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Maximizing detection probability for effective large-scale nocturnal bird monitoring

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Abstract

Aim: Our specific objectives were to (a) estimate detection probabilities of nocturnal bird species, after taking into account survey-specific covariates, and (b) investigate the influence of site-specific covariates on owl and nightjar abundance, integrating effects of imperfect detection.

Innovation: We conceived a survey protocol to estimate probabilities of detection and estimates of abundance of owls and nightjars in a large area, the Basque Country, northern Spain.

Main Conclusions: Our results show that detection probability was strongly influenced by playback broadcast and by observer experience. Date irregularly affected species according to their reproductive periods, and we also found that vocal activity gradually diminished proportionally to the hour after sunset. Tawny owl (*Strix aluco*) was the most abundant and widely distributed species. Its abundance was positively related to forest areas (mainly pine timber forests) and decreased in large urban and agricultural areas. Open space species were less common. Barn owls (*Tyto alba*), little owls (*Athene noctua*), Eurasian scops owls (*Otus scops*) and long-eared owls (*Asio otus*) avoided forest areas, but showed different responses to agriculture, grass-fields, scrub and urban areas. Finally, European nightjar (*Caprimulgus europaeus*) was moderately frequent, and its abundance was favoured by scrub areas and, weakly, by eucalyptus patches, whereas it was negatively affected by large forest areas. We have shown that it is fundamental to consider the effects of survey-specific covariates in the methodology design and analytical development. Our results also indicate some ecological adaptations and population changes in the nocturnal bird community following an increase in urbanization and in the extent of timber plantations, and also the simplification of natural habitats.

KEYWORDS
abundance estimates, binomial N-mixture models, broadcast surveys, European nightjar, imperfect detection, observer experience, owls

1 | INTRODUCTION

Long-term and large-scale ecological monitoring programmes of secretive or elusive species are difficult and costly (Thompson, 2013). Datasets about distribution and abundance of a species, among others, are required to adequately develop management actions (Petitot, Manceau, Geniez, & Besnard, 2014). Managers and researchers expect to reach a profitable trade-off between available budgets (personnel, time and money) and results. Currently, ecologists and conservation practitioners hold a range of relatively "low cost" established and emerging technologies that can be used to increase the spatial and temporal scales at which they work (Marvin et al., 2016). Species distribution models (SDMs) and occupancy models are powerful tools to evaluate distribution, abundance and population trends (Kellner & Swihart, 2014). SDMs use a range of datasets collected through the time and the space with a high variety of positive records of a target species (Bradsworth, White, Isaac, & Cooke, 2017; Girini, Palacio, & Zelaya, 2017; Sarà, 2008), and they have become an important research tool to inform decision-making in conservation (Sofaer et al., 2019). Unfortunately, detection is rarely either perfect or constant due to observer error, environmental conditions and species rarity (Banks-Leite et al., 2014). It may result in bias in estimated relationships with ecological covariates and estimates of species distribution or abundance that are inaccurate or mask trends (Kellner & Swihart, 2014). Occupancy models use detection/non-detection data also collected using different methods from passive detectors such as remote cameras or acoustic recording devices, to questionnaires and specific surveys (Martínez-Martí, Jiménez-Franco, Royle, Palazón, & Calvo, 2016; Moeller, Lukacs, & Horne, 2018). However, failure to detect a species where it is present (imperfect detection) is a common source of error in the predictive ability of SDMs, which can have serious implications for the effectiveness of applications that rely on their predictions (Lahoz-Monfort, Guillera-Arroita, & Wintle, 2014). Occupancy models provide better accuracy than SDMs, although it does not always lead to a substantial improvement to predict the distribution of poorly detectable species (Comte & Grenouillet, 2013). Specific analytical methods are nevertheless required to obtain reliable benefits of these datasets (Jiménez-Franco et al., 2019).

Typically, relatively too much time and money are spent on data collection and not enough consideration is given to programme development, data management and analysis, interpretation, and reporting (Caughlan & Oakley, 2001). Lack of adequate programme development based on behavioural studies causes significant changes in the detection probability of the target species (Nijman, 2007). Many studies employ data from multiple sources, often relying on volunteer fieldwork, without a thorough understanding or critical evaluation of the influence of the background data quality, and its subsequent analytical transformation, on the research conclusions (Blanco et al., 2012). However, to date, it is widely assumed that data collection should be organized within a robust and statistically valid scheme, which optimally corrects for imperfect detection (Strebel, Schmid, Kéry, Sattler, & Knaus, 2020).

Nocturnal birds, especially owls, have drawn scientific attention to obtain a valuable method to measure their population size and trends. The conservation status and recent trends of most nocturnal species necessarily require the application of suitable monitoring programmes (BirdLife International, 2015). However, owls and nightjars are secretive species difficult to study due to their nocturnal behaviour and particular biology, which greatly differ among species (Zuberogoitia, Martínez, & Alonso, 2011). In addition, their detection probability is usually highly dependent on the skill of the observer, the period of the year, the weather and other factors (Jiguet & Williamson, 2010; Zuberogoitia et al., 2019). Although large-scale monitoring programmes are generally impractical, expensive and time-consuming, researchers have been developing specific methods to survey owls in different conditions (see, e.g., Bradsworth et al., 2017; Fröhlich & Ciach, 2017; Ibarra, Martin, Drever, & Vergara, 2014). However, large-scale censuses are still scarce and only a few cases consider the nocturnal bird community (Ibarra et al., 2014; Yahya, Puan, Azhar, Atikah, & Ghazali, 2016; Zuberogoitia & Campos, 1998).

Moreover, large-scale surveys of nocturnal species are affected by detection rates, which are typically low (Kissling, Lewis, & Pendleton, 2010; Wingert & Benson, 2018). Failure to account for detection rates in occupancy surveys can incorrectly identify occupied sites as vacant (MacKenzie et al., 2006; Stolen et al., 2019). Ideally, one would dedicate a sufficient survey effort to ensure that detection is perfect (Lahoz-Monfort et al., 2014). Prior knowledge of the target species has a very strong positive influence on detection probability (Brubaker, Kovach, Ducey, Jakubas, & O'brien, 2014). Knowledge of those factors affecting detection probability could also positively affect the results of models and should be considered to design the most robust survey possible (Kissling et al., 2010). Thus, recording data in ways that allow the modelling of the detection process should be a standard practice in future surveys (Lahoz-Monfort et al., 2014). It would be desirable to calibrate our estimates of the species' distribution and population, not only for population trend analysis but also for national breeding atlas and even wildlife–habitat studies (Freeman, Balmer, & Crick, 2006; Martínez-Martí et al., 2016).

This work was conceived to develop a valuable method easy to replicate and robust enough to evaluate population trends of owls and nightjars. During the last two decades, we have developed methodological works focused on specific owl surveys in the study area (e.g. Zuberogoitia et al., 2019; Zuberogoitia, Martínez, et al., 2011). We took advantage of this knowledge to programme a large-scale survey that should be conducted through one breeding season. Therefore, we designed this programme considering limiting factors, survey-specific covariates that may affect detection probability which, in turn, affect abundance models (see Lahoz-Monfort et al., 2014). Our specific objectives were to (a) estimate probabilities of detection of each species, after taking into account survey-specific covariates, and (b) investigate the influence of site-specific covariates on owl and nightjar abundance, integrating effects of imperfect detection.

