buckland *et al.* 2001), so that data were truncated at 150 m from the transect line.

The results of the RF modelling were used to predict urban pigeon abundance in Pamplona (148 500×500-m cells). Since transect abundance was quantified as the number of individuals counted twice for each transect (N_{obs}; i.e., sum), the value predicted by the RF model for each cell (N_{est}) was divided by two and multiplied by 4.1667 (250 000 m^2 of each cell / 60 000 m^2 covered by a transect), i.e. $N_{est} = 4.1667 \times N_{obs}/2$. We decided to use the sum of pigeons detected in the two replicates of each transect as the response variable of the RF models for two reasons: (1) the sum of birds detected fits a count distribution that only admits integer values (e.g. Poisson or negative binomial), which would not be satisfied by the average sum of odd-numbered counts; (2) working with the sum of birds in two replicates of the same transect increases the range of variation in the response variable, which facilitates the estimation of the RF models and increases their precision. The number of pigeons recorded in the two replicates of the 126 transects ranged from 0 to 108, which would have been reduced to 0–54 individuals per transect if the average number of pigeons had been used.

Such estimates ignore the fact that detectability is imperfect. Therefore, the value predicted by the RF model was corrected for the PD value. This was done by dividing the estimated number of birds (N_{est}) by the probability of detection: $N_{actual} = N_{est}/PD$. To estimate the size of the urban pigeon population in Pamplona, the N_{est} values of all 500 x 500-m cells in the municipality were summed (ΣN_{est}). Using resampling procedures with replacement (Davison & Hinkley 1997), 40 000 ΣN_{est} values were generated using the cells of the municipality. At the same time, 40 000 PD values were generated within their 95% confidence interval. Finally, the 40 000 ΣN_{est} values were divided by the 40 000 PD values to obtain 40 000 population size estimates (N_{actual}) after correction for detection bias. The 95% confidence interval (95%CI) of the estimate was obtained using the percentile method.

Taking into account the previous predictions of the RF models for the 500 x 500-m cells and the coverage of the most representative habitats in the municipality, eight main habitat typologies were defined for which pigeon densities and their 95% intervals were calculated using the percentile method. These habitats and their average characteristics are described in Appendix 1.

Statistical analyses were performed using R software (R Core Team 2023). The analysis packages used for the RFs were {*randomForest*} (Liaw & Wiener 2002), {*randomForestExplainer*} (Paluszynska *et al.* 2020), {*rfUtilities*} (Evans & Murphy 2018) and {*pdp*} (Greenwell 2017). The packages {*mrds*} and {*Distance*} (Miller 2016a, b) were used to calculate PD.

Results

The number of urban pigeons counted in all transects and at distances less than 150 m from the line transects was 2,059, giving a mean of 8.2 individuals per transect (range: 0–54 individuals). The number of transects with one or more contacts was 83 (65.8%).

RF model of habitat preference

The RF model was highly significant (R^2 = 0.90, P<0.01), although its predictive power was much lower (R^2 = 0.26; i.e. 26% of the variance in the 126 transect counts). The variable importance of predictors in the RF model explaining the spatial variation in pigeon counts per transect (Table 1) was highest for distance to the city centre (DISCEN), followed by distance to historic buildings (DISEDI) and large parks (DISPAR), garden cover (GARDEN), urban roads (URBVIA) and buildings (URBEDI). Geographical position (UTMX and UTMY) had a lower importance, albeit still of a relevant magnitude, suggesting that spatial constraints unrelated to urban structure explain some of the urban pigeon abundance at local level. The importance of the remaining variables was negligible.

The relationship between pigeon numbers and the variables with the greatest importance in explaining the variation associated with urban pigeon abundance (Figure 2) shows that abundance decreased with increasing distance

Table 1. Importance of predictor variables in the Random Forest model for predicting feral pigeon abundance in Pamplona. MMD: minimum depth of predictor variables in the branches of the regression trees (greater importance with lower value); MSE: increase in the Mean Squared Error value when removing the variable from the model (greater importance with higher value); NPI: contribution of variables to the purity (i.e. low variance) of pigeon count values at the nodes of the regression trees (greater importance with higher values).
Importància de les variables del model RF utilitzades per predir l'abundància de colom urbà a Pamplona. MMD: profunditat mínima de les variables predictores en les *ramificacions dels arbres de regressió (major importància com més baix* és *el valor); MSE: increment en el valor de Mean Squared Error en eliminar la variable del model (major importancia com més alt* és *el valor); NPI: contribució de les variables a la puresa (i.e., baixa variància) dels valors de recompte de coloms als nodes dels arbres de regressió (més gran com més valor). Les variables utilitzades són les següents: GRASS, pastures (prats, pastures); SCRPES, matolls i pastures; MATMED, matoll mediterrani; OAK, bosc de quercínies; DECID, arbrat de caducifolis; CONIFE, coníferes; WOODCUL, cultiu de llenyoses (vinya, etc); CULHER, conreus de caràcter herbaci (fonamentalment, cereal); AGRURB, horts urbans; URBEDI; urbanitzat i edificat; GARDEN, jardins, parcs urbans i altres espais verds a zona urbana; URBVIA, urbanitzat no edificat (carrers, places, etc.); URBOTR, un altre tipus de zones en* àrees *urbanes (e.g., polígons industrials, erms); WATER, aigua (riu, basses). DISPAR, distància* mínima a un gran *parc urbà; DISEDI, distància* mínima a un *edifici/monument històric; DISCEN, distància al baricentre geogràfic de Pamplona; UTMX, longitud; UTMY, latitud.*

