


# Factors influencing detectability and responses of Elf Owls to playback of conspecific vocalizations

Aaron D. Flesch,<sup>1,4</sup>  John Boone,<sup>2</sup> David Vander Pluym,<sup>2,5</sup> and Laura Beth Sabin<sup>3</sup>

<sup>1</sup>*School of Natural Resources and the Environment, University of Arizona, The Desert Laboratory on Tumamoc Hill, 1675 West Anklam Road, Tucson, Arizona 85745, USA*

<sup>2</sup>*Great Basin Bird Observatory, 1755 East Plumb Lane, Reno, Nevada 89502, USA*

<sup>3</sup>*Bureau of Reclamation, Lower Colorado River Multi-Species Conservation Program, P.O. Box 61470, Boulder City, Nevada 89006, USA*

Received 27 April 2021; accepted 14 June 2021

**ABSTRACT.** Broadcasting conspecific vocalizations is commonly used to survey secretive, inconspicuous, and uncommon species of birds, but information about how response behaviors vary across temporal and broad spatial gradients is limited for most species despite the importance of such data for guiding survey efforts. We assessed response patterns and detection probability of Elf Owls (*Micrathene whitneyi*) across broad ecological gradients in the Sonoran and Chihuahuan deserts of Arizona that spanned much of their breeding range in the United States. From March to June 2015–2017, we examined response times and distances of an estimated 587 Elf Owls detected during playback surveys at 1488 stations along 121 transects (193 km). Additionally, from April to June 2010–2011 and 2016–2017, we examined detection probability during 255 playback experiments at occupied nests and modeled the influence of spatial, temporal, moon illumination, vegetation, conspecific densities, and weather-related factors on detection probability. During transect surveys, response times were rapid (mean = 2.0 min), with 75% of detections within 3 min. Owls often responded close to broadcast stations (mean = 103 m), with only 25% of responses at distances > 140 m and none > 400 m. Response times were faster and from greater distances in the more arid western portion of our study area. During playback experiments at nests, detection probability averaged 0.65 and declined with increasing time of night, time of season, and noise levels. Detection probability also declined with increasing distance from target owls, but at lower rates in the western than the eastern portion of our study area. Spatial variation in detectability was primarily due to surveyors failing to detect responding owls in areas with higher owl densities in more resource-rich environments in the east, not differences in underlying responsiveness. Our results suggest that 5 or 6 min surveys within ~4 h of sunset and early in the breeding season will be most effective and that spacing survey stations from 100 to 150 m apart, depending on local densities and study objectives, is adequate for estimating occupancy and abundance with relatively low false absence rates.

**RESUMEN.** Factores que influyen en la detectabilidad y las respuestas de los tecolotes enanos al reproducción de vocalizaciones de conespecíficos

La transmisión de vocalizaciones conespecíficas se usa comúnmente para inspeccionar especies de aves reservadas, inconspicuas y poco comunes, pero la información sobre cómo los comportamientos de respuesta varían a lo largo de gradientes temporales y espaciales amplios es limitado para la mayoría de las especies a pesar de la importancia de estos datos para orientar los esfuerzos de muestreo. Evaluamos patrones de respuesta y probabilidad de detección del Tecolote enano (*Micrathene whitneyi*) a través de gradientes ecológicos amplios en los desiertos Sonorenses y Chihuahuenses de Arizona que abarcaban gran parte de su rango de reproducción en los Estados Unidos. De marzo a junio de 2015–2017, examinamos los tiempos y las distancias de respuesta de un estimado de 587 de tecolotes enanos detectados durante censos de reproducción de vocalizaciones en 1488 estaciones a lo largo de 121 transectos (193 km). Adicionalmente, de abril a junio de 2010–2011 y 2016–2017, examinamos la probabilidad de detección durante 255 experimentos de reproducción de vocalizaciones en nidos ocupados, y modelamos la influencia de factores espaciales, temporales, de iluminación lunar, de vegetación, de densidades conespecíficas y relacionadas con el clima sobre la probabilidad de detección. Durante los censos de transectos, los tiempos de respuesta fueron rápidos (media = 2.0 min), con un 75% de detecciones en 3 min. Los tecolotes a menudo respondían cerca de las estaciones de transmisión (media = 103 m), con sólo el 25% de respuestas a distancias > 140 y ninguna a > 400 m. Los tiempos de respuesta fueron más rápidos y desde mayores distancias en la parte occidental más