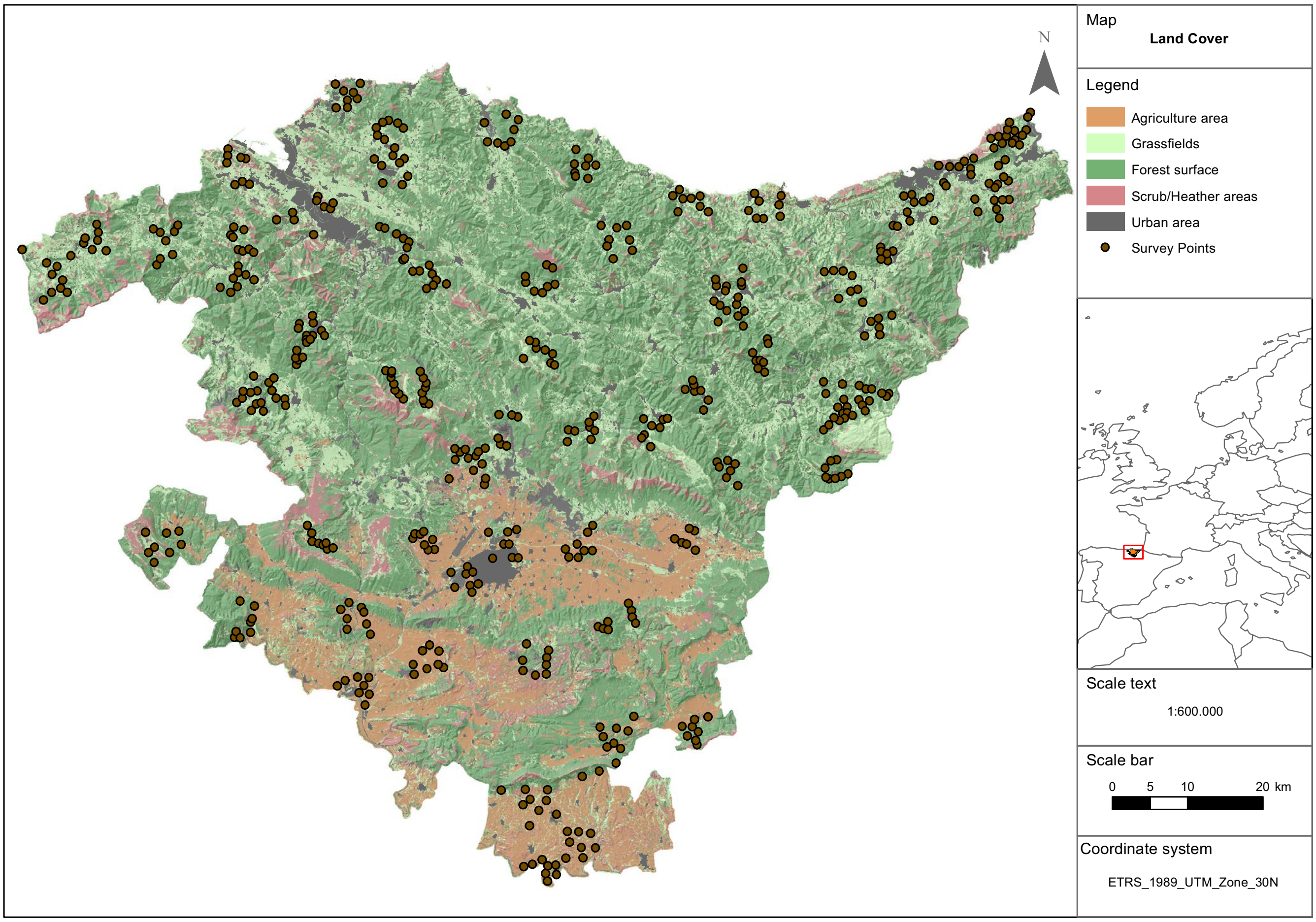

FIGURE 1 Land cover and survey points of the study area, Basque Country

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in the Basque Country, northern Spain (7,234 km^2, lying between 42° and 43°N and 1° and 3°W; Figure 1). There are two clearly defined areas (roughly north and south). The northern area, Cantabric region, runs along the coast of the Bay of Biscay. It has an Atlantic climate and mild temperatures with a thermic oscillation of 12°C from the coldest to the hottest months and 1,200–2,000 mm of rainfall distributed throughout the year (www.euskalmet.euskadi.net). The landscape is mountainous and densely populated, with extensive urban and industrial areas, mainly located in valley floors and on the gentler slopes. Forestry plantations (*Pinus radiata* and *Eucalyptus* spp.) have become widespread in the last 80 years, gradually replacing grazing land for extensively reared livestock, traditional agricultural activities, as well as a few remnants of native forest. The other area, of some 2,500 km^2, lies to the south and is situated in a transition area to the Mediterranean climatic region. The climate is dry with a thermic oscillation of 17°C from the coldest to the hottest months, and the landscape is dominated by arable lands, vineyards, Mediterranean scrub and holm-oak woods in the sloping areas.

2.2 | Survey design and survey protocol

Survey methods were based on the methodology used in the little owl (*Athene noctua*) census carried out in the Basque Country (Zuberogoitia, Zabala, & Martínez, 2011), in which we conducted a large-scale detection/non-detection survey encompassing all the Basque Country. However, in the present case, we considered all the owl species and also European nightjars (*Caprimulgus europaeus*).

First, we randomly selected 65 5 × 5 km Universal Transverse Mercator (UTM) squares that represented all the vegetation types of the Basque Country. These UTMs were considered our sampling units (SUs). Second, we randomly selected eight survey points (SPs) in each SU. The SPs were chosen according to the main habitat types at each SU, considering a minimum distance of 1 km between two SPs. All the SPs were established before the beginning of the surveys and were kept without change until the end of the study. In all, we surveyed 521 SPs which will be considered the sampling sites for our hierarchical models (Figure 1).

We considered seven survey periods in 2018 (one per month through January to July, most of the breeding cycle of the target species; Zuberogoitia, Martínez, et al., 2011). In each period,

TABLE 1 Results of owls and nightjars surveys in the Basque Country between January and July 2018. Number of survey points (SP) with positive results, and number of surveys with 0–9 individuals detected

		Number of individuals per SP/survey period							
Species	Positive SP	0	1	2	3	4	5	6	9
Eagle owl	13 (2.5%)	2,567	15	2					
Boreal owl	1 (0.2%)	2,582	2						
Tawny owl	371 (71.4%)	1,826	479	177	80	13	9		
Long-eared owl	29 (5.6%)	2,551	30	3					
Short-eared owl	3 (0.6%)	2,581	3						
Barn owl	151 (29.0%)	2,382	175	23	4				
Scops owl	109 (20.9%)	2,430	113	30	5	3	1	1	1
Little owl	73 (14.0%)	2,493	79	12					
European nightjar	162 (31.1%)	2,379	155	42	7			1	

we surveyed between four (minimum) and eight (maximum) SPs per SU, being the average of six SPs surveyed per SU and survey period.

In each SP, we developed a three-period survey protocol for owl and nightjar census: 5-min waiting for spontaneous voices, 5 min of playback broadcast voices of only one species and 5-min waiting in silence. Therefore, we spent 15 min per survey in each SP. All the surveys were developed during the first hours after dusk. Surveying eight SP in a SU required on average 180 min, and therefore, only one or a maximum of two SUs were surveyed per night. Surveys were conducted on calm and dry nights, and they were suspended if it started to rain or wind increased, reducing owl detectability (Braga & Motta-Junior, 2009; Lengagne & Slater, 2002; Zuberogoitia et al., 2019).

We noted every owl species and nightjars in each survey, considering those that were detected in the first 5-min spontaneous, during the 5-min broadcast period and during the last 5-min silent period. We broadcast playback voices of only one species per survey period. The species were chosen according to the annual maximum peak of response to playback broadcasts in our study area. In this sense, we broadcast voices of eagle owls (*Bubo bubo*) in January (Martínez & Zuberogoitia, 2003), tawny owls (*Strix aluco*) in February (Zuberogoitia et al., 2019; Zuberogoitia & Martínez, 2000), long-eared owls (*Asio otus*) in March (Martínez, Zuberogoitia, Colás, & Macía, 2002), barn owls (*Tyto alba*) in April (Zuberogoitia & Campos, 1998), Eurasian scops owls (*Otus scops*) in the last weeks of April and first weeks of May (Zuberogoitia, Martínez, et al., 2011) and little owls during June and the first half of July (Zuberogoitia, Zabala, et al., 2011). There were no records of boreal owls (*Aegolius funereus*) in the study area, although we also included survey points with broadcast voices of this species in mountain old forest areas in January (Badosa, López, Potrony, Bonada, & Gil, 2012). Similarly, although there were no records of breeding attempts of short-toed owls (*Asio flammeus*) in the study area, we considered the courtship main period of this species in Spain (Onrubia, 2016) and included some surveys in open areas broadcasting voices of the species in March and April. We did not use broadcast voices of nightjars.

