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Factors affecting spontaneous vocal activity of Tawny Owls *Strix aluco* and implications for surveying large areas

IÑIGO ZUBEROGOITIA,[1,2]* GORKA BURGOS,[2] JOSÉ ANTONIO GONZÁLEZ-OREJA,[3] JON MORANT,[2]
JOSÉ ENRIQUE MARTÍNEZ[4,5] & JABI ZABALA ALBIZUA[6]
[1] *Estudios Medioambientales Icarus S.L., C/San Vicente 8, 6ª Planta. Dpto 8. Edificio Albia I. 48001, Bilbao, Spain*
[2] *Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, 20014 Donostia-S. Sebastián, Spain*
[3] *Facultad de Ciencias Biológicas, BUAP, Benemérita Universidad Autónoma de Puebla, Ciudad Universitaria, Edificio 112-A, 72570 Puebla, Mexico*
[4] *Bonelli's Eagle Study and Conservation Group, Apdo. 4009, 30080 Murcia, Spain*
[5] *Departamento de Ecología e Hidrología, Universidad de Murcia, Campus de Espinardo, 30100 Murcia, Spain*
[6] *Sebero Otxoa 45 5 B, 48480, Arrigorriaga, Spain*

To use vocalizations properly for the estimation of owl population size, it is important to identify how environmental factors affect owl calling behaviour. Here, we analyse how intrinsic and extrinsic factors modify the vocal activity of Tawny Owls *Strix aluco* in two areas of northern Spain. From March 2013 to May 2015, we radiotracked 20 Tawny Owls and also undertook a systematic survey in which we collected data on spontaneous vocal activity (hoot/call) of the tagged owls, plus their mates and neighbours (36 untagged owls). After 223 nights in Valle de Mena and 224 in Duranguesado we obtained a total of 8791 records of vocal activity. The annual proportion of surveys on which an owl called was 6.3% and did not differ between the study areas. Vocal activity of Tawny Owls varied with sex, annual cycle stage and weather. Male owls were significantly more vocal than females year-round, and vocal activity peaked during the incubation and post-breeding periods. Wind and rain adversely affected vocal activity of both sexes throughout the year. Tagged owls were detected more often than untagged owls, which we interpret as an observer effect because the systematic survey ensured that short distances to tagged owls increased the probability of detecting vocal activity. In fact, 2.8% of variation in vocal activity was due to detectability differences between tagged and untagged owls. We conclude that if fieldwork is carried out during the optimum period of the year for vocal detection (i.e. incubation, which in our case was around mid-April), and under good weather conditions (dry and calm nights), censuses based on spontaneous vocal activity would detect only approximately 12% of the true Tawny Owl population.

Keywords: detection probability, long-term census, observer capacity, rain, survey methods, systematic surveys, wind vocal activity.

Accurate estimates of the distribution and abundance of animal species are crucial to determine their conservation status and to design monitoring and conservation programmes (Noon *et al.* 2012). However, such estimates are often difficult to obtain for secretive or cryptic species with low detection probabilities (MacKenzie *et al.* 2002) or those that occur in inaccessible or remote areas (Crampton *et al.* 2017). Many of these species can be detected by sound (e.g. songs, calls), which is often used for population assessment (Dawson & Efford 2009). By using both spontaneous and elicited voices, wildlife biologists take

*Corresponding author.
Email: zuberogoitia@icarus.es

advantage of vocal recordings to census populations of species, such as owls or nightjars, whose behaviour or ecology reduce their detectability during traditional surveys (Delport *et al.* 2002, Zwart *et al.* 2014). Nevertheless, controversy exists regarding the use of spontaneous or broadcast calls. For several owl species, better results have been obtained using broadcasting methods than simply registering spontaneous calls (e.g. Martínez & Zuberogoitia 2003, Mori *et al.* 2014, Worthington-Hill & Conway 2017) and audio playbacks have the potential to elicit a response from otherwise silent birds. Consequently, playback methods have been widely applied for censusing owl populations and developing ecological and behavioural studies (Zuberogoitia & Campos 1998, Barnes & Belthoff 2008, Kajtoch *et al.* 2016, Tempel *et al.* 2016). On the other hand, these methods could induce individuals to move beyond their normal, defended area, causing bias in population estimates (Anich *et al.* 2009). Moreover, national or large-scale surveys of owls using playback are not practical because of difficulties in standardizing sound conditions such as call quality or volume that might affect owl responsiveness (Freeman *et al.* 2006). Currently, several national monitoring projects use spontaneous calls (e.g. Canada, Takats *et al.* 2001; UK, Freeman *et al.* 2006; Spain, Noctua 2017).

