

LANDSCAPE FEATURES INFLUENCING NESTING-SITE SELECTION OF *COLUMBA LIVIA* AND *PATAGIOENAS MACULOSA* IN A SOUTH AMERICAN DESERT CITY

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ABSTRACT.— Urban centers are dominated by species adapted to human presence. The intensity of human activity has a strong influence on habitat selection by animal populations across landscapes. The objectives of this study were to assess the abundance and the spatial distribution of the nests of two species of pigeons (*Columba livia* and *Patagioenas maculosa*), and evaluate the effects of human factors on the probability of nesting-site selection in different urban zones within a desert city. Nest abundance increased for *Columba livia* in city centers and for *Patagioenas maculosa* in zones away from them, in green areas. The most important variables influencing the probability of nesting-site selection by *Columba livia* were distance to the main square, distance to food sources and the interaction between distance to food sources and distance to water, along with type and height of buildings. For *Patagioenas maculosa*, the variables influencing the probability of nesting-site selection were distance to water, human population density, distance to food sources and the interaction between human population density and distance to food sources, along with tree height and diameter of tree canopy. This species selected *Platanus × hispanica* and *Morus* spp. as nesting sites. Nesting sites could be a limiting factor for these species, and our results have important implications for choosing appropriate control strategies for the management of urban pigeons in desert environments.

KEY WORDS: *desert city, nesting site, resource selection, spatial distribution, urban ecology.*

RESUMEN. CARACTERÍSTICAS DEL PAISAJE QUE INFLUYEN EN LA SELECCIÓN DE SITIOS DE NIDIFICACIÓN DE *COLUMBA LIVIA* Y *PATAGIOENAS MACULOSA* EN UNA CIUDAD DE DESIERTO EN AMÉRICA DEL SUR.— Los centros urbanos están dominados por especies adaptadas a la presencia humana. La intensidad de la actividad humana tiene una fuerte influencia sobre la selección del hábitat en poblaciones animales. Los objetivos de este estudio fueron estimar la abundancia y la distribución espacial de los nidos de dos especies de palomas (*Columba livia* and *Patagioenas maculosa*) y evaluar los efectos de factores humanos sobre la probabilidad de selección de sitios de nidificación en diferentes zonas en una ciudad de desierto. La abundancia de nidos de *Columba livia* aumentó en el centro de la ciudad y para *Patagioenas maculosa* en zonas alejadas del centro, en áreas verdes. Las variables más influyentes en la probabilidad de selección de sitios de nidificación para *Columba livia* fueron distancia a la plaza principal, distancia a las fuentes de alimento y la interacción entre la distancia a las fuentes de alimento y la distancia al agua, además del tipo y la altura de los edificios. Para *Patagioenas maculosa* las variables más influyentes en la probabilidad de selección de sitios de nidificación fueron la distancia al agua, la densidad poblacional humana, la distancia a las fuentes de alimento y la interacción entre la densidad poblacional humana y la distancia a las fuentes de alimento, además de la altura del árbol y el diámetro de la copa. Además, esta especie seleccionó *Platanus × hispanica* y *Morus* spp. como sitio de nidificación. Los sitios de reproducción podrían ser un factor limitante para estas especies; los resultados de este estudio tienen importantes implicancias para la elección de estrategias apropiadas de control en el manejo de palomas de ambientes urbanos en zonas desérticas.

PALABRAS CLAVE: *ciudad de desierto, distribución espacial, ecología urbana, selección de recursos, sitio de nidificación.*

Urban areas are characterized by drastic environmental changes and high levels of disturbance (Niemelä 1999). In turn, the abundance of resources upon which animals depend, such as vegetation cover, food and nesting places, may change positively or negatively with urban development (Jokimäki and Suhonen 1998). This depends on the rapid adaptation of species to urban changes. As result, urban centers are dominated by a few widely distributed species that are adapted to human presence (Villegas and Garitano-Zavala 2010, Morelli et al. 2016). The Rock Pigeon (*Columba livia*) is a species adapted to human presence (Ryan 2011) and is likely the most recognized, widespread and abundant pest species inhabiting cities in the American and European continents (Pimentel et al. 2000, Savard et al. 2000). Its breeding colonies are primarily concentrated in city centers (Sacchi et al. 2002), and breeding pairs occupy a defined nesting territory for many years forming large colonies (Hetmanski and Barkowska 2007). The Spot-winged Pigeon (*Patagioenas maculosa*) instead, despite being a species exhibiting synanthropic behaviours (Fernández-Juricic et al. 2004), concentrates its breeding nests mostly in suburban areas and urban fringes (Leveau and Leveau 2004). Recently, this species has considerably expanded its distribution range from its typical rural habitat to urban habitats of Argentina (Leveau and Leveau 2012). Moreover, these urban pigeons have a strong direct impact not only on other species but also on humans (Savard et al. 2000, Clergeau et al. 2001). Their droppings accumulate above and below their nesting sites producing structural damage in buildings (Gómez-Heras et al. 2004, Magnino et al. 2009, Spennemann and Watson 2017). Another major problem is the dust from droppings floating in the air (source of bacterial, fungal and viral infections) that can be inhaled posing a risk to human and animal health (Casanovas et al. 1995, Vallvé et al. 1995, Adesiyun et al. 1998, Haag-Wackernagel and Moch 2004, Marques et al. 2007).