<sup>4</sup>Corresponding author. Email: flesch@email.arizona.edu

<sup>5</sup>Present address: Museum of Natural Science and Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA

árida de nuestra área de estudio. Durante los experimentos de reproducción de vocalizaciones en nidos, la probabilidad de detección fue de un promedio de 0.65 y disminuyó al avanzar la noche, la temporada y al aumentar los niveles de ruido. La probabilidad de detección también disminuyó al

augmentar la distancia a los tecolotes objetivo, pero a tasas más bajas en la parte oeste que en la parte este de nuestra área de estudio. La variación espacial en la detectabilidad se debió principalmente a que los censistas fallaron en detectar tecolotes respondiendo en áreas con mayor densidad de tecolotes en entornos más ricos en recursos en el este, no a diferencias en la capacidad de respuesta subyacente. Nuestros resultados sugieren que 5 o 6 min de censos dentro de ~4 h antes de la puesta del sol y temprano en la temporada reproductiva serán los más efectivos, y que un espaciamiento de las estaciones de censo de 100 a 150 m, dependiendo de las densidades locales y los objetivos de estudio, es adecuado para estimar la ocupación y abundancia con tasas de falsas ausencias relativamente bajas.

*Key words:* broadcast surveys, detection probability, ecological gradients, *Micrathene whitneyi*, response distance, response time, Sonoran desert, tape playback surveys

Broadcasting conspecific vocalizations can increase detection rates compared to non-elicited surveys for many bird species and, hence, is a frequently used technique for surveying raptors, marsh birds, and other cryptic species (Fuller and Mosher 1981, McGarigal and Fraser 1985, Mosher et al. 1990, Gerhardt 1991, Sutherland et al. 2004, Conway and Gibbs 2005). The relationship between response rates (e.g., raw number of respondents per unit effort) obtained during these surveys and true detection probabilities (e.g., probability of detecting an individual that is present during sampling), however, is poorly understood for many species. Detection probabilities and response rates vary with a range of spatial, temporal, observer, and survey- and weather-related factors (Fuller and Mosher 1987, Hardy and Morrison 2000, Conway and Simon 2003, Seavy 2004, Flesch and Steidl 2007, Barnes and Belthoff 2008, Conway and Gibbs 2011). Understanding these patterns is fundamental for designing reliable survey and monitoring programs because when detectability is  $< 1.0$ , uncorrected estimates may bias inferences (Pollock et al. 2002, Tyre et al. 2003).

An aspect of variation in detection probability that has received little attention in terrestrial systems is spatial variation across broad geographic regions that may differ in climate, vegetation, and densities of focal species (Conway and Gibbs 2011, Hagihara et al. 2018). In contrast, temporal variation in detection probability linked to differences in territorial, breeding, and other behaviors across time of day or night and season has been much better studied (Kennedy and Stahlecker 1993, McLeod and Anderson 1998, Flesch and Steidl 2007, Conway et al. 2008), likely because temporal gradients are less challenging to sample across than broad geographic regions. Regardless, protocols

developed in one area of the geographic range of a species are often applied elsewhere without determining if and how detection probability might vary spatially, potentially influencing inferences from statewide and multi-regional survey and monitoring efforts. If such variation exists and the ratio of a derived index (e.g., total observed count) and true parameter value (e.g., abundance) varies systematically across space, inferences about populations could be biased (Yoccoz et al. 2001, Williams et al. 2002, Bart et al. 2004).

