FACTORS SHAPING OCCURRENCE PROBABILITY OF A GENERALIST RAPTOR SPECIES ACROSS AN URBAN-RURAL GRADIENT

FACTORES QUE AFECTAN A LA PROBABILIDAD DE PRESENCIA DE UNA RAPAZ GENERALISTA A LO LARGO DE UN GRADIENTE URBANO-RURAL

Nerea PAGALDAi¹^{*}, Javier Rodríguez-Pérez^{1, 2}, Arkaitz Arnaiz¹ and Juan Arizaga¹

SUMMARY.-Urbanization constitutes one of the most intensive and fast spreading factors explaining biodiversity loss worldwide. The extension of urban areas and landscape configurations affects the ability of raptors to exploit urban patches. The Tawny Owl Strix aluco is a forest-dwelling nocturnal species with a wide distribution range that is well-adapted to urban environments. However, it remains unknown which habitat factors explain its presence in urban-associated landscapes. Our main objective is to determine the effect of urban landscapes on the probability of occurrence of Tawny Owls along an urban-rural gradient. It is expected that Tawny Owls will be able to use urban patches that have (1) at least 30% tree cover thanks to gardens/parks for hunting but (2) they will not use those with high noise levels (i.e., highways). Our research was carried out in the municipality of Donostia-San Sebastian in the Basque Country, Northern Spain. Data were obtained from a survey conducted in 2017. The municipality was divided into 329 square cells, of which 251 were surveyed. Tawny Owls were detected in 141 cells, and we found that nocturnal noise level and scrub cover contributed most to explaining the probability of Tawny Owl occurrence; with nocturnal noise having a significant negative effect on occurrence probability, and scrub cover a positive effect, probably because the species uses open or semi-open areas to hunt (but woodland to breed). Overall, it can be concluded that the very noisy and/or urbanized parts of the city comprised a non-optimal habitat for the species. - Pagaldai, N., Rodríguez-Pérez, J., Arnaiz, A. & Arizaga, J. (2023). Factors shaping occurrence probability of a generalist raptor species across an urban-rural gradient. Ardeola, 70: 75-88.

Key words: agglomeration noise, city ecology, GAM, presence-absence, San Sebastian, *Strix aluco*, Tawny Owl, urban environments.

* Corresponding author: npagaldai@aranzadi.eus

Twitter: @npagaldai

Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, 20014 Donostia-San Sebastian, Spain.

² Institute for Multidisciplinary Research in Applied Biology (IMAB), Depto. Ciencias del Medio Natural, Centro Jerónimo de Ayanz, Universidad Pública de Navarra (UPNA), Campus Arrosadía, 31006 Pamplona, Spain.

RESUMEN.-La urbanización es una de las causas más intensivas y rápidas que explican la pérdida de biodiversidad a nivel mundial. La extensión de las áreas urbanas y la configuración del paisaje afectan la habilidad de las rapaces para explotar parches urbanos. El cárabo euroasiático Strix aluco es una especie forestal nocturna con una amplia distribución y bien adaptada a los ambientes urbanos. Sin embargo, siguen siendo desconocidos qué factores relacionados con el hábitat explican su presencia en ambientes urbanizados. Nuestro objetivo general es el de determinar el efecto que tienen los paisajes urbanos en la probabilidad de presencia del cárabo euroasiático a lo largo de un gradiente urbano-rural. Se espera que el cárabo sea capaz de usar los parches urbanos que tengan (1) un mínimo número de jardines/parques con árboles para cazar; y (2) un limitado nivel de ruido durante la noche (ej. autopistas). Nuestro estudio se llevó a cabo en Donostia-San Sebastián, en el País Vasco, norte de España. Los datos se obtuvieron mediante un censo realizado en 2017. El municipio se dividió en 329 cuadrículas y 251 de ellas fueron censadas. Se detectaron cárabos en 141 cuadrículas, y obtuvimos que el ruido nocturno y la cubierta de matorral fueron las variables que más contribuyeron a explicar la probabilidad de presencia; el ruido nocturno tuvo un significativo efecto negativo en la probabilidad de presencia, mientras que la cubierta de matorral tuvo un efecto positivo, probablemente porque la especie utiliza áreas abiertas o semiabiertas para cazar (pero bosques para criar). En general, se puede concluir que las zonas más ruidosas y urbanizadas de la ciudad componen un hábitat no óptimo para la especie. - Pagaldai, N., Rodríguez-Pérez, J., Arnaiz, A. y Arizaga, J. (2023). Factores que afectan a la probabilidad de presencia de una rapaz generalista a lo largo de un gradiente urbano-rural. Ardeola, 70: 75-88.