The selection of a habitat is determined by the availability of patches suitable for use. This approach has been especially employed in theoretical and empirical studies of foraging behaviour (Orians and Wittenberger 1991). A suitable habitat may need to contain a mixture of patches that provides opportunities for

all of the activities required for successful reproduction. The success of an individual under those circumstances depends strongly on the local distribution of resources and on density of conspecific individuals already settled in the area. Among the available procedures that quantify relative use of habitat resources, the resource selection function is undoubtedly the most popular (McLoughlin et al. 2010). Also, the distribution and intensity of human activity has a strong influence on habitat selection by animal populations across entire landscapes. For instance, increases in the population density of *Columba livia* depend on its selection of habitats where human population density is high (Senar et al. 2009, Hetmanski et al. 2011), whereas there is no information on this subject for *Patagioenas maculosa*. In addition, both species take advantage of food directly or indirectly provided by humans (Sol et al. 1998, Buijs and Van Wijnen 2001, Villegas and Garitano-Zavala 2010, Leveau and Leveau 2016), selecting habitats where food availability is abundant (Senar et al. 2017, Stock and Haag-Wackernagel 2016). Moreover, *Columba livia* selects habitats with tall buildings that provide roosting and nesting sites and a better aerial view of possible food resources. They also offer a safe refuge from predators and vehicular collisions (Menon and Mohanraj 2016). In turn, *Patagioenas maculosa* selects habitats with green areas, such as parks with abundant trees (Leveau and Leveau 2016), since it spends a considerable amount of time perching, resting, preening, and singing in them (Fernández-Juricic et al. 2004). It also selects tall trees that provide nesting sites and availability of shelter sites (Fernández-Juricic et al. 2004).

Bendjoudi et al. (2015) provide the only study that evaluated population density of two species of Columbidae (*Columba palumbus* and *Streptopelia decaocto*), and how habitat modifications and urbanization are an advantage for these populations to invade and expand in a city. Most of the literature addresses population density of *Columba livia* and variables likely to explain this parameter (Sacchi et al. 2002, Menon and Mohanraj 2016, Rose et al. 2006, Bendjoudi et al. 2015), but leave aside nesting-site availability in the habitat. Availability of an optimal habitat for nesting can be an important factor influencing the response of the population to be controlled

(Fernández-Juricic et al. 2004). Therefore, our study focused on recording the nesting sites of two species of pigeons, *Columba livia* and *Patagioenas maculosa*, and the factors that influenced their selection in a city. We hypothesized that nesting-site selection by birds is affected by human factors that could have an impact on the availability of places to nest, and therefore, on reproductive success. Within this framework, the objectives of this study were to assess the abundance and the spatial distribution of the nests of these species, and evaluate the effects of human factors on the probability of nesting-site selection in different urban zones within a desert city.

METHODS

The study was conducted in San Juan, a city located in central Argentina. The urban conglomerate is located in the central-north part of Tulum Valley (31°S, 68°W). San Juan has a population of 681055 inhabitants which, according to censuses carried out in 2001 and 2010, is mainly urban (593383 inhabitants), as the city concentrates 73% of the provincial population in a space that represents 2% of the total provincial surface area. The city is distinguished by having old and modern buildings, both presenting ornamental mouldings that provide favourable nesting sites, attracting a large number of birds. The city is situated in the ecoregion Monte of Plains and Plateaus (Brown et al. 2006). The area exhibits high aridity and high thermal oscillation, with an average annual temperature of 17°C (Labraga and Villalba 2009) and an annual precipitation below 100 mm, concentrated in the warm months (spring and summer).