Elf Owls (*Micrathene whitneyi*) are nocturnal insectivores that nest in cavities in arid and semi-arid environments in the southwestern United States and adjacent northwestern Mexico (Henry et al. 2020). As likely the most abundant raptor in the Arizona Uplands subdivision of the Sonoran Desert, Elf Owls can occur at remarkably high densities in desert woodlands with giant saguaro cacti (*Carnegiea gigantea*) that provide nest cavities (Glinski 1998, Henry et al. 2020). In the northwestern portion of their breeding range, populations of Elf Owls have declined to near-extirpation levels due to loss of gallery forests along the lower Colorado River and are listed as endangered in California and as a covered species under the Lower Colorado River Multi-Species Conservation Program (Halterman et al. 1989, Rosenberg et al. 1991, Lower Colorado River Multi-Species Conservation Program 2004). As a result, efficient and reliable survey methods are needed to address conservation goals. Although broadcasting conspecific vocalizations increases response rates of Elf Owls (Hardy and Morrison 2000), no data are available concerning detection probability, factors that influence detection probability, or the degree to which response behaviors might vary spatially.

In the Sonoran Desert, Elf Owls occur across broad gradients in aridity and

vegetation structure. Areas at lower elevations in the northern and western portions of their distribution are more arid, often with less vegetation, especially in uplands, whereas higher-elevation environments to the east and south are less extreme (Shreve 1951, Brown 1982). These elevation, climate, and vegetation gradients can influence habitat use and the relative importance of resources to wildlife in these systems (Flesch and Steidl 2010) and may also contribute to variation in detection probability.

We examined the responses patterns of Elf Owls to broadcasts of conspecific calls across broad environmental and spatial gradients that spanned nearly the entire breeding range of the species in the Sonoran and Chihuahuan deserts of the southwestern United States. We also estimated detection probability during playback experiments at occupied nests across the study region and modeled the influence of spatial and temporal factors, vegetation obstruction, moon illumination, weather, and conspecific densities on detection probability, and assessed the implications of our results for surveys and population estimation.

## METHODS

**Study area.** We surveyed across lowland (~150–1250 m asl) western and southeastern Arizona from March to June 2010–2011 and 2015–2018 (Fig. S1). Sites in the western portion of our study area were mainly in the Bill Williams River watershed. This region is in the Lower Colorado River Valley subdivision of the Sonoran Desert where upland vegetation cover was lower and trees are often restricted to riparian areas. Sites in the eastern portion of our study area, in contrast, were in the Gila, Salt, and Verde river watersheds at higher elevations. This region spans areas of the Arizona Upland subdivision of the Sonoran Desert, semi-desert grasslands, and Chihuahuan desertscrub and has greater tree cover in uplands and more saguaro cacti. Riparian vegetation in both regions was dominated by cottonwood-willow (*Populus fremontii*, *Salix* spp.), mesquite (*Prosopis* spp.), and tamarisk (*Tamarix* spp.) woodland. Average annual rainfall varied from ~10–25 cm in the arid west to ~30–40 cm in the more mesic east.

**Design and surveys.** We used call broadcasts in two different ways during the breeding season to assess different aspects of responsiveness of Elf Owls. First, we surveyed along transects to assess response times (e.g., time from initiation of broadcast to first response), response distances (e.g., distance between surveyors and initial location of responding owls), and overall response rates of Elf Owls and to locate sites for experimental trials. Second, we conducted playback experiments at Elf Owl nests that we confirmed were occupied to estimate detection probability and assess how it varied with spatial, temporal, and other factors such as moon illumination, vegetation density, weather, noise, and local conspecific densities. Surveys along transects were implemented only once per site across a larger number of sites we selected across the study area. In contrast, experiments at nests involved more intensive repeated test trials at the same nests replicated at five distances (i.e., 50, 100, 150, 200, and 250 m) at fewer sites selected to capture a broad range of environmental variation across the study region.