Palabras clave: cárabo, ecología de ciudades, entornos urbanos, GAM, presencia-ausencia, ruido de aglomeración, San Sebastián, *Strix aluco*.

INTRODUCTION

Urbanization, a process which involves the development of modern urban infrastructures (Gu, 2020), constitutes one of the most intensive and rapidly increasing threats to biodiversity worldwide (Aronson et al., 2014). Urbanization decreases species homogenization and richness as a consequence of landscape modification for human-based purposes, although at the same time it provides new opportunities or resources for some species, leading to increases in population sizes (Melles et al., 2003). The response of a species to urbanization is related to its life history and habitat requirements (Evans et al., 2011). For instance, the urban habitat is typically occupied or used by generalist, plastic species that occur over a broad range of habitats, hence they naturally have biological and evolutionary adaptations that allow them to exploit novel environments (Li et al., 2021). In the particular case of predators, generalist species, in terms of both habitat use and diet, are likely to use urban areas because they provide novel opportunities and benefits for their breeding performance (Kettel *et al.*, 2018; Callaghan *et al.*, 2019; Palacio, 2020). It is therefore important to understand whether environmental factors associated with the urban habitat are decisive for maintaining long-term populations of generalist species. This is crucial, because (1) urbanization continues to increase worldwide and (2) promoting biodiversity in cities is important to increase resilience against climate change, as well as having socio-economic benefits.

In urban areas the occurrence of a raptor species is usually related to its population density in the surrounding non-urban areas (Leveau *et al.*, 2022). Most urban raptors are species typical of woodland habitats and occupy small forested areas and/or forage in open habitats (Boal, 2018). The ability of a raptors to exploit an urban patch is affected by the number of other urban areas around it, such as towns and cities, and the landscape configuration itself (Pagaldai *et al.*, 2021). The quantity and size of green zones, number of trees and the presence of pets (cats and dogs) is known to have a direct impact on bird richness in cities (i.e., Gonçalves *et al.*, 2021). For instance, the Cooper's Hawk *Accipiter cooperii* occupies urban territories which include large native trees and areas with native vegetation, where prey is apparently more common than in places with nonnative vegetation (Boggie & Mannan, 2014).

Raptors play a role as biodiversity sentinels (Natsukawa, 2021), their presence commonly being linked with higher levels of biodiversity and more structured ecosystems. For instance, Goshawk Accipiter gentilis breeding sites could usefully be employed as a conservation surrogate to identify and preserve habitat hotspots for wintering birds in urban ecosystems (Natsukawa, 2021). In the particular case of nocturnal raptors, hunting success depends on both hearing and vision, meaning that the amount of urban development could hamper their capacity to successfully hunt resources in highly urbanized areas (Fröhlich & Ciach, 2019). The Tawny Owl Strix aluco is a forest-dwelling nocturnal species with a wide distribution range that is well adapted to urban environments (Mikkola, 1983; Pagaldai et al., 2021). It has been demonstrated by Sergio et al. (2005) that the presence of Tawny Owls is correlated with bird species richness, while Gonçalves et al. (2021) observed that gardens with bushes in urban landscapes are those with the richest and most abundant bird communities. However, it remains to be elucidated which habitat factors explain Tawny Owl presence under urban-associated landscapes.

Our main objective here is to determine the effect of urban landscapes on the probability of occurrence of Tawny Owls along an urban-rural gradient. For this purpose, we used data collected in the city of DonostiaSan Sebastian (Northern Iberian Peninsula), which hosts a relatively abundant and welldistributed Tawny Owl population (Arizaga *et al.*, 2021). Hypothetically, Tawny Owls will be able to use urban patches with at least a 30% of their area covered by gardens/ parks with trees for hunting; but will not use areas with high nocturnal noise levels (i.e., highways) as hunting areas. It is expected that habitats with well-structured vegetation and forest with a natural structure i.e., it includes scrub, will have a positive effect on the Tawny Owl occurrence.