Nests were surveyed along 16 line transects (Silvy 2012) approximately 2.4 km long and 20 m wide (38.65 km long in total). The width of the line transects allowed sampling both sides of the road, including public groves of trees, houses and buildings. The exact location of each nest along each transect was determined with a GPS device. These transects were visited from winter 2012 to spring 2013. We stratified the sampling by three urban zones based on type of building, presence of green areas and vehicular and pedestrian traffic: zone 1 is an area surrounded by commercial and administrative buildings in the center of the city with high traffic, zone 2 includes

neighbourhoods with almost all apartments and houses with yards, public green areas and medium traffic, and zone 3 is composed of residential and private neighbourhoods, houses with yards, public green areas and vacant lots, with low traffic (Fig. 1).

In order to evaluate nest spatial distribution for each species for the spring and winter seasons, we used the nesting sites recorded in each season, and random points where nests were absent (potentially available nesting sites), generated at random with the QGIS software (QGIS Development Team 2016) on the same transects where nests were sampled. These points were separated at least 100 m from nesting sites. Sixty six potentially available sites were sampled in zone 1, 150 in zone 2, and 156 in zone 3. We compared used nesting sites (active and inactive) versus potentially available nesting sites in order to assess the probability of nesting-site selection (Thomas and Taylor 1990).

Eleven explanatory variables were considered for modelling the probability of nesting-site selection; these variables were divided into three categories: urban, building and green variables. Urban variables were: (1) human population density, the number of

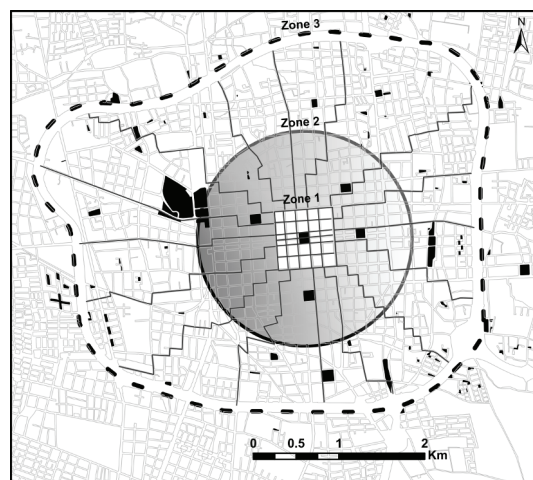


Figure 1. Map of the study area in San Juan city, Argentina, showing transect routes (continuous dark grey lines), green areas (in black), and city blocks (light grey lines). Three urban zones were considered: zone 1 (grey area from center of main square to continuous line), zone 2 (grey area), and zone 3 (area from grey area to thick broken line).

humans per ha for each of the sites (CEFOCA 2010), which is assumed to positively influence the abundance of pigeons (Hetmanski et al. 2011), and we also assume to positively influence on nest abundance; (2) distance to food sources, the minimum distance (m) between restaurants or coffee shops and nesting sites; (3) distance to water, the minimum distance (m) between water fountains and nesting sites; and (4) distance to the main square, the minimum distance (m) between the main square of San Juan city and nesting sites. Building variables were: (5) height of buildings (m); (6) number of strata in buildings (flat areas where pigeons can build their nests; e.g., air conditioners, mouldings, cornices, balconies); and (7) type of buildings, a categorical variable including vertical buildings (buildings with more than two stories) and horizontal buildings (with two or less than two stories). Finally, green variables were: (8) distance to green areas, the minimum distance (m) between green areas of at least 1 ha, such as parks and squares, which is assumed to have a positive influence on the presence of pigeons (Leveau and Leveau 2016); (9) tree height (m); (10) diameter of tree canopy, the mean diameter taken along both, east-west and south-north axes; and (11) tree species, a categorical variable including *Morus* spp., *Melia azedarach*, *Platanus × hispanica* and other species (all tree species with less than 15 individuals recorded). All distances were measured with the QGIS software (QGIS Development Team 2016) whereas all heights were estimated through a basic trigonometric formula using measurements of the horizontal distance to eye and the distance from eye to top, measured with a laser distance meter.

To determine whether there was a difference in abundance of *Columba livia* and *Patagioenas maculosa* nesting sites among zones and the interaction between species and zone, we fitted Generalized Linear Mixed Models with Poisson error distribution. We used `glmer` function from *lme4* package. Nest abundance was analyzed with a Negative Binomial error distribution with a log-link function, which is a combination usually recommended to model count data with overdispersion, using `glmm.a` function from *glmm ADMB* package and *R2admb* package. In order to account for variation inherent to transect length in each stratum sampled, we included length as a

random factor. We assessed the significance of each fixed effect using the Wald test (Sokal and Rohlf 1995, Murtaugh 2014).