Variable	MMD	MSE	NPI
Distance to the geographical barycentre of Pamplona (DISCEN)	2.44	138.2	12296.6
Minimum distance to a historic building/monument (DISEDI)	2.48	76.5	9092.2
Minimum distance to a large urban park (DISPAR)	2.68	108.9	8003.1
Gardens, urban parks and green spaces in urban areas (GARDEN)	2.74	33.2	6414.0
Non-built-up urban areas (streets, squares, etc.) (URBVIA)	2.80	42.1	6419.8
Urban and built-up (URBEDI)	2.82	36.2	6487.4
Longitude (UTMX)	3.14	17.9	5147.0
Latitude (UTMY)	3.26	15.9	4262.9
Other types of areas in the city (e.g. industrial areas) (URBOTR)	3.87	3.2	2757.6
Herbaceous crops (mainly cereal) (CULHER)	3.97	28.9	2473.2
Water (rivers, ponds) (WATER)	4.64	-4.8	2084.4
Grassland (meadows, pastures) (GRASS)	5.03	9.5	1545.1
Other deciduous woodlands (DECID)	5.60	-1.5	742.5
Urban orchards (AGRURB)	6.22	-0.3	136.5
Pastures with shrubs (SCRPAS)	6.27	-1.3	263.5
Mediterranean scrubland (MATMED)	6.88	-0.1	130.1
Coniferous woodlands (CONIFE)	6.92	0.5	109.3
Woody crops (vines, etc) (WOODCUL)	7.37	0.1	21.6
Oak woodlands (OAK)	7.48	0.2	8.8

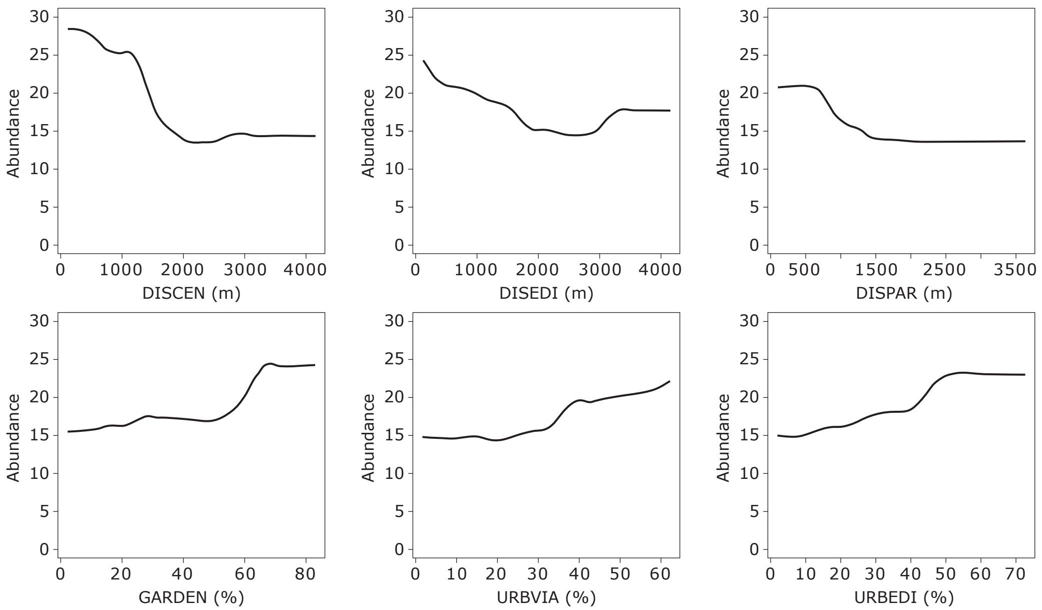
from the centre of Pamplona, historic buildings and large parks, but increased as the proportion of park and built-up areas increased (whether buildings, streets, squares or roads). However, there is a clear lack of linear relationships. The local maxima and minima observed in the graphs of the relationships are a consequence of the uncertainty associated with the gregariousness of the studied species, which makes it difficult to analyse the complex phenomenon of variation in pigeon abundance at such a detailed scale (126 200×300-m transects). Maximum local pigeon abundance was reached at the geographical barycentre of Pamplona; density decreased sharply along a radius of about 2,000 m from the city barycentre but then remained stable (Fig. 2, effect of DISCEN on abundance). Similarly, abundance decreased with increasing distance from nearby historic buildings (mostly up to 1500 m; DISEDI) or a large park if more than 500 m away (DISPAR). Considering the coverage of different urban land types, maximum pigeon abundance was reached when the relative area of urban streets, avenues or squares (URBVIA) increased, and in areas with more than 60% gardens (GARDEN) and 45% buildings (URBEDI).