Playback records were built according to our own experience (e.g. Zuberogoitia & Campos, 1998). We included a mix of territorial and mating voices of males and females of each species in tracks of 5 min (just the time needed for each survey). Voices were downloaded from xeno-canto (https://www.xeno-canto.org/), choosing only those clear and adequate for each case, recorded on other parts of the species range, and according to our previous experience. The volume of the playback broadcast was enough to be heard by an

TABLE 2 Overall number of individuals of each species detected per survey period (month). Results obtained during specific broadcasting surveys in bold

	January	February	March	April	May	June/ July
Eagle owl	**13**	3	1	0	0	0
Boreal owl	**1**	1	0	0	0	2
Tawny owl	199	**446**	103	154	145	123
Long-eared owl	6	1	**15**	5	3	6
Short-eared owl	0	1	**0**	1	1	0
Barn owl	12	7	35	**126**	25	28
Scops owl	0	1	5	40	**132**	42
Little owl	9	4	9	15	14	**52**
European nightjar[a]	0	0	6	10	86	164

[a]Note that European nightjar was not recorded with broadcasting surveys.

observer at 300 m but not as much as to produce distortion noises at close distances.

2.3 | Variables for the analyses

The number of individuals (abundance, from 0 to a maximum of 9 individuals) of each species detected per SP was considered the response variable, a zero-inflated Poisson random variable (Table 1). We recorded two types of predictive variables, those that could affect species detectability (survey covariates) and those that could affect our ecological response variables, that is species abundance (site covariates).

We chose five survey covariates that could affect detectability. We noted whether individuals responded to conspecific broadcast voices or produced spontaneous calls (BROAD). We also considered the experience surveying owls of each observer (EXPER), being “0” for those researchers who had no experience surveying owls and “1” for those researchers that had developed owl surveys (see, e.g., Zabala et al., 2006; Zuberogoitia, Zabala, et al., 2011). We considered linear and quadratic effects of the Julian days (1 January = 1, 31 December = 365; DATE, DATE^2) to control for seasonal effects. Survey hour (HOUR) was measured counting each hour from the sunset in the study area (https://tierra.tutiempo.net/calendario/calendario-solar-de-euskadi-sp019021.htm) to the survey moment. Surveys should have been conducted on dry and calm nights, although it was impossible to effectively control some parameters as wind (WIND) and temperature (T), and therefore, we obtained detailed information about the wind speed (km/hr) and T (°C) of the 15-min survey period at each SP. We obtained these data from the nearest meteorological stations (n = 27) to each SP (http://www.euskalmet.euskadi.eus).

We also selected 11 site-specific covariates that could affect species abundance, the regional climatic situation (REG) of the SP, being Cantabric region (1), Subcantabric region (2) and Mediterranean region (3; for more details, see Zuberogoitia, Zabala, et al., 2011), and the altitude (ALT) m a.s.l. of the SP. Moreover, we established a 565 m radius obtaining 1-km^2 buffer area for each SP. The 521 buffer areas were overlapped with vegetation and urban digital maps (www.geoeuskadi.eus) to obtain the percentage of vegetation types (FIELD—grass-fields; AGR—agriculture area; SCRUB—scrub and heather areas; DEC—deciduous forest;

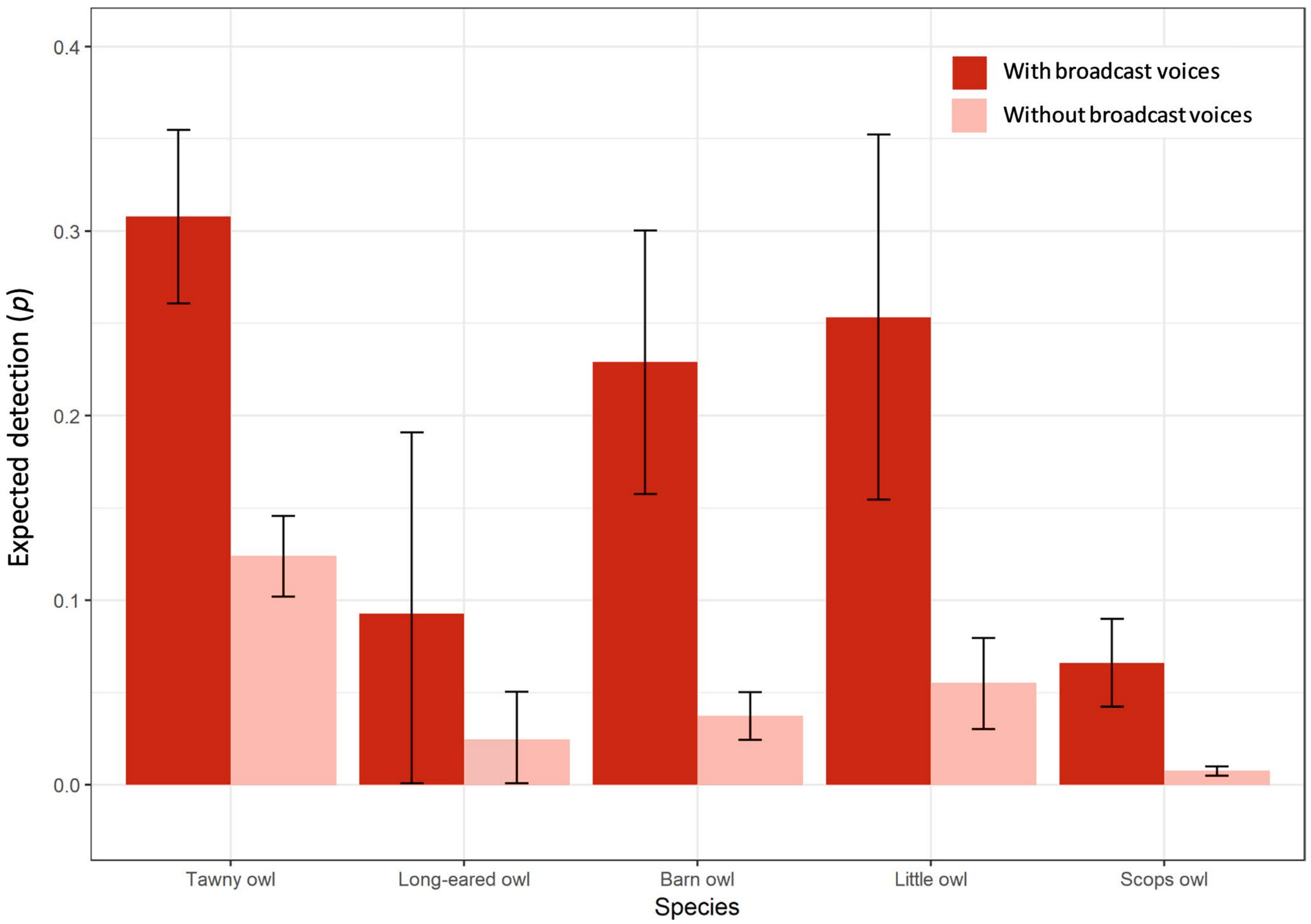

FIGURE 2 Expected detection probability (p) of owls and nightjars of the Basque Country in relation to broadcast voices (1: with, 0: without broadcast voices) that include this covariate in the top-ranked model. Error bars show standard error bounds. Predictions were made at average values of the other covariates. Eagle owl, short-eared owl and boreal owl were not considered in the models due to the scarce numbers of positive records

TABLE 3 Untransformed coefficients and standard error of survey-specific covariates related to detection probability (p) estimated by the top-ranked models of owls and nightjars surveys of the Basque Country. Eagle owl, short-eared owl and boreal owl were not considered in the models due to the scarce numbers of positive records. Covariates: date (DATE), quadratic function of date (DATE$^{\wedge 2}$), survey hour (HOUR), wind speed (WIND), temperature (T), broadcast voices (BROAD), observer experience (EXPER). Blank cells refer to those covariates that were not selected in the most parsimonious models

	Int	DATE	DATE$^{\wedge 2}$	HOUR	WIND	T	BROAD	EXPER
Tawny owl	−2.07 (0.21)	−0.003 (0.00)		−0.05 (0.02)	−0.01 (0.01)		1.15 (0.08)	0.23 (0.08)
Long-eared owl	−3.69 (1.11)			−0.15 (0.13)			1.41 (0.35)	
Barn owl	−3.43 (0.36)	0.004 (0.002)		−0.08 (0.05)			2.04 (0.17)	0.34 (0.19)
Little owl	−317 (0.49)			−0.08 (0.08)	−0.07 (0.03)		1.77 (0.23)	0.65 (0.25)
Scops owl	−5.23 (0.40)	0.02 (0.00)					2.24 (0.20)	0.66 (0.26)
European nightjar	−6.77 (0.42)	0.04 (0.003)		−0.35 (0.07)		−0.05 (0.03)	NA	0.72 (0.20)

HOLM—holm-oak forest; PINE—pine plantations; EUC—eucalyptus plantations; FOR—forest surface, including timber plantations; URB—urban area). For open areas species, barn owl and little owl, we joined forest types (DEC, HOLM, PINE and EUC) in a unique covariate (FOR), whereas for the rest of species, we considered the forest types in the analysis.