We evaluated nest spatial distribution using the R nearest neighbour index for the winter and spring periods (Clark and Evans 1954). The R index is calculated as the ratio between the observed and the expected mean distance, under the assumption of a random process, and ranges from 1 (random distribution) to 0 (maximum aggregation conditions). Distances between nests were measured using the QGIS software (QGIS Development Team 2016). Nest spatial patterns were assessed using SaTScan statistics (Kulldorff 2009) and the Bernoulli purely spatial model (Kulldorff and Nagarwalla 1995, Kulldorff 1997) for the winter and spring periods. In the Bernoulli model, the cases are represented by a binary variable symbolized by 0 (potentially available sites) or 1 (nesting sites). The standard purely spatial model draws circular windows on the study area centered on each data point. SaTScan estimates the likelihood ratio between the total number of cases and controls within the window and the combined total number of cases and controls in the data set. The likelihood function is maximized over all locations and sizes of the window, and the one with the maximum likelihood is the most likely cluster (Turnbull et al. 1990). The distribution and statistical significance of clusters were explored using a Monte Carlo procedure, with 999 simulations. The null hypothesis was rejected for probability values of 0.05 (Dwass 1957).

We used Generalized Linear Models to assess the probability of nesting-site selection. We ran two types of models: (1) general models with urban variables, using the same explanatory variables for the two species and some interactions of interest between variables (distance to food sources with distance to water for *Columba livia*, and human population density with distance to food sources for *Patagioenas maculosa*); and (2) species-specific models for each species, with different explanatory variables for *Columba livia* (building variables) and *Patagioenas maculosa* (green variables). For these models we used a logistic regression equation, with 1 for nesting sites, and 0 for potentially available nesting sites. We used the information-theoretic approach as a model selection procedure (Burnham and

Table 1. Spatial patterns of nests of *Columba livia* and *Patagioenas maculosa* in spring and winter in San Juan city, Argentina. Values of the mean (\pm SE) observed distance, the mean expected distance under the assumption of a random process, and of the R index (and its significance) are shown.

	Observed (m)	Expected (m)	R	P ^a	n
<i>Columba livia</i>					
Spring	265.53 (\pm 2.00)	277.55	0.85	*	48
Winter	257.47 (\pm 2.60)	286.64	0.80	**	45
<i>Patagioenas maculosa</i>					
Spring	96.85 (\pm 10.70)	180.34	0.50	***	125
Winter	103.19 (\pm 9.50)	161.81	0.61	***	167

^a ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$.

Anderson 2002, Garamszegi 2011), based on the second-order Akaike Information Criterion corrected for small size samples (*AICc*) (Burnham and Anderson 2002). We evaluated the Akaike weight (w_i) of each model and the relative importance of the explanatory variables (Burnham and Anderson 2002). We previously performed a correlation analysis to identify multicollinearity in order to remove correlated variables (Kutner et al. 2005). However, we included all variables in the analysis because all coefficient values were lower than 0.8. Models were tested using R (R Core Team 2016). We also used *MuMIn* to select the best models (Barton 2016). We assessed the significance of the interaction effect using the Wald test (Sokal and Rohlf 1995).

For *Patagioenas maculosa*, we calculated Manly’s index to obtain a tree species selection function, which estimates the probability that a randomly selected used resource unit would be in category *i* if all categories were equally frequent in the original population of available resource units (Manly et al. 2002). An index value of $1/k$ (k = number of tree species) indicates no selection, a value $>1/k$ indicates selection, and a value $<1/k$ indicates avoidance. To test the reliability of the index, we estimated 95% confidence intervals by bootstrapping, taking a random sample with replacement (200 times) of used and available locations in all tree species. The selection index was considered statistically significant when the confidence interval did not contain the $1/k$ value.

RESULTS

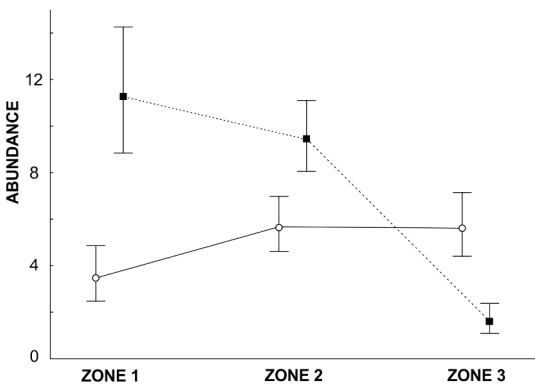


Figure 2. Mean (\pm SE) abundance of nests of *Columba livia* (filled squares) and *Patagioenas maculosa* (open circles) across three urban zones in San Juan city, Argentina.