MATERIALS AND METHODS

Study area

Our research was carried out in the city of Donostia-San Sebastian (43.31283 latitude, -1.97499 longitude; 60km^2 ; Figure 1), in the Basque Country, Northern Spain. It is a coastal city located in the Eurosiberian region (sub province Cantabro-Atlantic) on the southeastern part of the Bay of Biscay. Apart from a number of industrial estates and highly-transited public spaces (and their nodes), the city is surrounded by Atlantic countryside, comprised by a mosaic of patches of grasslands, native deciduous forest and tree plantations (mostly Monterey Pine Pinus radiata). Overall, the municipality has recently been reported to host 90 breeding bird species, including a Tawny Owl population that is well- and widely distributed across the area (Arizaga et al., 2021).

Bird survey

Vocal activity of Tawny Owls reaches its peak during the incubation period, which lasts from February to April. A survey was conducted during this period –February and the first 15 days of March– in 2017 to obtain the data for this study. Data collection was carried out during the night when vocal activity is at its highest, hence allowing us to maximize detectability (Zuberogoitia *et al.*, 2018).

The municipality was divided into 329 square cells of 500×500m and we surveyed 251 of them (76% of the total available, Figure 1). To estimate detectability, 14 of the 240 surveyed cells were surveyed twice and another 10 cells were surveyed 4 times.

However, data obtained from these 'extra' surveys was not included in the models due to the way the field work was carried out. The survey was carried out during the first hours after dusk (normally, from dusk to +6 h). Most of the cells that were not sampled were excluded due to their inaccessibility (i.e., private land, steep slopes, etc.). The territory of a Tawny Owl pair is in fact bigger than the scale of our survey unit (31.11ha in urban areas) (Burgos & Zuberogoitia, 2018),



Pagaldai, N. et al.; Ocurrence probability of an urban raptor

FIG. 1.—The study area, and its borders, is shown in the map. The dark grey area shows the buildings, making it possible to identify the urban area. The grid used for the survey is also shown, the light grey cells represent those surveyed, while the uncoloured ones are the ones that could not be surveyed. The black dots are the locations where the Tawny Owls responded to the recorded calls.

[En el mapa está representado el área de estudio con sus fronteras. El área de color gris oscuro representa los edificios, haciendo posible identificar el área urbana. La cuadrícula usada durante el censo también está representada. Las celdas de color gris claro representan las celdas censadas, mientras que las transparentes son las que no se pudieron censar. Los puntos negros son las localizaciones donde los cárabos respondieron al reclamo.] so the survey data obtained here was only useful for studying its presence-absence, not to calculate abundance.

In each cell, a location as close as possible to the centroid was selected as the survey point. For the Tawny Owl, better results have been obtained using broadcasting methods rather than simply registering spontaneous calls (Worthington-Hill & Conway, 2017). Consequently, each survey used a threeperiod survey protocol: 5-min of recorded calls, 5-min waiting for spontaneous calls and 5-min of recorded calls. The recordings, which included a mix of territorial and mating calls of both sexes (in a track lasting 5 min), were constructed based on our own experience (i.e., Zuberogoitia et al., 1998). The calls used were downloaded from xenocanto (https:/xeno-canto.org/). The volume of the recording was loud enough to be heard by an observer at a distance of ca. 300m, but not so high as to create distortion at closer distances. The minimum number of individual owls detected in each cell was notated and considered as an object variable for the statistical models.

Environmental variables

We considered a total of nine environmental variables (Table 1) extracted at the scale of our bird survey (i.e., 500×500 m): (1) the shortest distance (m) from the cell centroid to the nearest river (RIV); (2) the percentage of the area occupied by buildings (BUI); (3) the percentage of the area occupied by forest (FOR); (4) the percentage occupied by crops (CRO); (5) the percentage occupied by scrub species (SCR); (6) the percentage occupied by fields (grasslands) (FIE); (7) the mean night-time crowd noise (NOI); (8) Tawny Owl nest box density (In 2014, we had placed 100 nest boxes for Tawny Owls across much of the municipality) (BOX); (9) the garden largest patch index, defined

as the surface area of the largest patch of garden in the cell (LPI). The RIV variable was measured for each cell using the Basque Government's river shapefile and in R. Percentages of land cover type (building, forest, crop, scrub, field) were obtained by digitalizing main habitats from the Basque Government's 2017 Orthophotos. The nocturnal noise variable was obtained from a shape layer available from the municipality of Donostia-San Sebastian based on measurements taken in 2017 and we calculated the mean MhZ value for each 500 × 500m cell. The nest box density variable was calculated applying the 'heatmap' function in QGIS 3.4 (QGIS, 2022). The garden largest patch index variable was calculated for the garden habitat using the 'landscapemetrics' package in R (Hesselbarth et al., 2019).