Because vocalizations are used to estimate owl populations, it is important to identify environmental factors affecting owl calling (Conway *et al.* 2008). This is especially true for studies that compare population estimates across space or time (White 2005, Conway *et al.* 2008) and is important to correct for biases in detecting secretive and inconspicuous species (Manning 2011). Vocal activity in animals depends on (1) population density (more individuals not only calling at higher densities but also more frequently; Martínez & Zuberogoitia 2003, Nijman 2007, Laiolo & Tella 2008); (2) annual cycle stage (with animals calling more frequently during the mating and/or the breeding season; Zuberogoitia *et al.* 2011, Mori *et al.* 2014); and (3) environmental conditions (e.g. rain and wind; Francis *et al.* 2011a,b). Some bird species may develop behavioural responses to adapt song parameters to environmental noise (e.g. producing higher-frequency songs; Szymański *et al.* 2017) or adverse weather conditions (e.g. heavy rain, strong wind and low temperatures; Clark & Anderson 1997, Takats & Holroyd 1997, Lengagne & Slater 2002, Kissling *et al.* 2010).

Lack of information on vocal behaviour of the target species in large-scale surveys may result in large datasets with skewed data that require assumptions in order to be analysed (Blanco *et al.* 2012). In reality, detection of a target species depends on (1) availability (i.e. the presence of the species in the surveyed area during the time of the survey); (2) cue production (i.e. whether an owl that was available vocalized during the survey); and (3) detectability (i.e. whether an owl that was available and vocalized during the survey was actually heard by the surveyor; Kissling *et al.* 2010). In this context, we developed a field study to test how both intrinsic (species density, sex, and annual cycle stage) and extrinsic factors (i.e. weather) influenced the vocal activity of Tawny Owls *Strix aluco*, and to quantify our ability to detect owls known to be present through spontaneous calls.

METHODS

Study areas

The study was conducted in Valle de Mena (Burgos; 43°08′09″N, 3°19′44″W) and Duranguesado (Bizkaia; 43°11′36″N, 2°36′27″W) in northern Spain. The two areas have an oceanic climate, with mild temperatures and high precipitation rates. Valle de Mena (1942.6 ha) is a heterogeneous mountain landscape (319–1343 m a.s.l.) dominated by grass-fields for cattle (34.46%), surrounded by large deciduous forests (43.16%; *Quercus petraea* and *Quercus faginea*) in the valley, pine plantations (18.5%; *Pinus radiata*) on the lower slopes and beech/oak forests (3.88%; *Fagus sylvatica* and *Quercus pyrenaica*) on the upper mountain slopes. Most of the deciduous forests in the lower valley are younger than 50 years, whereas forests in the upper mountains are older than 100 years. Human population is concentrated in three small villages at the bottom of the valley, which is crossed by one small road, whereas slopes only have forest tracks. Although Duranguesado (1441.7 ha; 118–1026 m a.s.l.) is also a rural area, the human population is bigger, with small towns surrounded by isolated houses with small grass-fields for cattle, and orchards. Deciduous forests are almost absent (11.67%), with small patches of oak *Quercus robur* and beech *F. sylvatica* forest, while most of the landscape is dominated by fragmented patches of pine plantations (40.68%; *Pinus* *radiata*), including clear-cuts and selectively logged (thinned) areas. The first rotation of felling of pine stands occurs at 30–40 years of age. The landscape has an extensive network of roads and forest tracks.