The sampled environment includes an area of 18.77 km², and in this area we recorded a total of 385 nests. The mean (\pm SE) abundance of *Columba livia* nests was 7.29 ± 1.87 and for *Patagioenas maculosa* it was 5.13 ± 0.73 . The interaction between species and urban zone was significant ($\chi^2 = 6.6$, $df = 1$, $P = 0.01$, Wald test). Zone 1 had a higher abundance of nests of *Columba livia* than of *Patagioenas maculosa*, while in zone 3 nests of *Patagioenas maculosa* were more abundant than those of *Columba livia* ($Z = 2.53$, $P < 0.01$; Fig. 2).

Nest spatial distribution showed a significant aggregation (*R* values significantly lower than 1) in both species (Table 1). The Bernoulli purely spatial model for *Columba livia* nesting sites showed a similar clustering within the

Table 2. Best models explaining the probability of nesting-site selection with urban variables by *Columba livia* and *Patagioenas maculosa* in San Juan city, Argentina. MainSq: distance to the main square, FoodSour: distance to food sources, Water: distance to water, HumDens: human population density.

	K	ΔAIC_c	w_i
<i>Columba livia</i>			
MainSq + FoodSour + Water + FoodSour*Water	5	0.00	0.58
HumDens + FoodSour + Water + MainSq + FoodSour*Water	6	1.32	0.30
Null	1	157.80	0.00
<i>Patagioenas maculosa</i>			
HumDens + FoodSour + Water + HumDens*FoodSour	5	0.00	0.47
HumDens + FoodSour + Water	4	1.77	0.19
Null	1	47.44	0.00

urban zone 1 and part of the zone 2 in spring and winter (Fig. 3a). Nests of *Patagioenas maculosa* also showed similar clusters for spring and winter, including all three zones, although with a higher proportion in zones 2 and 3, including the largest park of the city (Fig. 3b).

With respect to the probability of nesting-site selection, we first ran the general models using urban variables (Table 2). In order of importance, the explanatory variables that were selected in the best model for *Columba livia* were distance to food sources, distance to the main square, distance to water and the

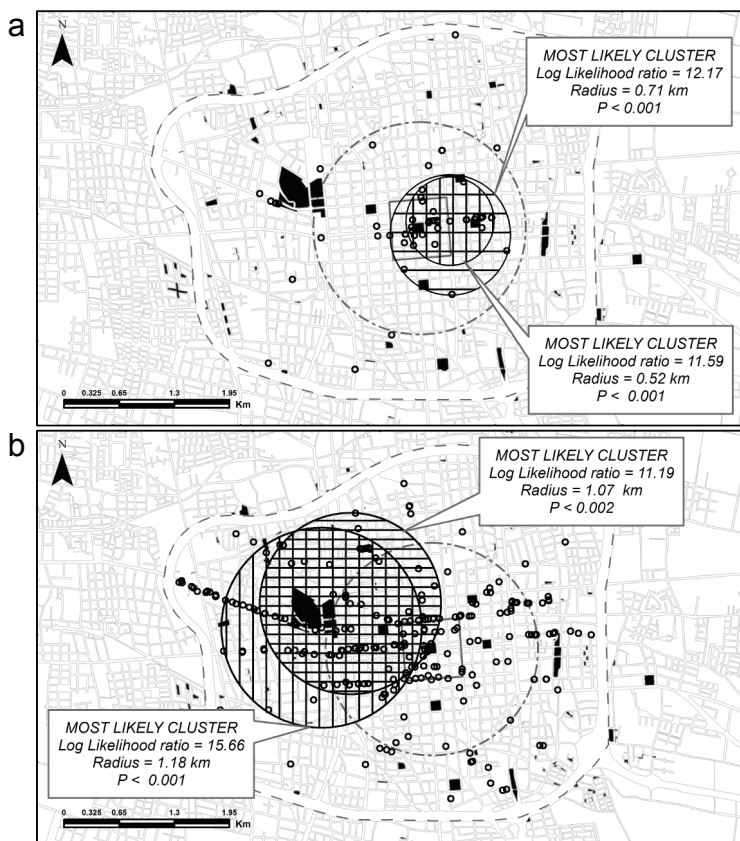


Figure 3. Spatial distribution of nests (open circles) of *Columba livia* (a) and *Patagioenas maculosa* (b) in San Juan city, Argentina, with the most likely clusters of nests in spring (large circles with vertical lines) and winter (large circles with horizontal lines). Urban zones, city blocks and green areas are shown as in figure 1.