Statistical analysis

Initially we had 14 habitat covariates, and we conducted certain correlation analyses using both the 'cor' (R Core Team, 2020) and the 'vif' (Naimi et al., 2014) function. After comparing the results that these analyses provided about correlation, which in fact coincided, we decided to drop 5 covariates (urban percentage, summer ndvi-Normalized Difference Vegetation Index-, winter ndvi, daylight road noise and daylight crowd noise) from the analysis. We then incorporated the remaining 9 covariates, where no correlation was found, into a Generalized Linear Model (GLM), and also into a Generalized Additive Model (GAM), without interactions, using owl presence as a binary response variable (0, absence; 1, presence). We performed the GLMs and GAMs that incorporated the nine environmental variables above as explanatory variables. Next, we ranked the best models using the 'dredge' function, which gave us the best model-which only included noise and scrub as covariates. All models

TABLE 1

All nine variables included in the models with each acronym, unit and description. [Las nueve variables incluidas en los modelos con sus respectivos acrónimos, unidades y descripciones.]

Acronym	Name	Unit	Description
RIV	Nearest river	Meter (m)	The shortest distance from the cell centroid to the nearest river
BUI	Building	%	The percentage of area occupied by buildings
FOR	Forest	%	The percentage of land occupied by forest
CRO	Crop	%	The percentage of land occupied by crops
SCR	Scrub	%	The percentage of land occupied by scrub
FIE	Field	%	The percentage of land occupied by fields (grasslands)
NOI	Nocturnal noise	MhZ	The mean night crowd noise
BOX	Nest box	density	Tawny Owl nest box density (In 2014, we put up 100 nest boxes for Tawny Owls, spread across much of the municipality)
LPI	Largest Patch Index of gardens	m ²	The garden largest patch index, defined as the area of the greatest garden patch

were run with the 'gam' function from the 'mgcv' package in R (Wood, 2011). In the case of the GAM models, the default thin plate splines smoothing parameter was chosen by the Restricted Maximum Likelihood (REML). Two basic functions (k) were used and then the 'gam.check' function (Wood, 2011) was employed to check if the value was appropriate. Due to the nature of the object variable, we used a binomial distribution of errors based on a logit link function. All statistical analyses were run in R software (R Core Team, 2022).

After running saturated GLM and GAM models (i.e., those models that included all the covariates), we compared them and chose if GLM or GAM fitted the data better (Table 2). Model comparisons were based on their

Akaike (AIC; Burnham & Anderson, 2004), R^2 and the Area Under the Curve (AUC) values. Those with higher values of R^2 and AUC were considered to have greater predicting capacity. The overdispersion parameters were also calculated for GLM and for GAM models. Models differing in less than 2 AIC units (Burnham & Anderson, 2004) were considered to fit the data equally well, so model averaging was done. We also calculated the RVI (Relative Variable Importance, Giam & Olden, 2016) values to ascertain which variables contributed most to the model in question. These values were calculated as the sum of Akaike weights. RVI is quantified in terms of the R^2 explained by each variable (Giam & Olden, 2016).

Table 2

Comparison between the saturated GLM and GAM models with respect to AIC (Akaike Information Criterion), R^2 (R-squared), AUC (Area Under the ROC Curve) and overdispersion. The GAM better fitted the data, so a comparison between the saturated, the best and the averaged GAM models is also shown (same criteria as above). In the averaged GAM model it was not possible to calculate the AIC, R^2 and overdispersion.

[Comparación de los modelos GLM y GAM con respecto al AIC (Criterio de Información Akaike), R^2 (R cuadrado), AUC (el Área bajo la curva ROC) y la sobredispersión. El GAM resultó ajustarse mejor a los datos, por lo que también se muestra la comparación entre los GAM saturado, mejor y promediado, siguiendo los mismos criterios previamente mencionados. No fue posible calcular el AIC, R^2 y la sobredispersión del GAM promediado.]

	AIC	GCV	\mathbb{R}^2	AUC	Overdispersion
GLM saturated	201.2813	0.4076	0.0855	0.7052	1.0860
GAM saturated	192.4544	0.2675	0.2358	0.8034	0.9590
GAM saturated	192.4544	0.2675	0.2358	0.8034	0.9590
GAM best	190.276	0.3262	0.0704	0.6972	1.0463
GAM averaged				0.7486	

RESULTS

Tawny Owls were detected in 141 of the 251 cells surveyed (i.e., 56% of the cells were occupied). During the survey, a total of 277 Tawny Owls responded to the recorded calls, more than half of them being males (159) and 83 of them females. The sex of the remaining 35 could not be established on the basis of their calls.