Trapping and handling Tawny Owls

Using mist-nets and broadcasting conspecific vocalizations, we successfully trapped and radiotagged 20 Tawny Owls (11 males and 9 females, Table S1), 10 individuals per study area. Trapped individuals were ringed, measured and fitted with a 13.39-g radio-transmitter (TW3 single celled tag; Biotrack Ltd, Wareham, UK), attached as a backpack harness made from Teflon ribbon. Gender and age determination was carried out following Martínez *et al.* (2002) and Zuberogoitia *et al.* (2018), as well as gender determination of tagged and untagged owls using vocal discrimination between the sexes (Galeotti 1998, Zuberogoitia 2002). After 20–30 min of handling, all Tawny Owls were safely released at their capture sites.

We assigned identity of untagged owls using a combination of: (1) individually distinct hoots that remain stable over the time and are essential for individual recognition (Galeotti & Pavan 1991, Galeotti 1998), (2) their territory location with respect to the tagged owls and (3) their behaviour with respect to tagged owls; for example, the home-ranges of mates overlap and they usually hoot close each other (Sunde & Bølstad 2004), and there are vocal interactions along boundaries between neighbours (Galeotti 1994).

Field monitoring

Tagged Tawny Owls were radiotracked from 1 March 2013 to 17 May 2015 in Valle de Mena, and from 9 October 2013 to 4 May 2015 in Duranguesado. A hand-held, three-element Yagi antenna, plus a TRX-1000S (Wildlife Materials Inc., Carbondale, IL, USA), an RX8910 and/or an RX-98H receiver (Televit International AB) were deployed to locate the tagged owls. We attempted to find each radiotagged owl on at least three nights per week, independently of weather conditions (including snowstorms and strong winds). To avoid bias due to autocorrelation (Kenward 2001), the activity of each owl was surveyed only once per night. To obtain accurate locations (< 10 m^2) of each individual, we applied the point sampling method, using homing and triangulation techniques. Thus, to detect vocal activity, we maintained distances between the observer and the tagged owls that were short enough (25–100 m) to detect vocalizations but long enough to avoid disturbance by the observer. In each survey, we noted whether the focal tagged Tawny Owl hooted/called (vocal activity = 1) or remained silent (vocal activity = 0). Surveys of vocal activity of tagged owls were considered ‘controlled surveys’ because we controlled for availability (*sensu* Kissling *et al.* 2010) by confirming the presence of the target species within the surveyed area. Controlled surveys began at dusk sometimes 1–2 h later. To avoid possible behavioural biases, the order in which owls were surveyed was varied throughout the study. During each controlled survey, we registered the vocal activity of the target individuals, and also of their mates and neighbours (whether tagged or not). We covered the entire study area for tagged owls every night. The average field sampling period (mean ± sd) was 98.2 ± 71.2 min per night in Valle de Mena and 100.6 ± 49.3 min per night in Duranguesado. In total, we monitored vocal activity of 10 tagged and 13 untagged Tawny Owls in Valle de Mena, and 10 tagged and 23 untagged Tawny Owls in Duranguesado. After 223 and 224 nights in Valle de Mena and Duranguesado, respectively, we had obtained 8791 records of vocal activity.

Data on owl identity, time, location, individual behaviour, vocal activity and weather conditions were recorded in the field and transferred to a GIS database (*Quantum GIS*; version 2.18.1). Weather conditions (precipitation, temperature and wind speed) for every 10-min period of each controlled survey were also obtained from two meteorological stations located within the study areas (www.euskalmet.euskadi.net) and we used our field notes to corroborate the meteorological data.

Two of the transmitters failed during the study period, one of them (BF4O) after 2 months and the other (DF2G) starting just 1 day after trapping, providing only irregular data. All the tracked owls except BF4O were alive at the end of the study.

Data analysis

We divided the Tawny Owl annual cycle into the following four periods: (1) pre-breeding, from November to January (Zuberogoitia & Martínez

2000); (2) incubation, from February to April, and including the pairing, laying and incubation periods (average laying date in our study area is 15 March ± 38.03 sd days; Zuberogoitia 2011); (3) chick-rearing (owlets), from May to July, when adult pairs are attending offspring; and (4) post-breeding, from August to October, the period of juvenile dispersal.