Table 3. Mean (\pm SE) estimate values, 95% confidence intervals and its relative importance for urban variables explaining the probability of nesting site-selection by *Columba livia* and *Patagioenas maculosa* in San Juan city, Argentina. Explanatory variables are described in table 2.

	Estimate	Lower 95% CI	Upper 95% CI	Importance
<i>Columba livia</i>				
FoodSour	-0.0112 \pm 0.0041	-0.0192	-0.0032	0.97
MainSq	-0.00132 \pm 0.00048	-0.00227	-0.00037	0.97
Water	-0.00232 \pm 0.00143	-0.00512	0.00048	0.94
FoodSour*Water	0.0000115 \pm 0.0000034	0.0000047	0.0000182	0.91
HumDens	-0.0188 \pm 0.0193	-0.0567	0.0191	0.36
<i>Patagioenas maculosa</i>				
HumDens	-0.0287 \pm 0.0100	-0.0482	-0.0092	0.99
Water	-0.000935 \pm 0.000305	-0.001532	-0.000337	0.98
FoodSour	-0.00316 \pm 0.00172	-0.00654	0.00021	0.96
HumDens*FoodSour	0.0000566 \pm 0.0000287	0.0000004	0.0001128	0.67
MainSq	0.000075 \pm 0.000158	-0.000235	0.000384	0.29

interaction between distance to food sources and distance to water (Table 3, Fig. 4). For *Patagioenas maculosa*, the best model included, in order of importance, the explanatory vari-

ables human population density, distance to water, distance to food sources and the interaction between human population density and distance to food sources (Table 3, Fig. 5).

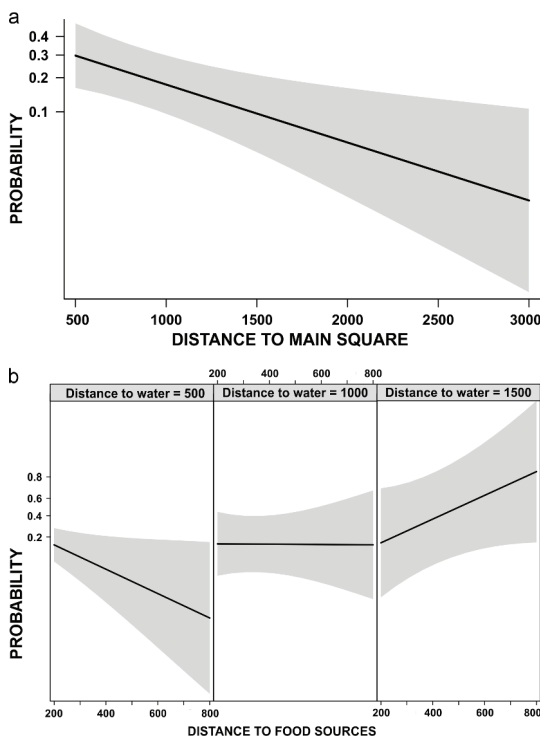


Figure 4. Effect plots showing the probability of nesting-site selection by *Columba livia* in San Juan city, Argentina, regarding the distance to the main square (a) and the interaction between distance to food sources and distance to water (b). Shaded areas represent the 95% confidence intervals.

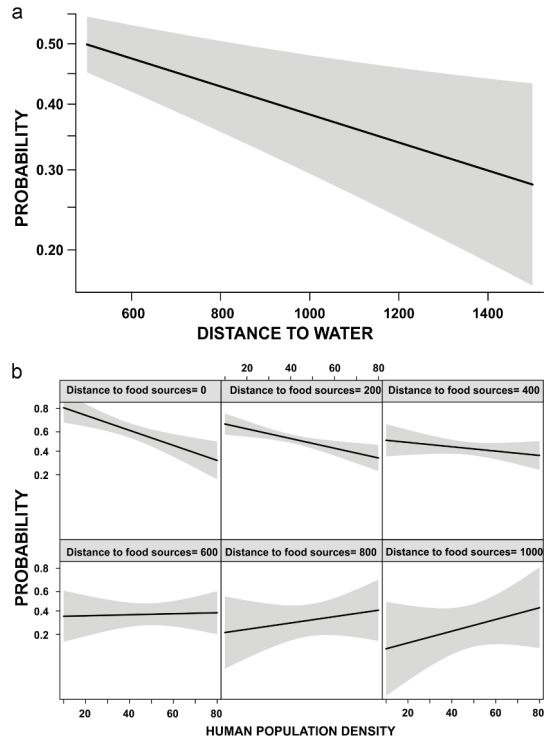


Figure 5. Effect plots showing the probability of nesting-site selection by *Patagioenas maculosa* in San Juan city, Argentina, regarding the distance to water (a) and the interaction between distance to food sources and human population density (b). Shaded areas represent the 95% confidence intervals.