2.4 | Data analysis

We developed binomial N-mixture occupancy models, in which we estimated abundance and detectability as a function of site-specific and survey-specific covariates using the log link function (Fiske & Chandler, 2011). Our sampling design considered 521 sites (SPs)

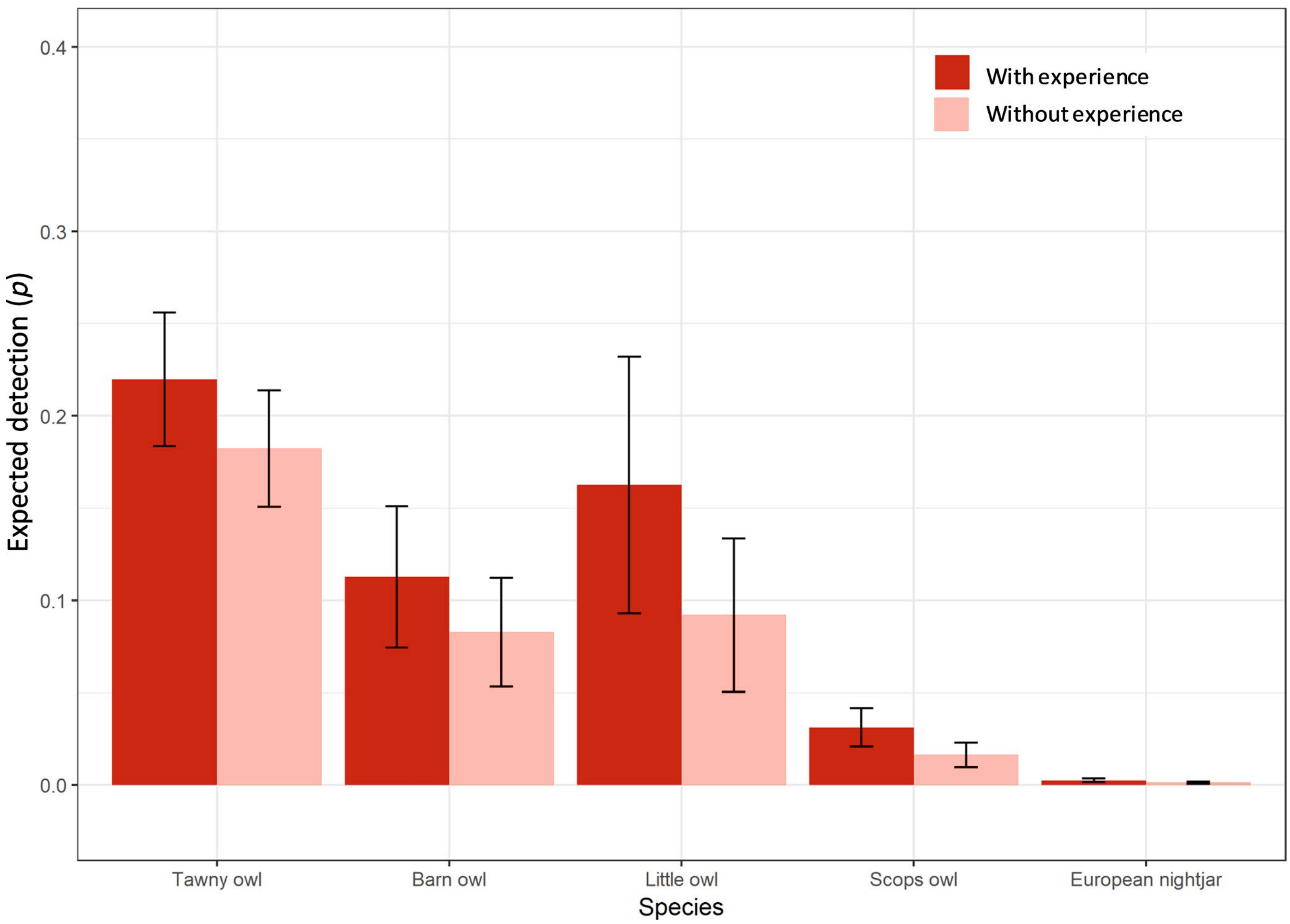

FIGURE 3 Expected detection probability (p) of owls and nightjars of the Basque Country in relation to observer experience (1: with experience; 0: without experience) that include this covariate in the top-ranked model. Error bars show standard error bounds. Predictions were made at average values of the other covariates. Eagle owl, short-eared owl and boreal owl were not considered in the models due to the scarce numbers of positive records

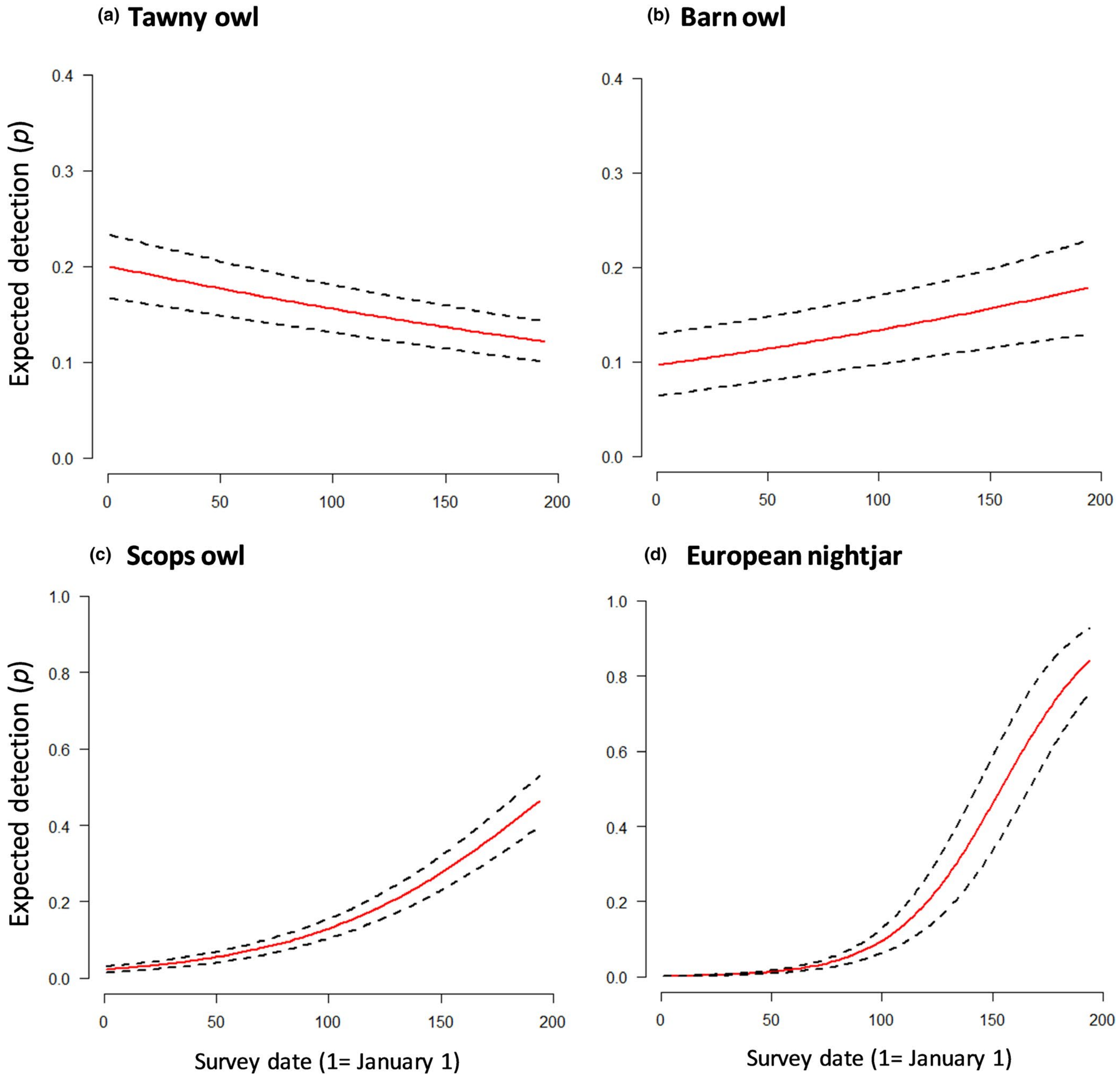

FIGURE 4 Expected detection probability (*p*) of owls and nightjars of the Basque Country along survey date (1 = 1 January) that include this covariate in the top-ranked model: a) tawny owl; b) barn owl; c) scops owl; d) European nightjar. Dashed lines show standard error bounds. Predictions were made at average values of the other covariates

in which we recorded the numbers of individuals for each species, considering from 4 to 8 temporal replicates for sites. Observations were generated by a combination of (a) a state process determining abundance (i.e. counts) at each site and (b) a detection process that yields observations conditional on the state process (Kéry, Royle, & Schmid, 2005; MacKenzie et al., 2002; Royle, 2004).