To test the association of intrinsic and extrinsic factors with vocal activity of Tawny Owls, we used generalized linear mixed models (GLMMs) with a binomial error distribution on the response variable (1 = hooting/calling; 0 = silent) and a logit-link function. We considered sex and annual cycle stage (i.e. period) as intrinsic categorical fixed effects. In addition, we considered study area as a categorical fixed effect reflecting differing population densities, and weather covariates as extrinsic predictors because they could affect vocalization rates and detectability of calls. The weather covariates were rain (L/m^2), wind speed (km/h) and temperature (°C). There was no collinearity between weather variables (pairwise correlation < 0.2 for all cases). Finally, we considered the tracked status of each Tawny Owl (tagged or untagged) as a fixed effect in order to test whether the close approach that was guaranteed to tagged owls increased the probability that vocalizations were detected. Individual owl identity entered the GLMMs as a random term (Table S1).

We applied an information theoretic approach and used Akaike's information criterion (AIC; Burnham & Anderson 2002). We first fitted the saturated (intercept and all main effects) model and then excluded explanatory variables that reduced the performance of the model in terms of AIC, one by one in a backward, stepwise procedure. We computed all our models, which were fitted by maximum likelihood methods using the Laplace approximation, using the 'glmer' function as implemented in the 'lme4' package (Bates *et al.* 2015) for R (R Core Team 2015). We also calculated model weight and the coefficient of determination explained by each model (Burnham & Anderson 2002). To this end, we followed the method proposed by Nakagawa and Schielzeth (2013) as implemented in the R package 'PiecewiseSEM' (Lefcheck 2015). Thus, we divided the amount of observed variation explained by the best model into a marginal coefficient of determination [R^2_m], attributable to fixed factors, and a conditional coefficient of determination [R^2_c], which includes both fixed and random factors. To estimate the amount of R^2 explained exclusively by one variable of interest [R^2_{part}], we computed the difference between the R^2_m of the best model and the R^2_m of the same model, excluding the variable of interest.

RESULTS

Twelve territorial pairs of Tawny Owls were registered in Valle de Mena (population density = 0.62 pairs/km^2) and 17 pairs in Duranguesado (population density = 1.18 pairs/km^2; Table S1).

Overall, annual vocal activity of Tawny Owls was low throughout the study: 6.3% ± 6.2% (range = 0.5%–28.5%, Table 1). Contrary to our expectations, vocal activity did not differ between the study areas, despite contrasting population densities (Tables 2 and 3). Vocal activity was influenced by both intrinsic (sex and annual cycle stage) and extrinsic (weather) factors. In addition, vocal activity was higher in tagged than in

Table 1. Spontaneous vocal activity of Tawny Owls in the two study areas (Valle de Mena and Duranguesado), classified by tracking status (tagged or untagged) and sex

	Valle de Mena		Duranguesado	
	Mean ± sd (range)	Sample size (*n*)	Mean ± sd (range)	Sample size (*n*)
Tagged				
Male	13.1 ± 10.8% (1.6–28.5%)	5	13.0 ± 7.9% (0.8–28.0%)	6
Female	3.3 ± 1.7% (0.8–5.0%)	5	6.8 ± 3.8% (3.9–12.4%)	4
Untagged				
Male	6.4 ± 6.6% (2.3–19.8%)	6	5.0 ± 4.1% (0.6–14.1%)	11
Female	4.9 ± 4.6% (0.5–12.2%)	7	3.0 ± 2.5% (0.6–7.7%)	12

Data show mean percentage of positive detections on controlled surveys ± standard deviation, range and number of monitored individuals per group (tagged and untagged).

Table 2. Correlates of spontaneous vocal activity of Tawny Owls from a GLMM

Model	Model structure	df	AIC	ΔAIC	wAIC	$R^2_{\mathrm{GLMM}(m)}$	$R^2_{\mathrm{GLMM}(c)}$
0	Null model	2	3885.7	127.88	0		0.22
1	Saturated model	11	3761.4	3.59	0.108	0.18	0.31
2	Saturated model-T	10	3759.7	1.96	0.273	0.18	0.31
3	Saturated model-(T and Areas)	9	3757.8	0.00	0.727	0.18	0.31

Model selection followed a backward, stepwise procedure. The saturated model included intrinsic (sex and period) and extrinsic (study area and weather: temperature (T), rain and wind) factors as well as tracking status (tagged or untagged) which could affect the vocal activity of Tawny Owls. ΔAIC: AIC difference between the current model and that with the lowest AIC value; wAIC: Akaike weight, df: degrees of freedom; $R^2_{\mathrm{GLMM}(m)}$: marginal variance, attributable to fixed factors; $R^2_{\mathrm{GLMM}(c)}$: conditional variance, which includes both fixed and random factors.