The saturated GAM showed a better fit with the data (Table 2.; GAM AIC: 192.45; GLM AIC: 201.28) and a higher predictive capacity than the saturated GLM (GAM AUC: 0.8034; GLM AUC: 0.7052) and we therefore retained the GAM model. The RVI values of the averaged GAM (AUC = 0.749) showed that the variables nocturnal crowd noise (0.88 RVI) and scrub percentage (0.70 RVI) contributed most to explaining probability of occurrence (Figure 2; Table 3); noc-

turnal crowd noise had a negative effect, whilst scrub showed a positive effect.

Several of the other environmental variables contributed, but to a lesser extent, to explaining the probability of occurrence. Specifically, forest, crop and field percentages had a positive effect on occurrence probability, whilst building percentage had a negative effect whereby 20% building cover resulted in a predicted occurrence of ca. 40% whilst building cover over 35% resulted in occurrence probability falling below 20% (Figure 3). Lastly, garden largest patch index, nearest river distance and nest box density variables showed no effect.

DISCUSSION

In this work we studied the effect of urban landscapes on the probability of occurrence



Pagaldai, N. et al.; Ocurrence probability of an urban raptor

FIG. 2.—The effects shown by the two variables that most explained Tawny Owl occurrence probability. A) Mean night crowd noise (MHz) and B) Scrub mean percentage (%). Dots are the model fitted values of presence probability. The line is the smoothed vector using the gam approach with the formula = $y \sim s$ (x, bs = "cs"). The standard errors are shown in grey.

[Los efectos mostrados por las dos variables que más explican la probabilidad de presencia del cárabo común. A) Media del ruido de aglomeración nocturna (MHz), y B) Porcentaje medio de matorral (%). Los puntos son la probabilidad de presencia de los valores ajustados al modelo. La línea es el vector suavizado utilizando la aproximación gam y la formula = $y \sim s$ (x, bs = "cs"). Los errores estándar están representados en gris.]

of Tawny Owls along an urban-rural gradient. Our study took place during the incubation season of the Tawny Owl meaning that we maximized the detection probability during our surveys. Our results indicate a detectability of 50%, while that estimated by Zuberogoitia et al. (2020) is around 30%, which likely demonstrates the weaknesses of using a single survey per location, as we did here, and indicates that more than one should be carried out in future studies. Even though we obtained a higher detectability value than Zuberogoitia et al. (2020), it is still a quite low value, and half of our negatives could indeed be false negatives. Thus, detectability should be taken into account

Ardeola 70(1), 2023, 75-88

for future studies. Overall, we detected the species in almost 60% of the survey area. This was assessed directly from positive/ negative counts, without considering the detection probability. Occupancy models including detection probability estimates are being increasingly applied to estimate the role of different factors that shape the spatial distribution of birds and other animal taxa with imperfect detection. However, in our particular case, we opted to use a simpler survey in order to cover a wider range of survey points comprising a rural-urban gradient, and therefore our survey design was not able to take into account this statistical approach.

TABLE 3

RVI (Relative Variable Importance) values of each variable included in the averaged GAM model. The highest two RVI values are written in bold. (RIV: shortest distance to the nearest river; BUI: building percentage; FOR: forest percentage; CRO: crop percentage; SCR: scrub percentage; FIE: field –grass-land– percentage; NOI: mean night crowd noise; BOX: nest box density; LPI: garden largest patch index). The p values of the variables included in the best model are in the right-hand column (* indicates a p value < 0.05). Blank cells means that these covariates were not included in the best model. [Valores RVI (Importancia Relativa de las Variables) de cada variable incluida en el modelo GAM promediado. Los dos valores RVI más altos están en negrita. (RIV: distancia más corta al río más cercano; BUI: porcentaje de edificios; FOR: porcentaje de bosque; CRO: porcentaje de cultivos; SCR: porcentaje de matorral; FIE: porcentaje de prados; NOI: media del ruido nocturno de aglomeración; BOX: densida de cajas nido; LPI: índice de parche más grande de jardín). Los valores p incluidos en el mejor modelo se encuentran en la columna de la derecha (* indica valor de p < 0.05). Las covariables con celdas blancas significan que estas covariables no fueron incluidas en el mejor modelo.]