Given the large number of potential candidate models to evaluate abundance and detection probabilities, model fitting was conducted following a two-phase approach. First, we performed model selection for detectability models in a hierarchical process considering all the possible combinations of the survey-specific covariates, including the null model, and keeping the abundance component constant; second, we performed abundance model selection in a hierarchical process considering all the possible combinations of the site-specific covariates, keeping the component for detection probability constant (Comte & Grenouillet, 2013). For abundance models, we rescaled the variables by subtracting the mean and dividing by the standard deviation (Hedlin & Franke, 2017) and we considered the quadratic function of the urban area (URB$^{\wedge 2}$). Finally, we performed model selection with the combination of the best detectability and abundance models. Models were ranked using the difference in Akaike's information criterion (ΔAIC) between each model and the

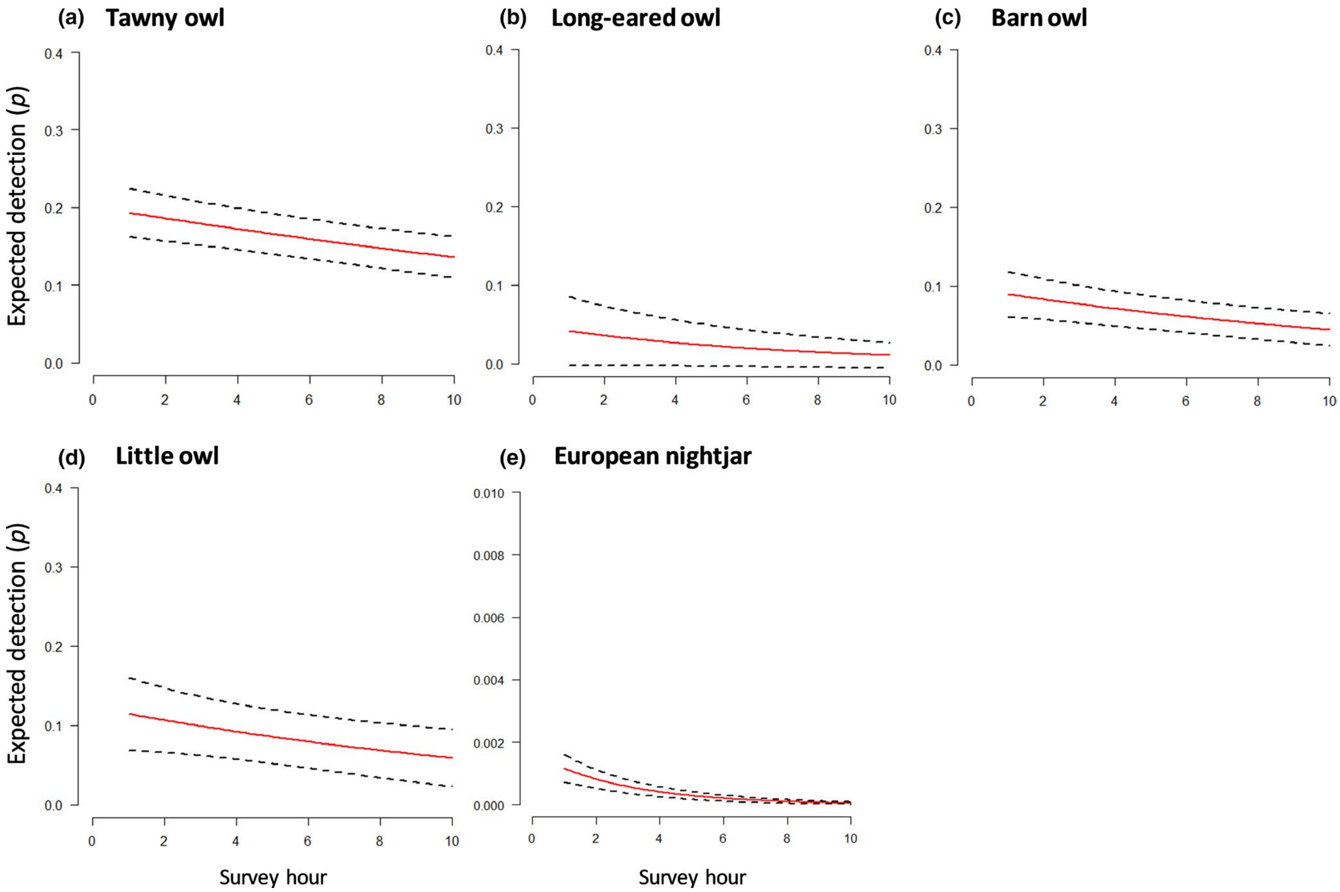

FIGURE 5 Expected detection probability (p) of owls and nightjars of the Basque Country along survey hour (survey hour counting each hour from the sunset to the survey moment) that include this covariate in the top-ranked model: (a) tawny owl; (b) long-eared owl; (c) barn owl;)d) little owl; European nightjar. Dashed lines show standard error bounds. Predictions were made at average values of the other covariates

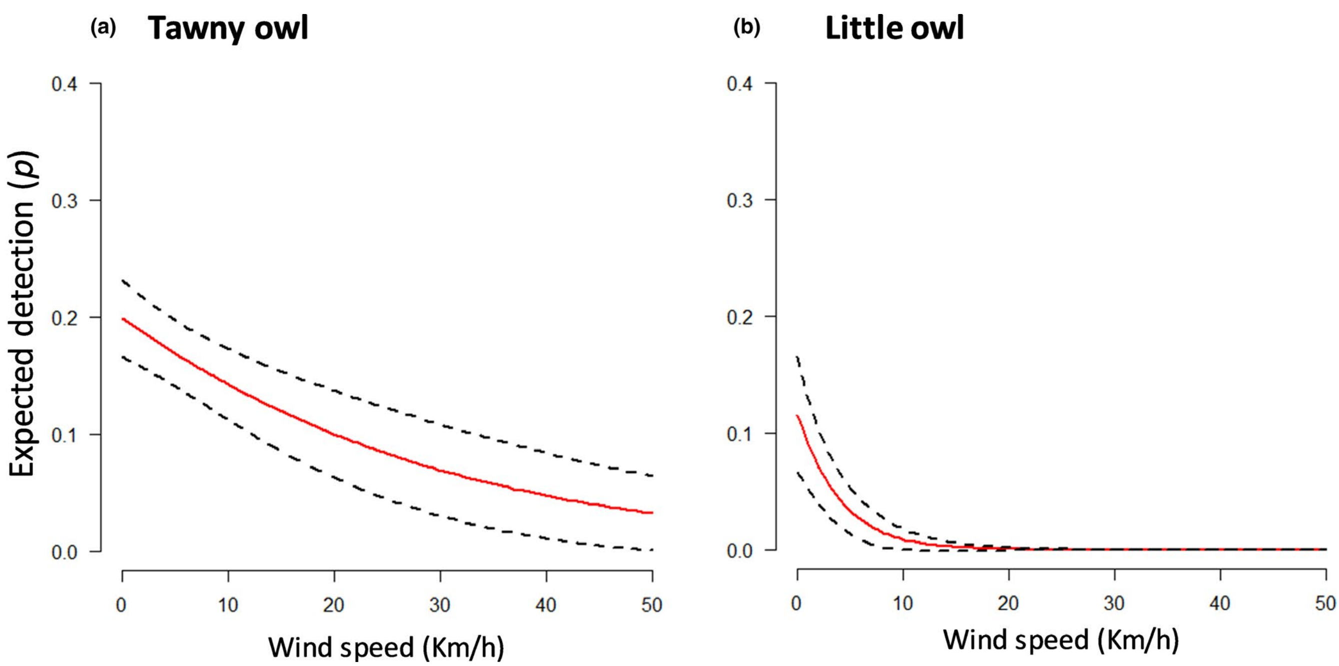

FIGURE 6 Expected detection probability (p) of owls and nightjars of the Basque Country along the wind covariate (km/hr) that include this covariate in the top-ranked model: (a) tawny owl; (b) little owl. Dashed lines show standard error bounds. Predictions were made at average values of the other covariates

best model supported (i.e. the model with the smallest AIC; Burnham & Anderson, 2002). We used the *pcount* function from the UNMARKED package (Fiske & Chandler, 2011), considering latent abundance as a Poisson distribution, and detectability as binomial distribution, as well as the identifiability problems described by Kéry (2018). We generated abundance maps of the species in R using the package RASTER (https://CRAN.R-project.org/package=raster).