Table 3. Parameter estimates for the most parsimonious model presented in Table 2.

Variable	Estimate	se	Z value	P	$R^2_{\mathrm{(part)}}$
(Intercept)	−3.04	0.21	−14.18	<0.001	
Factor(tracked)tagged	0.76	0.25	3.03	<0.01	0.028
Factor(sex)male	0.67	0.24	2.73	<0.01	0.024
Factor(period)owlets	−0.60	0.13	−4.55	<0.001	–
Factor(period)post-breeding	−0.10	0.11	−0.86	0.39	0.023
Factor(period)pre-breeding	−0.75	0.13	−5.75	<0.001	–
Rain	−4.06	0.92	−4.43	<0.001	0.105
Wind	−0.03	0.01	−4.07	<0.001	0.018

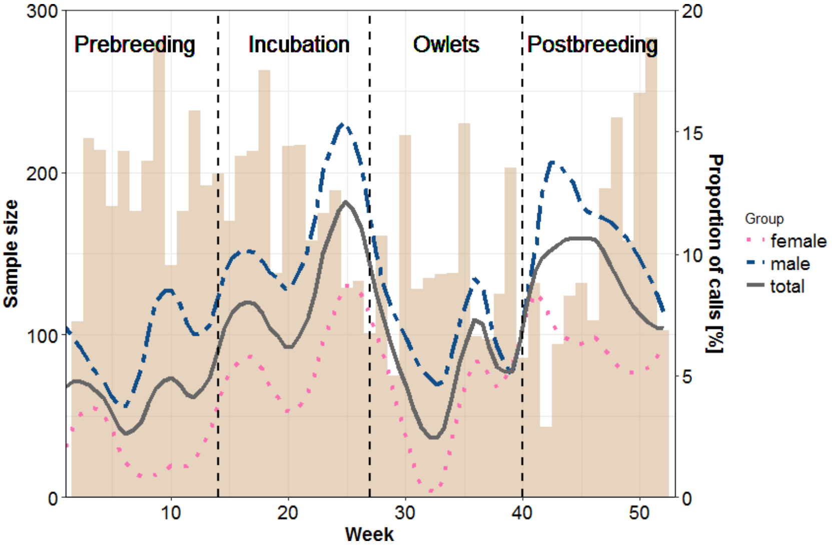

Figure 1. Proportion of vocal activity of Tawny Owls throughout the annual cycle (pre-breeding, incubation, owlets and post-breeding). The plot shows the ratio between the number of calls of each sex and the corresponding sample size (number of controlled surveys) on a weekly basis. Week 1 is the first week of November. Histograms show the number of controlled surveys (sample size).

untagged owls (Tables 1 and 3), as expected from the guaranteed detection and close approach to tagged owls. The most parsimonious model included all the predictor variables except for temperature and study area (Table 2). This model explained 31% of the total variability in the response data ($R^2_c = 0.31$), and the part attributable to fixed factors alone was $R^2_m = 0.18$.