Variables	RVI	Best model P values
RIV	0.35	
BUI	0.47	
FOR	0.43	
CRO	0.31	
SCR	0.70	0.055
FIE	0.25	
NOI	0.88	0.005*
BOX	0.20	
LPI	0.46	

The variables best explaining Tawny Owl occurrence across our survey area were the amount of noise at night (NOI) and amount of scrub cover (SCR), the former having with a negative effect on the response variable and the second, a positive effect. In other words, Tawny Owls tended to be detected in areas that were quieter and had a higher percentage of scrubs. Other habitat-related variables, including percentage of cover of urban zones or forest, had less importance in the models, the latter probably because it is not a limitation in our landscape. Regarding noise, it is necessary to take into account that this variable could also have an effect on detectability, i.e., lowering it. Thus, the species was less likely to be detected in noisy areas, thereby causing false negative counts. However, it is well known that owls tended to avoid noisy zones since these reduce their hunting success (Senzaki *et al.*, 2016; Fröhlich & Ciach, 2018), and as such our models demonstrate that an increase of 5MHz in noise level was linked to a decrease of ca. 25-30% in terms of the probability of occurrence of Tawny Owls (Figure 2). While taking imperfect detectability into account improves estimates, noise has also been



Pagaldai, N. et al.; Ocurrence probability of an urban raptor

FIG. 3.—The effects of the building percentage (%) variable on Tawny Owl occurrence probability. Dots are the fitted model values of presence probability. The line is the smoothed vector using the gam approach with the formula = $y \sim s$ (x, bs = "cs"). The standard errors are shown in grey.

[Los efectos mostrados por la variable de porcentaje de edificios (%) en la probabilidad de aparición del cárabo común. Los puntos son la probabilidad de presencia de los valores ajustados al modelo. La línea es el vector suavizado utilizando la aproximación gam y la formula = $y \sim s$ (x, bs = "cs"). Los errores estándar están representados en gris.]

previously analysed without taking detectability into account (Fröhlich & Ciach, 2018; Fröhlich & Ciach, 2019).

Scrubby areas were found to be especially attractive to the species. Those places with more than 40% of scrub cover showed occurrence probabilities exceeding 75%. Even though Tawny Owls preferred forest habitats, their home ranges often include open habitats where they hunt. Within our study site, scrubby areas comprise transition habitats, such as rural to forest, and these often have scattered tree stands or have a nearby forest patch, and therefore offer an excellent hunting habitat for the species (López-Peinado *et al.*, 2020). Since the sampling was carried out at night, we increased the probability of detecting foraging birds, which would be more likely to be found at these open or semi-open habitats as compared to in densely forested areas, which are of lesser importance as a hunting habitat for the species. The urban area of our study site has a very dense network of pathways and the size of the forest patches is relatively small (quite often <0.2 km²), so there are very few large wooded areas that are inaccessible and where the species may remain undetectable due to access problems.

Although statistically less important, other variables were also observed to have an impact on occurrence probability. Thus, built areas showed a negative impact on the Tawny Owl probability of occurrence, which could be in part a covariation with the noise at night, but other explanations are also possible: dense urban areas lack tree holes for nesting and also have no or very small green areas where sufficient prey can be found.

The size of the garden patches within the city had no apparent effect on occurrence probability. This could mean, on the one hand, that Tawny Owls simply ignore this variable given their higher dependence on other types of green areas, like scrubs and forest. Gardens also tend to be habitats with a considerable amount of human intervention, and are probably also subjected to a relatively high use of pesticides, which might reduce the amount of potential prey such as rodents. On the other hand, it is also true that Donostia-San Sebastian is a very green city with many natural or semi-natural habitat patches, from which the Tawny Owl might benefit, and which could mask the effect that size of garden patches might have in other circumstances.

Nest boxes were found to have no significant effect on occurrence probability. Thus, even though these boxes might help some pairs to settle in given areas which lack natural tree holes, it seems that the species has a sufficient amount of nesting areas irrespective of the use of these artificial nesting structures. In this context, it must be highlighted that our study site is a medium-size city (180,000 inhabitants), with a lot of green areas, both inside the city and across its periurban belt, still rich in Atlantic countryside with mosaics of pastures and small to medium-sized forest patches.