The model showed the existence of interactions (i.e. there are certain combinations of urban characteristics that maximise or minimise pigeon density). Abundance was highest when the distance to a historic building was less than 100 m, the distance to a large urban park was less than 600 m, the relative area occupied by parks and gardens exceeded 60%, and the coverage of other buildings was 10–20%. By contrast, the lowest abundances of pigeons occurred in areas 2,000 m or more from a historic building, more than 750 m from a large park, and the relative area of green space and buildings was less than 20%. These spatial configurations will serve as a useful guide for the urban pigeon management strategy in the municipality.

Population estimates

Extrapolating the transect count directly to the whole city of Pamplona (148 cells), we obtained a value of 1,209 individuals (2,059 individuals/2

Figure 2. Partial effect of the most influential variables in explaining the variation associated with the abundance of feral pigeons in Pamplona obtained from the application of a RF model. For the meaning of the acronyms, see Table 1. ABUNDANCIA on the Y-axis of the panels corresponds to the number of pigeons recorded in two visits to each 200-m transect.
Efecte parcial de les variables amb més pes a l'hora d'explicar la variació associada a l'abundància de coloms a Pamplona (per a les abreviatures vegeu Taula 1), obtingut a partir de l'aplicació d'un model RF. L'abundància a l'eix Y mesura el nombre de coloms registrat a les dues visites a cada transsecte de 200 m de longitud.



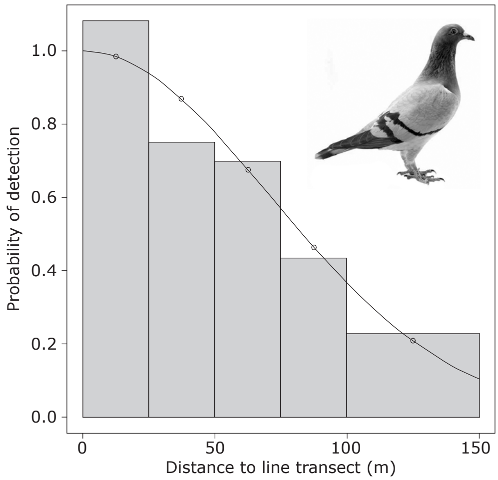


Figure 3. Detectability curve for feral pigeons in Pamplona obtained using a Distance Sampling model. N = 467 unique pigeon encounters of 2,059 individuals. *Corba de detectabilitat dels coloms a Pamplona obtinguda mitjançant un model de Distance Sampling. N = 467 contactes diferents amb coloms que inclouen 2.059 individus.*

repetitions/126 censused cells × 148 cells). However, the census area in each transect is only 0.06 km^2, detectability is imperfect, and the transects do not cover an identical proportion of the available habitat. Detection probability (PD) decreased non-linearly with distance from the observer (Fig. 3), estimated at 0.54 (SE = 0.04; 95%CI: 0.47–0.61; n = 467 pigeon contacts including 2,059 individuals). Flock size had no effect on the PD estimate (coefficient = +0.012, t = 0.992, P = 0.322). Extrapolating to the whole area of Pamplona, taking into account the PD and the predictions of the RF models, the urban pigeon population in Pamplona is estimated to be 8,030 individuals (95% CI: 6,483–9,860 individuals).

The distribution of urban pigeon abundance in Pamplona was not homogeneous. There is a higher concentration of urban pigeons around the historic centre of the city but their abundance decreases sharply towards peripheral areas (Fig. 4). Where maximum densities were reached, 200 individuals in 0.25 km^2 was exceeded, while in cells with the lowest values less than 10 individuals were recorded. There were 53 cells (35.8%) where pigeon density exceeded 200 birds/km^2 (or 50 individuals/500×500-m cell; Fig. 4).

Population densities

The urban pigeon density for Pamplona as a whole was on average 218 birds/km^2. This density, however, varied considerably between habitats (Table 2) and the highest figures were obtained in areas where there are historic buildings (exceeding 600 individuals/km^2). In urban sectors lacking nearby large green spaces or far from historic buildings, pigeon density decreased to an average of about 250 individuals/km^2. In undeveloped, peri-urban areas with crops, shrub or woodland environments, the density was much lower, with values of 10–50 individuals/km^2.