3 | RESULTS

Overall, we conducted 2,584 surveys in 521 SPs from January to July 2018 (Zuberogoitia et al., 2020). Tawny owl was the most abundant and widely distributed owl species in the study area, distantly followed by barn owl, Eurasian scops owl and little owl, whereas long-eared owl and eagle owl were scarce and patchily distributed, and short-eared owl and boreal owl were rare species in the study area (Tables 1 and 2). European nightjar appeared in 31.1% of the SPs.

3.1 | Factors affecting detection probability

Detection probability was strongly influenced by playback broadcast for all owl species modelled (Table 3; Appendix Table S1.1). In fact, surveys using broadcast voices considerably improved detection probability (Figure 2). Observer experience was another covariate affecting detection probability for all studied species except long-eared owl (Table 3), slightly increasing detectability, especially in little owl (Figure 3).

Date negatively affected tawny owl detectability, and positively, though weakly, affected barn owls, Eurasian scops owl and nightjars (Figure 4). These two last species are migratory species that arrive in spring for breeding. The survey hour also affected detectability in all species but Eurasian scops owls (Table 3). Vocal activity diminished proportionally to the hour after sunset, the first hour after dusk being the best for surveying owls and nightjars (Figure 5).

Finally, wind negatively affected detectability of tawny owls and little owls but had no effects for the other species (Figure 6). Temperature slightly affected European nightjars.

3.2 | Factors affecting abundance

Tawny owls were more abundant in mountain forest areas (mainly pine timber forests) of the northern area (Cantabric region) of the Basque Country (Figure 7), whereas large urban and agricultural areas, mainly those located in the south (Mediterranean region), negatively affected this species abundance (Table 4; Appendix S2, Figure S2.1.a). In contrast, long-eared owl's abundance was negatively affected by large forest areas, whereas it preferred Mediterranean scrub areas (Appendix S2, Figure S2.1.b).

Barn owls avoided forest areas, but their abundance was also affected by altitude, large urban and agricultural areas and scrub areas

TABLE 4 Untransformed coefficients of site-specific covariates related to abundance estimated by the top-ranked models of owls and nightjars surveys of Basque Country. Scarce species were not considered in the analysis. Covariates: regional climatic situation (REG), altitude (ALT) grass-fields (FIELD), agriculture area (AGR), urban area (URB), quadratic function of urban area (URB^2), pine plantations (PIN), scrub and heather areas (SCRUB), deciduous forest (DEC), eucalyptus plantations (EUC) and forest surface (FOR). For open areas species, barn owl and little owl, we joined forest types (DEC, HOLM, PINE and EUC) in a unique covariate (FOR), whereas for the rest of species, we considered the forest types in the analysis. NA refers to those covariates that were not included in the analysis. Blank cells refer to those covariates that were not selected in the most parsimonious models

	Int.	REG	ALT	FIELD	AGR	URB	URB^2	PIN	SCRUB	DEC	EUC	FOR
Tawny owl	2.24 (0.22)	−0.46 (0.09)	0.22 (0.05)		−0.31 (0.07)	−0.35 (0.06)		0.12 (0.04)				NA
Long-eared owl	−2.90 (1.22)	0.88 (0.30)						−0.41 (0.28)	0.22 (0.12)	−0.52 (0.27)		NA
Barn owl	−0.17 (0.24)		−0.36 (0.10)		−0.56 (0.14)	−0.32 (0.09)		NA	−0.32 (0.11)	NA	NA	−0.46 (0.09)
Little owl	−0.35 (0.36)		−0.39 (0.15)		0.35 (0.10)		−0.11 (0.08)	NA	0.17 (0.11)	NA	NA	
Scops owl	−0.82 (0.17)			0.33 (0.10)	0.34 (0.09)		0.04 (0.01)		0.17 (0.07)	−0.59 (0.16)		NA
European nightjar	0.11 (0.18)						NA		0.20 (0.04)	−0.18 (0.09)	0.02 (0.01)	NA

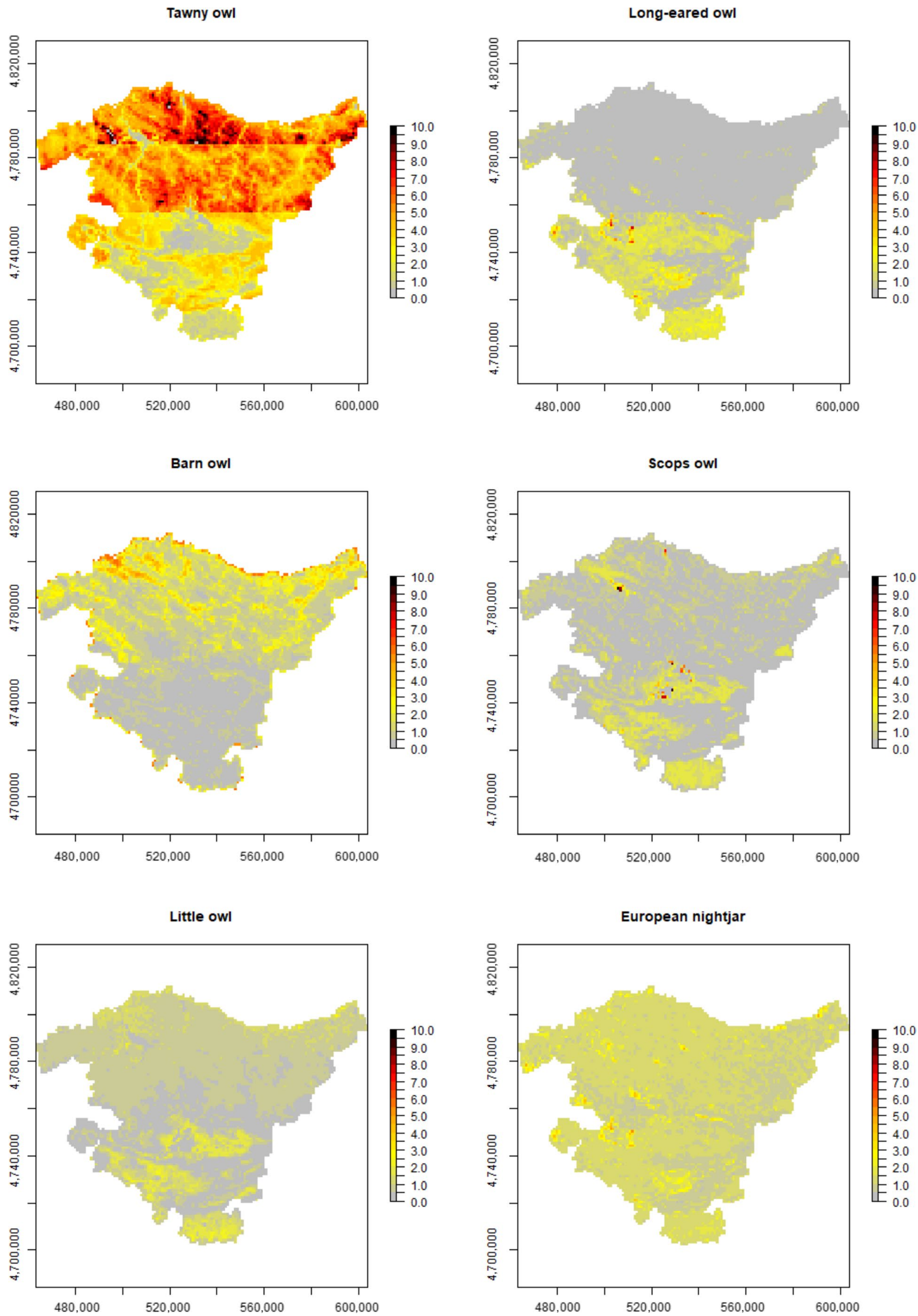

FIGURE 7 Species distribution maps of abundance estimates under the top-ranked model for data modelled at the 1-km^2 scale in the Basque Country. UTM coordinates are in Zone 30T. Number of individuals' estimates per 1 km^2 for the studied species: tawny owl, long-eared owl, barn owl, little owl, Eurasian scops owl and European nightjar