Table 4. Best models explaining the probability of nesting-site selection with species-specific variables by *Columba livia* and *Patagioenas maculosa* in San Juan city, Argentina. HeightBuild: height of buildings, Buildtype: type of buildings, Nstrata: number of strata in buildings, Treeheight: tree height, Canopy: diameter of tree canopy, Treesp: tree species, Distgreen: distance to green areas.

	K	ΔAIC_c	w_i
<i>Columba livia</i>			
HeightBuild + Buildtype	3	0.00	0.44
HeightBuild + Nstrata + Buildtype	4	0.57	0.33
Nstrata + Buildtype	3	2.49	0.13
HeightBuild + Nstrata	3	4.35	0.05
<i>Patagioenas maculosa</i>			
Treeheight + Canopy + Treesp	6	0.00	0.72
Treeheight + Canopy + Distgreen + Treesp	7	1.99	0.27
Canopy + Treesp	5	9.90	0.01
Canopy + Distgreen + Treesp	6	11.94	0.00

When we performed the species-specific models for each species, the best models for *Columba livia* included type of buildings, height of buildings and number of strata in buildings (Table 4). The probability of nesting-site selection increased with height of buildings, and was higher in vertical than in horizontal buildings (Table 5). For *Patagioenas maculosa*, the best model included diameter of tree canopy, tree species and tree height (Table 4). The probability of nesting-site selection increased with tree height and diameter of tree canopy (Table 5). Tree species also affected the probability of selection, with *Platanus × hispanica* and *Morus* spp. being the species which were positively associated with nesting (Table 5).

Values of the Manly's index indicated that *Patagioenas maculosa* selected *Platanus × hispanica* and *Morus* spp. and avoided *Melia azedarach*. Furthermore, *Platanus × hispanica* was selected three more times than *Morus* spp. (Fig. 6).

DISCUSSION

Our results revealed that *Columba livia* and *Patagioenas maculosa* use different nesting sites. *Columba livia* have high nest abundances around the main square of the city center. Our results coincide with the results found in other cities of the world (Sacchi et al. 2002, Przybylska et al. 2012). *Patagioenas maculosa* showed the opposite, being more abundant in zone 3. These results are similar to those found in Mar del Plata city by Leveau and Leveau (2012). These species select different nesting sites, probably because they have different habitat requirements. In addition, we found an aggregated spatial distribution of nests in both species. *Columba livia* was found mainly in zone 1 (city center) and in parts of zone 2, whereas *Patagioenas maculosa* was found in all zones, with a higher proportion in zones 2 and 3, including the largest green area. As in other studies, *Columba livia* is related to environments of the city center (Blair 1996, Sandström et al. 2006), whereas *Patagioenas maculosa* occurs outside it (Leveau and Leveau 2004). However, this is the first spatial analysis of cluster detection which compares the likelihood of selection by *Columba livia* and *Patagioenas maculosa*.



Figure 6. Values of the Manly's index (with 95% confidence intervals) showing tree species selection by *Patagioenas maculosa* in San Juan city, Argentina. Dashed line indicates the $1/k$ value.

Table 5. Mean (\pm SE) estimate values, 95% confidence intervals and its relative importance for species-specific variables explaining the probability of nesting site-selection by *Columba livia* and *Patagioenas maculosa* in San Juan city, Argentina. Explanatory variables are described in table 4.

	Estimate	Lower 95% CI	Upper 95% CI	Importance
<i>Columba livia</i>				
Intercept	-3.12 \pm 0.59	-4.29	-1.96	
Buildtype ^a				0.93
vertical buildings	1.89 \pm 0.73	0.44	3.34	
HeightBuild	0.12 \pm 0.06	0.01	0.25	0.85
Nstrata	0.28 \pm 0.19	-0.10	0.66	0.51
<i>Patagioenas maculosa</i>				
Intercept	-4.60 \pm 0.69	-5.96	-3.24	
Canopy	0.24 \pm 0.06	0.12	0.37	1.00
Treesp ^b				1.00
<i>Morus</i> spp.	1.34 \pm 0.56	0.23	2.44	
<i>Platanus</i> \times <i>hispanica</i>	1.98 \pm 0.59	0.82	3.14	
other species	0.96 \pm 0.66	-0.34	2.27	
Treeheight	0.20 \pm 0.06	0.08	0.33	0.99

^a Relative variable to value of horizontal buildings.