Discussion

The population of urban pigeons in Pamplona was estimated at around 8,000 birds distributed heterogeneously in terms of space and habitats. Proximity to the geographical centre of the city, large parks and historic buildings was the main environmental factor determining the presence of pigeons in Pamplona. The characteristics that gave the greatest abundances (around 650 pigeons/km^2) were proximity to historic buildings (<100 m) and large parks (<600 m), and a very high coverage (>60%) of green areas. By contrast, average densities in areas with

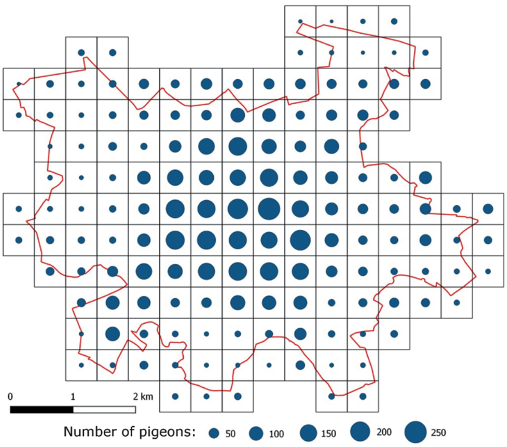


Figure 4. Spatial distribution of feral pigeon abundance in Pamplona (500 x 500-m grid cells) predicted using the RF model from Fig. 2 and Table 1. *Distribució espacial de l'abundància de coloms urbans a Pamplona (quadrícula de cel·les de 500×500 m), predita a partir del model RF de la Fig. 2 i Taula 1.*

Table 2. Density (birds/km^2) of feral pigeons in the most representative habitats of Pamplona. IC95% are the lower and upper limits of the 95% confidence intervals.
Densitat (ocells/km^2) de coloms als hàbitats més representatius de Pamplona. IC95% són els límits dels intervals de confiança al 95% de probabilitat.

Habitats	**Density (birds/km^2)**	**IC95%**
Woodland: coniferous	11.1	8.1–15.5
Woodland: deciduous (*Quercus* spp.)	38.6	30.3–49.5
Shrublands	19.9	16–25.7
Herbaceous crops	34.1	25.8–47.2
Urban orchards	57.9	49.2–69.5
Urban Areas with very few green spaces	274.1	256–294.3
Urban areas far from historical buildings	228	205.3–252.2
Urban areas near historical buildings	602.9	574.3–632.9

low garden coverage were around 250 pigeons/km^2, while densities in peri-urban agricultural habitats dropped to 40–50 pigeons/km^2. The fact that the distribution of urban pigeon abundance in Pamplona is highly explainable, both spatially and according to habitat types, makes it possible to design management actions aimed at avoiding or mitigating the impact of this commensal species on city and urban life (Dautel *et al.* 1999, Haag-Wackernagel & Moch 2004, Haag-Wackernagel & Geigenfeind 2008, Haag-Wackernagel & Bircher 2010, Przybylska *et al.* 2012).

Globally, the habitat preferences of urban pigeons in Pamplona were consistent with other urban areas where the factors influencing their distribution have been similarly analysed (Sacchi *et al.* 2002, Pascual *et al.* 2011, Przybylska *et al.* 2012, Anton *et al.* 2017). For example, the density in urban orchards and arable crops was only 40–50 birds/km^2, a density 12–15 times lower than that recorded in urban areas near historic buildings. The availability of old, vertically developed buildings, which mimic the rocky outcrops that make up its wild habitat and provide suitable breeding and roosting sites, appears to be an important determinant of the high population density of the Pamplona urban pigeon. Furthermore, the availability of buildings is also associated with a higher density of people and services (e.g. bars and restaurants in open-air terraces), which provide feeding opportunities. The preference for parks and gardens can similarly be attributed to pigeons relying on food sources that are either accidentally or intentionally provided through human activities.

The relatively low predictive power of the RF model is not due to the small sample size but, rather, to the gregarious nature of the study species, which creates variability in abundance estimates (Seoane *et al.* 2005, Estrada & Arroyo 2012, Carrascal *et al.* 2015). For instance, out of 465 contacts within a distance of <150 m, groups of 1–5 individuals were observed 369 times; conversely, larger groups of 30–40 individuals were recorded on only six occasions, including an instance of a flock of 73 birds. Such variability in flock size limits the certainty of the RF model predictions when comparing the predicted abundance per transect with the number actually observed. Repeating the RF model with the number of positive pigeon contacts per transect unit (rather than the sum of individuals detected) yields a highly significant model that explains a large proportion of the variance ($R^2 = 0.94$, $P < 0.001$) and also has a higher predictive power ($R^2 = 0.50$). Therefore, the model effectively estimates the frequency of occurrence within the municipality, although its ability to predict abundance is constrained by the gregarious nature of this pigeon.

On average, the density of urban pigeons throughout the municipality of Pamplona is 218 birds/km^2, a value significantly lower than the 846 birds/km^2 in Barcelona (Anton *et al.* 2017) but higher than the average of 60 birds/km^2 in San Sebastian (Arizaga *et al.* 2021), two cities located at similar latitudes in the north of the Iberian Peninsula. The densities in Pamplona are much higher than the averages obtained for many towns and cities in other areas of Spain (55–90 birds/km^2) (Carrascal & Palomino 2008) and is therefore one of the highest in Spain. It should also be noted that the lineal transects in Pamplona were carried out during the pre-breeding period, a time when only adult birds and no chicks were present. The urban pigeon population in Pamplona could easily double or even triple the estimate obtained for the study period when most of the yearling chicks have left the nest.