(Table 4, Appendix S2, Figure S2.1.c). Little owls avoided mountainous areas, but in contrast to barn owl, their abundance was favoured by agricultural and scrub areas and showed a negative quadratic effect of urban areas (villages and medium-sized towns, Appendix S2, Figure S2.1.d). Eurasian scops owls selected open areas, from Atlantic fields to agricultural areas and scrub areas, rejecting deciduous forests. Moreover, Eurasian scops owls were located in small rural areas and parks in the middle of some cities, large urban areas, explaining a weak quadratic effect of urban areas (Table 4, Appendix S2, Figure S2.1.e).

European nightjar abundance was highest in scrub areas and affected positively but weakly by eucalyptus patches, whereas it was negatively affected by large forest areas (pine and deciduous forests, Table 4, Appendix S2, Figure S2.1.f).

4 | DISCUSSION

Twenty years ago, we developed an intensive large-scale census of owls in Biscay, included in the current study area (Zuberogoitia & Campos, 1998), which was one of the first large surveys of the complete owl community in large areas. To date, we increased the study area to the whole Basque Country (more than threefold of the previous extent), but we could not apply the same intensive methodology, because of its excessive cost. Instead, we developed a survey protocol to obtain valuable information of nocturnal birds in a relatively short period (seven months) at a lower cost. The difference nevertheless is that Zuberogoitia and Campos (1998) obtained the population size of every owl species, and now, our results are expressed as detectability and abundance. These parameters, however, allow us to apply for monitoring programmes in a cost-effectively way, accounting for imperfect detection (Martínez-Martí et al., 2016), and to establish trends of populations using the same methods in future surveys (Jiménez-Franco et al., 2019; MacKenzie et al., 2006).

4.1 | Detection probability

Among the covariates affecting detection probability, the use of playback broadcast voices was the most obvious, improving results for all species as expected according to our previous experience (Zuberogoitia, Martínez, et al., 2011) and also other works with these and other owl species (Braga & Motta-Junior, 2009; Cooke et al., 2017; Kissling et al., 2010; Mori, Menchetti, & Ferretti, 2014; Wingert & Benson, 2018). Thus, incorporating call broadcast into future large-scale owl surveys should help biologists decrease false negatives (Regan, McClure, & Belthoff, 2018).

Observer experience was another important covariate that affected detection probability. This factor has been pointed out in different works, mainly for evasive and difficult to detect species (Booms, Schempf, McCaffery, Lindberg, & Fuller, 2010; Eglington, Davis, Joys, Chamberlain, & Noble, 2010; Johnston, Fink, Hochachka, & Kelling, 2018), but also for amphibians or insects, which require prior experience to find or for correct identification (MacKenzie et al., 2006; Petitot et al., 2014). In our case, all the observers had previously worked in different bird surveys, but not all had previous experience working with owls. Overall, 48% of the SPs were surveyed by experts. We had to reach a trade-off between the number of SPs surveyed per night/month and the number of observers involved in the project. This is a recurrent problem in most large-scale surveys because experts are scarce and more expensive than non-experts or volunteers. However, results can improve up to twofold for most of the species when experts are considered, and this magnitude might increase much more if volunteers (sometimes without any experience) are considered (Barata, Griffiths, & Ridout, 2017).

Knowledge of the biological cycle or vocal behaviour of every species is needed to adjust the date of the survey programmes (Flesch & Steidl, 2007; Olsen, Trost, & Hayes, 2002). Our results confirmed differences in detection probability for most species through the seasons that were related to specific breeding cycles, from eagle and tawny owls, the earliest breeders, until little and Eurasian scops owls, the latest ones (León-Ortega, Jiménez-Franco, Martínez, & Calvo, 2017; Zuberogoitia, 2002). In some cases, for example little owls, vocal activity reaches a maximum peak in spring (Zuberogoitia et al., 2007), but the best period to detect breeding territories is in June and July (Zuberogoitia, Zabala, et al., 2011).

Most of the owl and nightjar surveys are conducted during the first hours after sunset (Kissling et al., 2010; Raymond et al., 2019). Time negatively affected detection probability of all species, but Eurasian scops owls continued vocal activity through the night during courtship and heat seasons. These results condition programme development in large-scale surveys, as the optimal time to survey is reduced to the first hours after sunset, and therefore, one observer should only survey few SPs per night.

Weather conditions also affect detection probabilities, which in turn affect the survey programme. Rain and wind strongly affect vocal activity and observer capability to detect voices (Braga & Motta-Junior, 2009; Michel, Jiménez-Franco, Naef-Daenzer, & Grüebler, 2016; Zuberogoitia et al., 2019). Therefore, every nocturnal survey should be completed on calm and dry nights. However, in a large-scale survey project in which the number of experienced observers and the number of surveying hours per night are limited, it is difficult to adequately cover all the SPs during the bad weather seasons (winter and spring). This, in turn, increases the cost of the surveys, because observers must abandon the activity during adverse weather conditions, repeating the SPs on another occasion.

4.2 | Abundance

More than half of the study area is primarily covered by forest, both reforested for timber production (24.6% of pine and 2.6% of eucalyptus) and native deciduous forest (29.6%), whose extent has increased during the last decades, mainly in the medium and north of the study area, in detriment to open lands (http://www.nasdap.net/inventarioforestal). This is an ideal habitat for a generalist forest species, the tawny owl, that reaches maximum densities in pine plantations and oak forests fragmented with small grass-fields (Michel et al., 2016; Zuberogoitia, 2002), but reduces its densities in large homogeneous forest areas (Burgos & Zuberogoitia, 2018) and avoids young forests (Rumbutis et al., 2017). Tawny owl abundance showed a negative relation with open landscapes, mainly those agricultural landscapes located in the Mediterranean region and large urban areas. Tawny owls were also found in these types of habitats but at low abundance values. In fact, tawny owls show high flexibility to adapt to semi-arid landscapes, at the limits of its distribution range (Sánchez-Zapata & Calvo, 1999) and novel habitats too (Fröhlich & Ciach, 2019; Solonen, 2014).

Except for the long-eared owl, which is usually linked to agro-forestry systems and forest edges (Martínez & Zuberogoitia, 2004a), the rest of species we studied are not forest-dwelling ones. However, those habitat variables that favoured tawny owls negatively affected long-eared owls due to both differential habitat requirements and the effect of the intra-guild competition of tawny owls on long-eared owls (Zuberogoitia, 2002; Zuberogoitia, Martínez, Zabala, & Martínez, 2005). Therefore, the abundance of this species increased in the Mediterranean region, mostly associated with mixed habitat conditions (Emin et al., 2018), whereas its abundance was low or even null in some favourable habitats (grass-fields and heathlands) in the Cantabric and Subcantabric regions. In addition, the potential breeding area of long-eared owls in the north half of the study area suffered deep changes in the last decades. Open non-forested areas suffered a reduction due to a continuous increase of urban areas (i.e. urban areas increased from 41,680 ha in 2005 to 47,584 ha in 2018; http://www.nasdap.net/inventarioforestal) and to reforested surface. In the same way, the management of heathlands changed following Natura 2000 network (Evens et al., 2018) and even considering that Council Directive EEC/92/43 establishes the need to promote and maintain heathlands connectivity to improve the ecological coherence of the Natura 2000 network (Tapia, Regos, Gil-Carrera, & Dominguez, 2017). Heather patches are regularly cut to favour extensively grazed grasslands, and simultaneously, there was an increase of low-quality scrublands and clear-cuttings due to an increase of timber activity (e.g. timber area cut increased from 6,650 ha in 2016 until 8,580 ha in 2018). This activity creates a mosaic of early-seral stage communities within the matrix of medium-aged and older forest (Petty, 1996). Successional changes during a forest rotation provide different habitats and food resources for raptors to exploit, which favour some species, for example tawny owls, which obtain most of their food from clear-cuts, but also need older forest for roosting and breeding (Petty, 2011). However, intensive logging activities (i.e. clear-cuttings) alter successional states of vegetation and reduce open-land dwelling raptors (Tapia et al., 2017). In our study area, clear-cuts and pre-thicket sites do not constitute a suitable habitat for long-eared owls; on the contrary, the increase in availability and extension of these habitats seems to favour European nightjars. Our results, in accordance with previous work (Evens et al., 2017), show a negative effect of large forests on the abundance of nightjars. However, its abundance was high in scrubland areas, close to forests, where nightjars nest and forage (Sharps, Henderson, Conway, Armour-Chelu, & Dolman, 2015). Therefore, the increase of early-seral stage and afforested areas showed a positive effect on the species in the study area, with most of the populations in the northern, forested area (Appendix S2. Figure S2.1). Nightjar abundance was slightly related to eucalyptus plantations as they are harvested on a rotation of 12–18 years, whereas pine rotation is close to 35 years; therefore, clear-cuts are available sooner in eucalyptus plantations than in pine forests. In general, these temporal scrublands are low-quality habitats for birds (Goded et al., 2019), but they are positively selected by nightjars as breeding sites, moving to open lands for foraging (Evens et al., 2017).