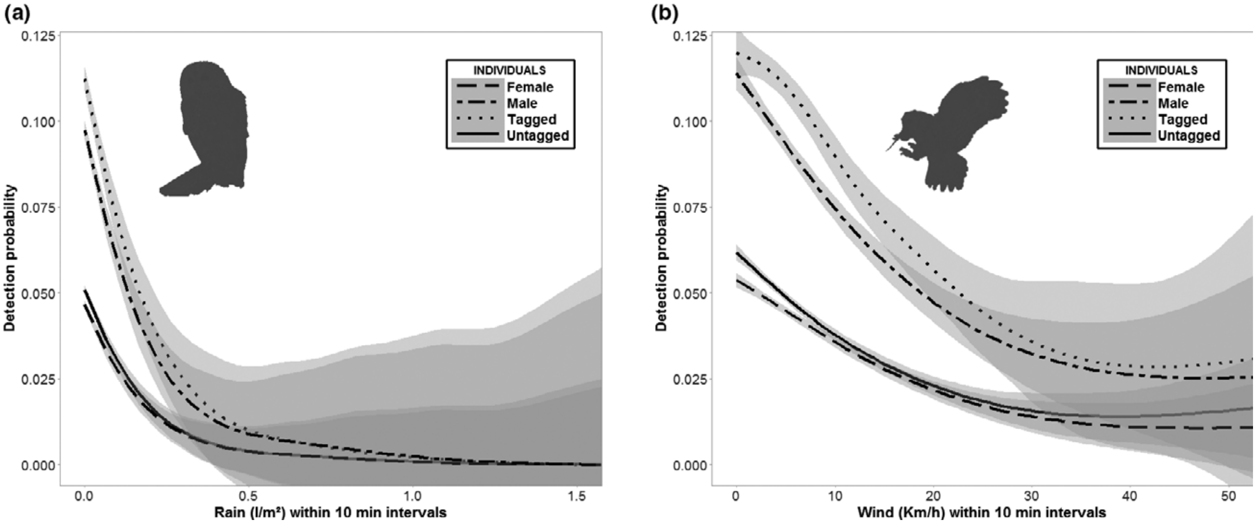

Figure 2. Detection probability of spontaneous calls of Tawny Owls in relation to rain (a) and wind speed (b) values recorded during the 10-min observation period. Detection probability (fitted values) was obtained from the most parsimonious model (model 3). Plots show differences between sexes (male and female) and tracked condition (tagged or untagged).

Male owls were more vocal than females but sex explained only 2.4% of the variation in vocal activity. Vocal activity was higher during the incubation and post-breeding periods than during the chick-rearing period and the first weeks of the pre-breeding period (Fig. 1), but the R^2_{part} of annual cycle stage was also very low (2.3%). Wind speed and rain affected vocal activity of both sexes throughout the annual cycle (Fig. 2). Rain and wind had a strong negative effect on the probability of detecting vocal activity (Fig. 2). Rain alone explained 10.5% of the total variation in the probability of vocal detection of an owl, whereas wind only explained 1.8%. Finally, the effect of owl tagging explained 2.8% of the total variability in the response data. Temperature did not show an effect on vocal activity because Tawny Owls had two different peaks of vocal activity through the year (Fig. 1), one in the coldest period (winter) and the second just at the end of the summer.

DISCUSSION

Our results show that vocal activity of the studied Tawny Owls was influenced by a combination of both extrinsic and intrinsic factors (i.e. weather conditions, and sex and annual cycle stage, respectively), plus the effect of tagging rendering owl vocalizations more easily detectable to observers due to the close approach to owls known to be present. In contrast to the telemetry study by Sunde and Bølstad (2004), in which males and females vocalized equally, our males were significantly more active than females year-round. When playback methods have been used, some authors have found that both males and females exhibit similar calling rates (Galeotti & Pavan 1993, Appleby *et al.* 1999), whereas other studies have reported that females exhibited significantly lower calling rates than males (Zuberogoitia & Martínez 2000, Worthington-Hill & Conway 2017). In fact, sex differences in spontaneous vocal activity are common in owl species (Martínez & Zuberogoitia 2002, Flesch & Steidl 2007, Barnes & Belthoff 2008, Korpimäki & Hakkarainen 2012).

In agreement with previous studies (Southern 1970, Zuberogoitia & Martínez 2000), Tawny Owls in our study sites showed two main peaks of vocal activity throughout the annual cycle, one during the ‘incubation’ period and another during the ‘post-breeding’’ period. The first period included courtship, laying and incubation, when both sexes showed the highest vocal activity. The same pattern was observed in a telemetry study of Flammulated Owls *Psiloscops flammeolus*, for which vocal activity was highest during pairing and incubation (Barnes & Belthoff 2008). Later in the year, during the owlet-raising period, adults invest more time hunting for and feeding offspring, and reduce vocal activity to occasional hooting, which is consistent with other owls (e.g. Ferruginous Pygmy Owl *Glaucidium brasilianum cactorum*; Flesch & Steidl 2007). During the dispersal of juveniles, adult Tawny Owls showed a second peak of hooting activity, probably related to territorial defence and re-organization of the population (Zuberogoitia & Martínez 2000, Sunde & Bølstad 2004). In autumn, territory ownership is asserted by newcomers or reasserted by territorial birds. Thus, there is a peak in Tawny Owl hooting to claim territory possession and prevent juvenile and floater owls from settling in occupied territories (Southern 1970).