The urban pigeon is now a globally distributed species, with a population estimated at between 165 and 330 million individuals (Haag-Wackernagel and Bircher, 2010). For Spain alone, Carrascal & Palomino (2008) estimated a population of 4.8 to 8.8 million birds. The abundance of pigeons in urban environments can lead to human-wildlife conflicts in the form of droppings, disease and nuisance behaviour, which can be managed and mitigated using humane, sustainable and safe methods. In recent decades, societal concern for animal welfare has grown and today non-lethal methods of wildlife management, especially in cities, are mandatory. To reduce the pigeon population in Pamplona, the following recommendations are thus proposed:

1) Seal as far as possible the cracks and holes used by pigeons to nest in buildings and make it difficult or impossible for pigeons to access ledges and areas where they also breed. In this context, it should be noted that there are species that also use holes in buildings for nesting, both birds (sparrows, jackdaws, redstarts, swifts, etc.) and other fauna (e.g. bats). These species, unlike pigeons, need to be protected and therefore a general sealing of cracks and gaps in buildings to prevent their use by these species would not be justified. The use of specific nesting boxes for bats, swifts or other birds can compensate at building level for the implementation of measures aimed at reducing the presence of pigeons (Domínguez 1999, Blanco 2003, Wortha & Arndt 2004, Luniak & Grzeniewski 2011, Schaub *et al.* 2015). As well, the use of physical deterrents such as spikes, nets, twine or angled coverings on pigeon roosting surfaces can help discourage pigeons from settling in certain areas. Bird spikes are the most effective non-lethal method of pigeon control on building facades. For example, Harris *et al.* (2016) showed that this deterrent reduced the pigeon population by 50% on the Muckleneuk campus of the University of South Africa.
2) Concentrate the capture of pigeons in large parks, especially those located in the city centre and within walking distance of historic buildings given that the feral population of pigeons in Pamplona is concentrated in the historic area and surrounding neighbourhoods (Rochapea, Ensanche and S. Juan), the north of Milagrosa, Azpilagaña and Iturrama, and the west of Mendebaldea. It should be noted, however, that trapping is ineffective in systems organised in metapopulations (Sol & Senar 1985). Culling has historically been a predominant method of urban pigeon population control, although its efficacy is questionable, both ethically and in terms of effectiveness. In Barcelona (Senar *et al.* 2009), despite the culling of more than 227,000 pigeons between 1991 and 2006 by the City Council's Public Health Agency, the number of pigeons in the city did not decrease and, moreover, an increase was observed in peripheral areas leading to a rise in the overall urban pigeon population. The removal of individuals is therefore not effective in the medium- to long-term unless it is accompanied by other measures such as reducing suitable breeding sites or removing feeding sites unless continuous trapping is performed (with all the ethical implications that it entails). However, we recommend mitigating extreme situations where high pigeon densities may be seriously affecting heritage conservation or human health. Such results suggest the need for alternative strategies, which are also less questionable from a social point of view.
3) Publicise the negative effects of feeding pigeons in urban areas by promoting a new awareness of the need to remove feeding points in large parks and squares; as well, the option of passing legislation to prohibit such practices could be contemplated. Senar *et al.* (2016) showed in Barcelona that reducing the amount of food provided by people to pigeons contributed to a 40% reduction in feral pigeon density in two experimental neighbourhoods, while no change was detected in the control neighbourhood. Stock & Haag-Wackernagel (2016) demonstrated that the removal of supplementary food (i.e. the creation of a shortage of artificially sourced food for the species) increases reproductive failure and reduces productivity by up to half. Better waste management to limit food availability including more secure wastebins and the frequent cleaning of public spaces may also deter pigeons from congregating in urban areas where there are high concentrations of people and restaurants.

Acknowledgements

This study was funded by Pamplona City Council. Daniel Sol and an anonymous reviewer helped improve a first version of the paper. Claire Jasinski translated the original Spanish version of the manuscript into English.

Resum

Mida de la població i factors que influeixen en la distribució del colom urbà *Columba livia f. domestica* a Pamplona