We expected the two open area specialist species (i.e. the barn owl and little owl), to be positively related to agro-pastoral areas, but our results did not support this anticipated relationship. On the one hand, the abundance of these two species decreased with altitude, as has been previously reported (Zuberogoitia, 2002). There were few records of these species in grasslands and heathers of the highlands. This could be related to weather conditions in the Basque Mountains, where the maximum precipitation values for the whole study area (close to 2,000 L/m^2; www.Euskalmet.euskadi.eus) are obtained. In fact, barn owl is sensitive to bad weather conditions (Altwegg, Roulin, Kestenholz, & Jenni, 2003, 2006; Zuberogoitia, 2000). Likewise, scrublands do not favour the foraging behaviour of barn owls (Arlettaz, Krähenbühl, Almasi, Roulin, & Schaub, 2010), and the species was scarce, or even absent, in heathlands and early-seral stages of deciduous forest and afforested areas, whereas little owl abundance was positively related to this type of habitat, although avoiding afforested areas. On the other hand, previous works in the study area showed a clear relationship between the two species and grasslands and agriculture areas (Aierbe, Olano, & Vázquez, 2001; Zabala et al., 2006; Zuberogoitia, 2002) as it occurs all through their range (Andersen, Sunde, Pellegrino, Loeschecke, & Pertoldi, 2017; Hindmarch, Krebs, Elliott, & Green, 2012; Taylor, 1994; Van Niewenhuyse, Génot, & Jonson, 2008). However, these habitats also suffered severe transformations during the last decades, being the most affected habitats for the urban increase and also partially affected by logging activities. Fragmentation and reduction of grasslands drove the extinction of isolated populations of both species (see Alonso, Caballero, Orejas, Sáez, & Yánez, 1999; Zabala et al., 2006; Zuberogoitia, Martínez, et al., 2011). An increase of road network and traffic along them can increase rates of barn owl–vehicle collisions (Regan et al., 2018), which also negatively affect population abundance, distribution and persistence (Borda-de-Água, Grilo, & Pereira, 2014; Grilo et al., 2012; Hindmarch et al., 2012; Silva et al., 2012). Moreover, the negative response of barn owls to agricultural landscapes is a new problem that has also been detected through the species range in Spain (Escandell, 2012), and it is also affecting many species in Europe (Chrenková, Dobrý, & Sálek, 2017; Michel, Naef-Daenzer, Keil, & Grüebler, 2017; Rey-Beyanas et al., 2010; Stoate et al., 2009). In fact, barn owls largely occupied and prospered in these habitats until recently, and population declines of the species were related to foraging habitat loss, an increase of road network and shortage of suitable breeding sites (Arlettaz et al., 2010; Askew, Searle, & Moore, 2007; Hindmarch et al., 2012; Martínez & Zuberogoitia, 2004b). Nowadays, the effect of intensive farming plus the abuse of agro-chemical biocides accelerated the habitat homogenization and biodiversity loss and it is related to a reduction of barn owl population viability (Bruce, Christie, & Kirwan, 2014; König & Weick, 2008; Schmid, 2002).

In contrast, Eurasian scops owl abundance was positively related to all the open habitat covariates. Habitat requirements of Eurasian scops owls are associated with open fields (scrubland, orchards, pastures and grasslands) close to forest edges, mainly river forest and small tree patches, where they find holes in trees for breeding and insect-rich areas for foraging (Denac, Kmecl, & Koce, 2019; Martínez, Zuberogoitia, Martínez, Zabala, & Calvo, 2007; Sergio, Marchesi, & Pedrini, 2009). In our study area, the species shows periodical cycles related to weather conditions in southern areas of the Iberian Peninsula. Rainy springs in central areas of the Iberian Peninsula seem to negatively affect species local abundance, associated with population increases in our study area (Zuberogoitia, Martínez, et al., 2011). In fact, during the study survey, it was a population peak of the species, passing from being a scarce and rare species in the Basque Country (Aierbe et al., 2001; Alonso, Orejas, Zuberogoitia, & Martínez, 2003; Zuberogoitia, 2002) to reach 20.4% of the SPs in 2018. Moreover, urban populations of Eurasian scops owls have increased during the last years, mainly in city gardens where programmes of nest boxes settlement are often carried out (Berian, 2008; Mori, Ancillotto, Menchetti, & Strubbe, 2017; Vrezec, 2001). The species occupies little towns, where they breed in old buildings and forage in orchards and surrounding fields, or occupy nest boxes in city gardens and forage on typical urban insects (e.g. cockroaches) and birds (R. Alonso, pers.comm.; Esperón et al., 2013).

Finally, eagle owls are still scarce in the Basque Country, mainly distributed in the Mediterranean region (southern study area). However, as it occurs in other European areas, eagle owls started to successfully breed in urban areas preying on alternative species (e.g. rats and pigeons; Penteriani & Delgado, 2019). Short-eared owls bred for the first time in our study area, with only one secure and three possible breeding events during the study period, all in extensive grasslands. We also registered the first record of boreal owl in a stand of mature mixed forest of beeches and pines with pastoral grasslands, located at 1,000 m a.s.l. The species could have been unnoticed in these habitats, similar to those found in other regions of its global range (Brambilla et al., 2013; Domahidi, Shonfield, Nielsen, Spence, & Bayne, 2019; Korpimäki & Hakkarainen, 2012; López et al., 2010). In fact, the south-westernmost European population of the species is located in the Pyrenees, 160 km from our record (Mariné, Lorente, Dalmau, & Bonada, 2005), and this distance is included within the breeding dispersion range of the species in the Pyrenees (Badosa et al., 2012). Castro, Muñoz, and Real (2008) included the Basque Mountains in the distribution projections modelled for the species.

5 | CONCLUSION

Large-scale surveys are needed to obtain data to apply towards species conservation. However, we have shown that previous efforts focused on the knowledge of biology and behaviour of the target species are needed to adequately develop survey programmes and to correct the effects of imperfect detection on the results. Likewise, to reduce the effect of imperfect detection it is fundamental to consider the effects of survey-specific covariates in the methodology design and the analytical development, mainly those that we can a priori manage as the use of broadcast voices, observer experience or the survey time. Our results also indicate some ecological adaptations and population changes in the nocturnal bird community following an increase in urbanization and the extent of timber plantations, and also the simplification of natural habitats. This information is crucial to design future monitoring programmes across our study area, as well as other large-scale areas, and to adopt management actions for conservation purposes.

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DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.dncjsxkwg

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BIOSKETCH

Our research team focuses the interest on ecology and ethology researches of raptors and owls in Spain. During the last two decades, we developed studies on vocal behaviour of owls and survey methods that have been the basin of the current work.

Author contributions: IZ originally formulated the idea and developed methodology; IZ, CGdB, GB, ML and 19 people more (see Acknowledgements) conducted fieldwork; IZ and MVJF performed statistical analyses; CGdB processed habitat data and GIS; and IZ, MVJF, JEM, JAGO, GB, JZ, ML and NP wrote the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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