Weather conditions affected vocal activity of Tawny Owls, probably by affecting the ability of owls to hear each other and inhibiting the calling behaviour of some individuals (Morrell *et al.* 1991, Braga & Motta-Junior 2009). Wind and rain produce noise which also influences both detection and discrimination of bird voices by the receiver (either conspecific individuals or human observers; Lengagne *et al.* 1999, Kissling *et al.* 2010). Fröhlich and Ciach (2018) showed that the mean audibility range for humans of calling Tawny Owls in urban noisy areas was 313 m. Lengagne and Slater (2002) reported that territorial calls of forest-dwelling Tawny Owls could be discriminated from 614 m in dry conditions but only 74 m during rain (i.e. an eightfold difference). In this paper, we show how the probability of detecting the vocal activity of Tawny Owls fell in soft rain, reaching almost zero with rain values above an average of 0.3 L/m^2 in 10-min intervals, whereas the reduction in detection probability was less pronounced in response to increasing wind speed. In fact, it was possible to detect Tawny Owls with wind speeds over 50 km/h. Indeed, we even recorded Tawny Owls hooting during heavy rain and strong winds, mainly during the ‘incubation’ period (winter), but the detection range in such situations was only a few tens of metres (Fig. 2). Accordingly, of 22 pairs of Tawny Owls studied by Lengagne and Slater (2002), 82% and 86% of birds apparently called on two dry and calm nights, but only 14% and 5% on two rainy nights. However, in this case it is difficult to determine how much of this reduction is due to the presence of fewer vocalizing owls or to the observer’s inability to hear those vocalizations (Kissling *et al.* 2010).

Our results suggest that bias in detecting owls in poor weather is also caused by observer failure to detect owls. Our controlled surveys ensured short distances to tagged owls, which then increased detection rate of vocal activity relative to that for untagged owls. Telemetry studies of owls via the homing technique require short distances to ascertain the position of the tagged owl in the dark. During telemetry surveys, vocal activity of the target owl is easy to detect because short distances ensure detection of even soft, low-volume calls. Conversely, observers could not guarantee to approach untagged owls as closely, so that these birds were more likely to be outside detection range when vocalizing (e.g. Berg & Stork 2004, Padgham 2004, Slabbekoorn *et al.* 2007).

According to Rosenstock *et al.* (2002) the probability of detecting a common diurnal land bird at any given perpendicular distance varies according to numerous factors, including weather, observer experience and the conspicuousness of the target species. These factors are even more important at night, when darkness limits the main sense of human observers. During nocturnal surveys there is a high dependence on auditory detection, which depends on how well the information is transmitted through the environment and discriminated by the receiver (Lengagne & Slater 2002, Flesch & Steidl 2007). Human listening ability is conditioned by both environmental conditions, which limit audible range, and the hearing ability and previous experience of the observer (e.g. intuitions about what information might be available to be heard; Gaver 1993). As found by Reid *et al.* (1999), it is therefore possible that detection rates in our study might be greater than in large-scale surveys involving inexperienced observers.

Our results have important implications for the design of future surveys to estimate the presence of Tawny Owls in large areas. It would be desirable to calibrate our estimates of the distribution and abundance of the studied species, not only for population trend analysis but also for national breeding atlases and studies of habitat associations (Freeman *et al.* 2006). We must consider that censuses based on spontaneous vocal activity may detect no more than *c.* 12% of the true population even when the census is carried out in the best stage of the annual cycle (i.e. the ‘incubation period’), which in our case was around mid-April, and under good weather conditions (dry and calm nights). Moreover, we would need to adjust the error associated with the use of large numbers of non-experienced observers in any large-scale census. Observer ability to hear owl vocalizations is critical and must be considered an important factor when selecting personnel to develop field surveys (Barnes & Belthoff 2008).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Data of monitored Tawny Owls in the two study areas ('Valle de Mena' and 'Duranguesado').