Les condicions ambientals i tròfiques que ofereixen els nuclis urbans sovint donen peu a poblacions molt nombroses dels coloms urbans *Columba livia f. domestica*, que a nivell local provoquen, entre d'altres, problemes de salubritat i de conservació del patrimoni pels seus excrements. Per això, estimar les mides poblacionals de coloms i definir els patrons espacials de la seva abundància són crucials des del punt de vista de la gestió en àmbits urbanitzats. En aquest article s'estima l'abundància de coloms a Pamplona així com els factors que expliquen la seva variabilitat a nivell local (cobertures de sòl, distàncies a elements d'interès per als ocells com ara grans parcs o edificis històrics i variables geogràfiques). El model Random Forest de la seva abundància a escala local en cel·les de 0,25 km^2 va tenir un poder explicatiu altíssim, encara que el seu poder predictiu va disminuir com a conseqüència del gregarisme de l'espècie. L'abundància va baixar quan es va incrementar la distància al centre, a edificis històrics o a grans parcs, i va augmentar quan també ho va fer la proporció de superfície coberta de parcs i substrat urbanitzat. La població de colom urbà a Pamplona es va estimar en 8.030 individus (IC95%: 6.483-9.860). La densitat estimada de colom urbà per al conjunt de Pamplona va ser, de mitjana, de 218 aus/km^2, si bé va variar considerablement entre hàbitats: els valors més elevats es van assolir en zones urbanes enjardinades amb presència d'edificis històrics (on es van superar els 600 individus/ km^2, al 35,8% de les cel·les de 0,25 km^2 es van estimar més de 200 individus). Quan el nucli urbà no tenia grans àrees enjardinades properes, o va quedar lluny d'edificis històrics, la densitat de coloms va baixar a mitjanes d'uns 250 individus/km^2. En conclusió, encara que la densitat de coloms urbans a Pamplona no arriba als nombres observats a d'altres ciutats del nord d'Espanya, com Barcelona, els seus patrons de preferències d'hàbitat són consistents amb allò documentat en altres regions europees. Identifiquem zones específiques on aplicar un control poblacional basat en la prohibició d'alimentació, la gestió de deixalles i la gestió de les façanes per dificultar l'accés dels coloms a llocs de descans i nidificació.

Resumen

Tamaño de la población y factores que influyen en la distribución de la paloma urbana *Columba livia f. domestica* en Pamplona

Las condiciones ambientales y tróficas que ofrecen los núcleos urbanos a menudo dan pie a poblaciones muy numerosas de las palomas urbanas (*Columba livia f. domestica*), que a nivel local provocan, entre otros, problemas de salubridad y de conservación del patrimonio por sus excrementos. Por ello, estimar los tamaños poblacionales de palomas y definir los patrones espaciales de su abundancia son cruciales desde el punto de vista de su gestión en ámbitos urbanizados. En este artículo se estima la abundancia de palomas en Pamplona así como los factores que explican su variabilidad a nivel local (coberturas de suelo, distancias a elementos de interés para las aves como grandes parques o edificios históricos y variables geográficas). El modelo *Random Forest* de su abundancia a escala local en celdas de 0,25 km^2 tuvo un altísimo poder explicativo, aunque su poder predictivo disminuyó como consecuencia del gregarismo de la especie. La abundancia bajó cuando se incrementó la distancia al centro, a edificios históricos o a grandes parques, y aumentó cuando también lo hizo la proporción de superficie cubierta de parques y sustrato urbanizado. La población de paloma urbana en Pamplona se estimó en 8030 individuos (IC95%: 6483-9860). La densidad estimada de paloma urbana para el conjunto de Pamplona fue, en promedio, de 218 aves/km^2, si bien varió considerablemente entre hábitats: los valores más elevados se alcanzaron en zonas urbanas ajardinadas con presencia de edificios históricos (superándose los 600 individuos/km^2; en el 35,8% de las celdas de 0,25 km^2 se estimaron más de 200 individuos). Cuando el núcleo urbano careció de grandes áreas ajardinadas cercanas, o quedó lejos de edificios históricos, la densidad de paloma bajó a medias de unos 250 individuos/km^2. En conclusión, aunque la densidad de palomas urbanas en Pamplona no alcanza los números observados en otras ciudades norteñas de España, como Barcelona, sus patrones de preferencias de hábitat son consistentes con lo documentado en otras regiones europeas. Identificamos zonas específicas donde aplicar un control poblacional basado en la prohibición de alimentación, la gestión de desechos y la gestión de las fachadas para dificultar el acceso de las palomas a lugares de descanso y nidificación.

References

Anton, M., Herrando, S., Garcia, D., Ferrer, X. & Cebrian, R. 2017. *Atles dels ocells nidificants de Barcelona*. Barcelona: Ajuntament de Barcelona/ICO/UB/Zoo.

Arizaga, J., Laso, M., Rodríguez-Pérez, J., Zorrozua, N., Pagaldai, N. & Carrascal, L.M. 2021. *Atlas de aves nidificantes en San Sebastián*. Donostia: Sociedad de Ciencias Aranzadi - Ayuntamiento de San Sebastián.

Blanco, G. 2003. *La chova piquirroja en edificios históricos de Segovia: un modelo de conservación del patrimonio natural y artístico*. Segovia: Caja Segovia.

Breiman, L. 2001. Random forests. *Machine Learning* 45: 15–32.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2001. *Introduction to distance sampling*. Oxford: Oxford University Press.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2007. *Advanced distance sampling*. Oxford: Oxford University Press.

Carrascal, L.M., Aragón, P., Palomino, D. & Lobo, J.M. 2015. Predicting regional densities from bird occurrence data: validation and effects of species traits in a Macaronesian Island. *Divers. Distrib.* 21: 1284–1294.

Carrascal, L.M. & Palomino, D. 2008. *Las aves comunes reproductoras en España. Población en 2004-2006*. Madrid: SEO/BirdLife.

Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M.L. & Dinetti, M. 2002. Avifauna homogenisation by urbanisation: Analysis at different European latitudes. *Biol. Conserv.* 127: 336–344.

Cutler, D.R., Edwards, T.C., Beard, K.H., Cutler, A. & Hess, K.T. 2007. Random forests for classification in ecology. *Ecology* 88: 2783–2792.

Dautel, H., Scheurer, S. & Kahl, O. 1999. The pigeon tick (*Argas reflexus*): its biology, ecology, and epidemiological aspects. *J. Med. Microbiol. Virol. Parasitol. Infect. Dis.* 289: 745–753.

Davison, A.C. & Hinkley, D.V. 1997. *Bootstrap methods and their application*. Cambridge: Cambridge University Press.

Dell'Omo, A. 1996. *Il ruolo degli escrementi dei piccioni nella bioalterazione delle rocce.* Tesina di Università degli Studi di Roma "La Sapienza". Roma: Facoltà di Scienze Matematiche, Fisiche e Naturali, Dipartimento di Biologia Animale e dell'Uomo.

Domínguez, L. 1999. *Ecología de la Grajilla (Corvus monedula Linnaeus 1758) en la provincia de Madrid. Tesis doctoral*. Madrid: Universidad Complutense de Madrid.

Estrada, A. & Arroyo, B. 2012. Occurrence vs abundance models: Differences between species with varying aggregation patterns. *Biol. Conserv.* 152: 37–45.

Evans, J.S. & Murphy, M.A. 2018. rfUtilities. R package version 2.1-3. Available at: [https://cran.r-project.org/package=rfUtilities.

Giunchi, D., Gaggini, V. & Baldaccini, N. 2007. Distance sampling as an effective method for monitoring feral pigeon (*Columba livia f. domestica*) urban populations. *Urban Ecosyst.* 10: 397–412.

Greenwell, B.M. 2017. pdp: An R Package for Constructing Partial Dependence Plots. *The R Journal* 9: 421–436.

Haag-Wackernagel, D. & Bircher, A.J. 2010. Ectoparasites from feral pigeons affecting humans. *Dermatology* 220: 82–92.

Haag-Wackernagel, D. & Geigenfeind, I. 2008. Protecting buildings against feral pigeons. *Eur. J. Wildl. Res.* 54: 715–721.

Haag-Wackernagel, D. & Moch, H. 2004. Health hazards posed by feral pigeons. *J. Infection* 48: 307–313.

Harris, E., Crom, E., Labuschagne, J. & Wilson, A. 2016. Visual deterrents and physical barriers as non-lethal pigeon control on University of South Africa's Muckleneuk campus. *SpringerPlus* 5: 1884.

Jacob, G., Prévot-Julliard, A. & Baudry, E. 2014. The geographic scale of genetic differentiation in the feral pigeon (*Columba livia*): implications for management. *Biol. Invasions* 17: 23–29.

Johnston, R.F. & Janiga, M. 1995. *Feral pigeons*. Oxford: Oxford University Press.

Keller, V., Herrando, S., Voříšek, P., Franch, M., Kipson, M., Milanesi, P. *et al.* 2020. *European Breeding Bird Atlas 2: Distribution, Abundance and Change*. Barcelona: European Bird Census Council - Lynx Edicions.

Leveau, L.M. 2013. Bird traits in urban–rural gradients: how many functional groups are there? *J. Orn.* 154: 655–662.

Liaw, A. & Wiener, M. 2002. Classification and Regression by randomForest. *R News* 2: 18–22.

Luniak, M. & Grzeniewski, M. 2011. Nest-boxes for the common swift *Apus apus* experience from Poland. *Ecologia Urbana* 23: 3–5.

Miller, D.L. 2016a. *Package 'Distance'. Version 0.9.6*.

Miller, D.L. 2016b. *Package 'mrds'. Version 2.1.17*.

Newton, I. 2013. *Bird populations*. London: Collins New Naturalist Library.

Paluszynska, A., Biecek, P. & Jiang, Y. 2020. randomForestExplainer: Explaining and Visualizing Random Forests in Terms of Variable Importance. R package version 0.10.1. Available at: https://CRAN.R-project.org/package=randomForestExplainer.

Pascual, J., Senar, J.C., Uribe, F. & Riba, D. 2011. *Determinació dels factors ambientals que incideixen en la distribució dels coloms a la ciutat de Barcelona*. Barcelona: Museu de Ciènces Naturals de Barcelona/Agència de Salut Pública de Barcelona.

Przybylska, K., Haidt, A., Myczko, Ł., Ekner-Grzyb, A., Rosin, Z.M., Kwieciński, Z. *et al.* 2012. Local and landscape-level factors affecting the density and distribution of the Feral Pigeon *Columba livia* var. *domestica* in an urban environment. *Acta Ornithol.* 47: 37–45, 39.

R Core Team 2023. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rivera-Milán, F., Boomer, G. & Martínez, A. 2014. Monitoring and modeling of population dynamics for the harvest management of scaly-naped pigeons in Puerto Rico. *J. Wildlife Manage.* 78: 513–521.