Tawny Owls can colonize new environments (Mak *et al.*, 2021; Gryz & Krauze-Gryz, 2018) depending on the surrounding habitat and urban habitat structure (Fröhlich & Ciach, 2018; Fröhlich & Ciach, 2019). Our study area is surrounded by forested areas

and has a high Tawny Owl density, which makes it more likely for the species to occur in the urban area (Leveau et al., 2022). This could lead the species to colonize the urban territory of Donostia-San Sebastian without problem. Nevertheless, at a local scale, the nocturnal noise in our study site is detrimental to the occurrence of the species, confirming what Fröhlich & Ciach (2018) found previously. Even though gardens can be expected to have an effect on the species occurrence probability, the scrub percentage has a greater effect. In conclusion, the probability of Tawny Owls entering urban areas increases if these areas are not noisy and have plenty of scrubs. So, overall, it can be stated that the very dense and urbanized parts of the city comprised a non-optimal habitat for the species, in accord with Pagaldai et al. (2021). Only by understanding the ecological needs of the species in this novel habitat will we be able to design and promote cities with greater capacity to host more biodiversity.

ACKNOWLEDGEMENTS.—N. Pagaldai was supported by a Basque Government predoctoral fellowship grant (PRE_2018_1_0004). The local government of San Sebastian gave us all the permits necessary to carry out the survey. We also want to thank all the volunteers that helped with the fieldwork. Two anonymous referees provided valuable comments that helped us to improve an earlier version of this work.

AUTHOR CONTRIBUTIONS.—Study conception: JA, JR, NP; Methodology: JA; Formal analysis: JR, NP; Research – data/ evidence collection: AA, NP; Resources: JA; Data curation: NP; Writing/ manuscript preparation – writing the initial draft: NP; Writing/manuscript preparation – critical review, commentary or revision: JA, JR, AA, NP; Writing/manuscript preparation – visualization/ data presentation: NP; Supervision: JA; Project administration: JA; Funding acquisition: JA.

REFERENCES

- Arizaga, J., Laso, M., Rodríguez-Pérez, J., Zorrozua, N., Pagaldai, N. & Carrascal, L.M. (2021). Atlas de aves nidificantes de San Sebastián / Donostiako hegazti habiagileen atlasa. Donostiako Udala, Osasun eta Ingurumen Saila; Aranzadi Zientzia Elkartea, Donostia.
- Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S., Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L., Kühn, I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U., Pysek, P., Siebert, S., Sushinsky, J., Werner, P. & Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B*, 281: 20133330.
- Boal, C.W. (2018). Urban raptor communities: Why some raptors and not others occupy urban environments. In, C.W. Boal & C.R. Dykstra, (Eds.): *Urban Raptors*, pp. 36-50. Island Press, Washington, DC.
- Boggie, M.A. & Mannan, R.W. (2014). Examining seasonal patterns of space use to gauge how accipiter responds to urbanization. *Landscape and Urban Planning*, 124: 34-42.
- Burgos, G. & Zuberogoitia, I. (2018). A telemetry study to discriminate between home range and territory size in Tawny Owls. *Bioacustics*, 29: 109-121.
- Burnham, K.P. & Anderson, D.R. (2004). Multimodel Inference: Understanding AIC and BIC in Model Selection. *Sociological methods & Research*, 33: 261-304.
- Callaghan, C.T., Major, R.E., Wilshire, J.H., Martin, J.M., Kingsford, R.T. & Cornwell, W.K. (2019). Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of ecological and life history traits using a novel continuous measure of bird responses to urbanization. *Oikos*, 128: 845-858.
- Evans, K., Chamberlain, D., Hatchwell, B.J., Gregory, R.D. & Gaston, K.J. (2011). What makes an urban bird? *Global Change Biology*, 17: 32-44.
- Fröhlich, A. & Ciach, M. (2019). Nocturnal noise and habitat homogeneity limit species richness

of owls in an urban environment. *Environmental Science and Pollution Research*, 26: 17284-17291.