^b Relative variable to value of *Melia azedarach*.

The most important urban variables influencing the probability of nesting-site selection by *Columba livia* were distance to the main square, distance to food sources and the interaction between distance to food sources and distance to water, which were included in the best models. This indicates that feeding sites play an important role in determining nest distribution (Haag-Wackernagel 1995, Ryan 2011). The interaction between distance to food sources and distance to water suggests that the range of activity of this species is less than 500 m during the breeding season, at least in desert cities, where water is a limiting resource. Although *Columba livia* has enough flexible individual foraging strategies (Rose et al. 2006), in our study its nesting sites were always near food and water sources. These resources probably explain *Columba livia* nesting sites because the high energy demand of nestlings cannot be met under conditions of food scarcity (Stock and Haag-Wackernagel 2016). In addition, the height of buildings positively affected the probability of nesting-site selection. This agrees with previous studies, which showed a positive relationship between density and tall buildings in this species (Sacchi et al. 2002, MacGregor-Fors and Schondube 2011). Also, we found that the probability of nesting-site selection was higher in vertical than in horizontal buildings,

suggesting a preference for constructions of two stories or higher. These results are similar to those reported by Przybylska et al. (2012), who showed that the most important variable influencing this species' density was the cover of tall buildings. Sacchi et al. (2002) showed that this species selected areas with old buildings, because new ones had less availability of holes and openings for nesting. Nevertheless, in San Juan city there are not old buildings because the city was destroyed during the earthquake of 1944, but air conditioners probably serve in a similar way.

Urban variables influencing the probability of nesting-site selection by *Patagioenas maculosa* were distance to water, human population density, distance to food sources and the interaction between human population density and distance to food sources. The most important variable was human population density, which negatively affected the probability of nesting-site selection. However, this is a new urban species found in several cities of South America (Leveau and Leveau 2005, Villegas and Garitano-Zavala 2010) and the success of an invasive bird species to colonize urban habitats is associated with its gradual adaptation to these environments, which results in an increase in its population density over time. This species, within the city, prefers nesting in sites with many trees, as are

zone 2 and zone 3. Therefore, this species behaves like many other native bird species in urban areas, which are affected by human presence and human population density (Ortega-Álvarez and MacGregor-Fors 2009, Buijs and Van Wijnen 2001). In fact, pedestrians have been identified as a factor that disrupts the foraging of some birds, and often forces them to move away, which decreases their chances of using sites packed with forage (Fernández-Juricic et al. 2001). Another important variable was distance to water, the probability of nesting-site selection increasing as distance to water sources decreases. This may be because *Patagioenas maculosa* is granivorous (Blendinger and Ojeda 2001) and, as seeds contain very little moisture, these birds are surface water dependent (Fisher et al. 1972). The interaction between human population density and distance to food sources was another variable related to the probability of nesting-site selection. The likelihood of this species finding nests increases as distance to food decreases. Probably, in winter, when seeds are scarce, they could use other available foods such as bread crumbs and food scraps discarded by restaurants and coffee shops, like other species that choose nesting sites near food sources. With respect to species-specific variables, tree height and diameter of tree canopy positively affected the probability of nesting-site selection. As highlighted by other studies, tree cover is a key element to maintain bird species within urban areas (Villegas and Garitano-Zavala 2010, MacGregor-Fors and Schondube 2011, Leveau 2013). In fact, trees are one of the most important vegetation components for birds inhabiting urban areas for roosting, hiding and foraging (Paker et al. 2014, Rousseau et al. 2015). Also, selecting these nesting sites can provide benefits for reproduction because they hide nests, and dense canopies protect eggs and chicks against predators. In addition, *Patagioenas maculosa* had preference for certain types of trees to make its nests, selecting *Platanus × hispanica*, followed by *Morus* spp., probably because this species feeds on fruits and sprouts of these trees, and avoided *Melia azedarach* trees.

In summary, the most important urban variables affecting nesting in *Columba livia* were related to building characteristics and to food and water availability, whereas nesting of

Patagioenas maculosa was related to water and food availability, human density and the presence of some large tree species. We consider that nesting sites could be a limiting factor for these species. Although *Columba livia* has a notable nesting site choice plasticity, since it breeds in cavities, bridges, on balconies, windowsills and many other places, in our study it always selected tall buildings. Similarly, *Patagioenas maculosa* always selected tall trees with dense canopies as nesting sites. Both species select nesting sites near food sources and water. These results have important implications for choosing appropriate control strategies for the management of urban pigeons in desert environments.

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