Rose, E., Nagel, P. & Haag-Wackernagel, D. 2006. Spatio-temporal use of the urban habitat by feral pigeons (*Columba livia*). *Behav. Ecol. Sociobiol.* 60: 242–254.

Sacchi, R., Gentilli, A., Razzetti, E. & Barbieri, F. 2002. Effects of building features on density and flock distribution of feral pigeons *Columba livia* var. *domestica* in an urban environment. *Can. J. Zoolog.* 80: 48–54.

Schaub, T., Meffert, P.J. & Kerth, G. 2015. Nest-boxes for Common Swifts *Apus apus* as compensatory measures in the context of building renovation: efficacy and predictors of occupancy. *Bird Conserv. Int.* 26: 164–176.

Senar, J., Carrillo, J., Arroyo, L., Montalvo, T. & Peracho, V. 2009. Estima de la abundancia de palomas (*Columba livia var. domestica*) de la ciudad de Barcelona y valoración de la efectividad del control por eliminación de individuos. *Misc. Zool.* 7: 62–71.

Senar, J.C., Montalvo, T., Pascual, J. & Peracho, V. 2016. Reducing the availability of food to control feral pigeons: changes on population size and composition. *Pest Manag. Sci.* 73: 313–317.

Seoane, J., Carrascal, L.M., Alonso, C.L. & Palomino, D. 2005. Species-specific traits associated to prediction errors in bird habitat suitability modelling. *Ecol. Model.* 185: 299–308.

Sol, D. & Senar, J.C. 1985. Urban pigeon populations: stability, home range and the effect of removing individuals. *Can. J. Zoolog.* 73: 1154–1160.

Stock, B. & Haag-Wackernagel, D. 2016. Food shortage affects reproduction of Feral Pigeons *Columba livia* at rearing of nestlings. *Ibis* 158: 776–783.

Uribe, F., Senar, J.C., Colom, L. & Camerino, M. 1985. Morfometría de las palomas semidomésticas (*Columba livia* var. *domestica*) de la ciudad de Barcelona. *Misc. Zool.* 73: 339–345.

Wormuth, H.J. 1994. *Zum Problem der verwilderten Haustauben*. Berlin: Merkblatt des Robert von Ostertag-Instituts des Bundesgesundheitsamtes.

Wortha, S. & Arndt, E. 2004. Acceptance of nest boxes by the Common Swift (*Apus apus*) in Berlin. *Ber. Vogelschutz* 41: 113–126.

Appendix 1. Habitat characteristics used for estimating feral pigeon densities in Pamplona by habitat types (relative surface area of land uses, average distances to large urban parks, historical buildings and the centroid of Pamplona). Abbreviations: see Methodology and Table 1.
Característiques (superfície relativa dels usos del sòl, distàncies mitjanes a grans parcs urbans, edificis històrics i el baricentre de Pamplona) dels hàbitats que s'utilitzen per a l'estimació de densitats de coloms a Pamplona, segons tipus d'hàbitat. Abreviatures: vegeu Metodologia i Taula 1.

HABITAT	GRASS	SCRPAS	MATMED	OAK	DECID	WOODCUL	CULHER	CONIFE	AGRURB
Woodland: coniferous	8.8	10.4	14.8	7.1	0.0	1.9	13.7	42.7	0.0
Woodland: deciduous (*Quercus* spp.)	2.2	23.3	5.6	32.9	4.1	0.0	6.8	16.8	0.0
Shrublands	0.1	3.6	38.1	3.8	0.0	1.0	24.3	15.1	0.0
Herbaceous crops	3.9	1.3	0.0	0.0	1.7	0.6	79.9	0.4	1.0
Urban orchards	8.1	0.0	0.0	0.0	0.0	0.1	2.1	0.0	38.2
Urban areas with very few green spaces	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Urban areas far from historical buildings	1.1	0.0	0.0	0.0	3.2	0.0	0.7	0.0	0.0
Urban areas near historical buildings	2.2	0.2	0.0	0.0	0.2	0.0	0.0	0.0	1.0

HABITAT	URBEDI	GARDEN	URBVIA	URBOTR	WATER	DISPAR	DISEDI	DISCEN
Woodland: coniferous	0.1	0.1	0.1	0.1	0.0	2496	2673	3469
Woodland: deciduous (*Quercus* spp.)	2.1	1.2	2.9	2.0	0.0	2461	2669	3546
Shrublands	1.0	6.1	6.2	0.8	0.0	2137	2571	3358
Herbaceous crops	1.5	3.2	5.0	1.0	0.5	887	2807	2826
Urban orchards	17.2	5.7	16.7	1.1	10.8	1450	2653	2430
Urban Areas with very few green spaces	43.4	16.5	37.6	2.3	0.3	955	1806	1910
Urban areas far from historical buildings	38.2	28.7	24.8	0.0	3.3	234	91	745
Urban areas near historical buildings	14.2	59.2	17.4	3.0	2.6	953	1732	2131