- Fröhlich, A. & Ciach, M. (2018). Noise pollution and decreased size of wooded areas reduces the probability of occurrence of Tawny Owl Strix aluco. Ibis, 160: 634-646.
- Giam, X. & Olden, J.D. (2016). Quantifying variable importance in a multimodel inference framework. *Methods in Ecology and Evolution*, 7: 388-397.
- Gonçalves, S.F., de Paula Lourenço, A.C., de Sousa Bueno Filho, J.S. & Barbosa de Toledo, M.C. (2021). Characteristics of residential backyards that contribute to conservation and diversity of urban birds: A case study in a Southeastern Brazilian city. Urban Forestry & Urban Greening. 61: 127095.
- Gryz, J. & Krauze-Gryz, D. (2018). Influence of habitat urbanization on time of breding and productivity of Tawny Owl (*Strix aluco*). *Polish Journal of Ecology*, 66: 153-630.
- Gu, C. (2020). Urbanization. In, A. Kobayashi (Ed.): *International Encyclopedia of human Geography (second Edition)*, pp. 141-153. Elsevier.
- Hesselbarth, M.H., Sciaini, M., With, K.A., Wiegand, K. & Nowosad, J. (2019). Landscapemetrics: an open-source R tool to calculate landscape metrics. *Ecography*, 42: 1648-1657.
- Kettel, E.F., Gentle, L.K., Quinn, J.L. & Yarnell, R.W. (2018). The breeding performance of raptors in urban landscapes: a review and metaanalysis. *Journal of Ornithology*, 159: 1-18.
- Leveau, L.C., Gorleri, F.C., Roesler, I. & González-Táboas, F. (2022). What makes an urban raptor? *Ibis*, 164: 1213-1226.
- Li, J., Dirzo, R., Wang, Y., Zeng, D., Liu, J., Ren, P., Zhong, L. & Ding, P. (2021). Rapid morphological change in a small mammal species after habitat fragmentation over the past half-century. *Diversity & Distributions*, 27: 2615-2628.
- López-Peinado, A., Lis, A., Perona, A.M. & López-López, P. (2020). Habitat preferences of the Tawny Owl (*Strix aluco*) in a special conservancy area of eastern Spain. *Journal of Raptor Research*, 54: 402-413.
- Mak, B., Francis, R.A. & Chadwick, M.A. (2021). Living in the concrete jungle: A review and

socio-ecological perspective of urban raptor habitat quality in Europe. *Urban Ecosystems*, 24: 1179-1199.

- Melles, S., Glenn, S. & Martin, K. (2003). Urban bird diversity and landscape Complexity: Speciesenvironment associations along a multiscale habitat gradient. *Conservation Ecology*, 7: 5.
- Mikkola, H. (1983). *Owls of Europe*, pp. 136-156. T. & A.D. Poyser.
- Naimi, B., Hamm, Na., Groen, T.A., Skidmore, A.K. & Toxopeus, A.G. (2014). Where is positional uncertainty a problem for species distribution modelling. *Ecography*, 37: 191-203.
- Natsukawa, H. (2021). Raptor breeding sites indicate high taxonomic and functional diversities of wintering birds in urban ecosystems. *Urban Forestry & Urban Greening*, 60: 127066.

- Pagaldai, N., Arizaga, J., Jiménez-Franco, M.V. & Zuberogoitia, I. (2021). Colonization of Urban Habitats: Tawny Owl Abundance Is Conditioned by Urbanization Structure. *Animals*, 11: 2954.
- Palacio, F.X. (2020). Urban exploiters have broader dietary niches than urban avoiders. *Ibis*, 162: 42-49.
- QGIS.org (2022). *QGIS Geographic Information System*. QGIS Association. http://www. qgis.org
- Senzaki, M., Yamaura, Y., Francis, C.D. & Nakamura, F. (2016). Traffic noise reduces foraging efficiency in wild owls. *Scientific Reports*, 6: 30602.
- Sergio, F., Newton, I. & Marchesi, L. (2005). Top predators and biodiversity. *Nature*, 436: 192.



- R Core Team (2020) R: A Language and Environment for Statistical Computing; R Foundation for Statistical Computing: Vienna, Austria, 202. Available online: https://www.R-project.org/
- Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society* (*B*), 73: 1.
- Worthington-Hill, J. & Conway, G. (2017). Tawny Owl *Strix aluco* response to call-broadcasting and implications for survey design. *Bird Study*, 64: 205-210.
- Zuberogoitia, I. & Campos, L.F. (1998). Censusing owls in large areas: A comparison between methods. *Ardeola*, 45: 47-53.

- Zuberogoitia, I., Burgos, G., González-Oreja, J.A., Morant, J., Martínez, J.E. & Zabala, J. (2018). Factors affecting spontaneous vocal activity of Tawny Owls *Strix aluco* and implications for surveying large areas. *Ibis*, 161: 495-503.
- Zuberogoitia, I., Martínez, J.E., González-Oreja, J.A., González de Buitrago, C., Belamendia, G., Zabala, J., Laso, M., Pagaldai, N. & Jiménez-Franco, M.V. (2020). Maximizing detection probability for effective large-scale nocturnal bird monitoring. *Diversity & Distributions*, 26: 1034-1050.

Recieved: July 21, 2022 Major revision: October 06, 2022 Accepted: November 28, 2022

Editor: José Hernán Sarasola