We surveyed along transects of call broadcast stations spaced at 150-m intervals and surveyed by single surveyors. Locations for these surveys were selected non-randomly in accessible areas across the study area and included areas with broad gradients in vegetation structure. To select survey locations, we considered 12 survey strata across all possible combinations of three riparian vegetation types (1-exotic riparian dominated by tamarisk, 2-xeric riparian dominated by mesquite, and 3-mesic riparian dominated by broadleaf trees), three upland vegetation types (1-desert woodland, 2-arborescent desertscrub, and 3-desert shrubland), and areas with and without saguaro cacti. Given greater interest and higher variability in the structure and composition of mesic riparian vegetation, we focused more sampling effort in this type than in exotic and xeric riparian vegetation. We arranged transects to sample both riparian and adjacent upland vegetation by “zig-zagging” linear transect segments at angles of  $\sim\pm 30^\circ$  orientation of the main stream channel and extending segments ~100 m into upland vegetation. The number of stations per transect ranged from three to 19 and averaged  $10.5 \pm 0.3$  (SE). Most surveys were conducted from

March to June 2015, with 8% during the same months in 2016–2017. All surveys began at dusk and continued for up to ~4 h after dusk.

At each station, we broadcast the common territorial chatter call of Elf Owls (song type A; Ligon 1968) at a volume of ~70 dB at 1 m from the broadcast speaker and at ~60 dB at 30 m with use of Fox Pro game callers. Call broadcasts at each station included an initial 60 s of passive listening, followed by three 1-min periods of alternating 25 s of broadcasted calls followed by 35 s of silence, and a final 60 s of passive listening. Each 25-s sequence of recorded calls included six chatter notes (see Ligon 1968: 16) recorded from a single individual in the western portion of the study area. In using just one recording from a single individual, we assumed particular characteristics of this owl's call did not influence our results, which seemed reasonable based on initial efforts with different call types. This total of 5 min per station generally included an additional 1–2 min, however, in the form of incidental passive listening while we recorded data and packed field gear, but was occasionally longer at the last station along transects. Although responses during these periods were rare, we considered them when evaluating response patterns because they included relevant information. For each owl response, we noted the time from the initiation of broadcasts to the response, the bearing, and estimated the distance from surveyors to each responding owl. We used these data together with information on response timing, simultaneous responses, and observations of owl behavior and movements to determine if owls observed along transects were the same or different individuals to minimize double counting and improve independence. We relied on simultaneous responses to differentiate individuals unless non-simultaneous responses were from locations significant distances (e.g., ~200 m) apart, and directions and timing of responses suggested they were from two or more individuals. To assure accurate estimates of response distances, we trained observers using owls at known distances at night and practiced estimation across different wind, noise, and vegetation conditions, and estimated distances > 100 m to the nearest 25–50 m. No surveys were conducted during periods of

continuous precipitation or when wind created consistent noise (e.g., > 12 km/hr).

Guided by results of our transect surveys, we selected a subset of occupied areas from across the study region for playback experiments. These experiments were conducted by both a surveyor who broadcast calls from a point at one of five fixed distances from nests (50, 100, 150, 200, and 250 m), and an observer positioned within 25 m of nests. We inspected cavities with a pole-mounted video camera to confirm nest contents before tests. We randomized the order of test distances at each nest, tested 92% of nests only once at each distance in a year, and conducted no more than one test per week at the same nest to minimize possible habituation to broadcasts. Before tests, we observed nests and areas around them for  $\geq 10$  min to confirm owl presence. We then initiated a standard 5-min call playback procedure as described above from one of the five predetermined test distances. Where necessary after surveys, we also listened for an additional 5 min to confirm owl presence and that responses were from target pairs and conducted observations and nest checks within 1 week of tests to confirm occupancy. Surveyors and observers stationed around nests independently recorded all Elf Owl responses during these periods, estimated positions of responding owls, and compared notes following each experiment. Tests were considered positive if surveyors independently detected target owls that observers confirmed were in fact the target pair, and only tests at sites known to be occupied were considered. Most playback experiments at nests were conducted from April to June 2016–2017, with 22% conducted during these same months during a pilot study in 2010–2011. During pilot efforts, playback experiments were conducted only at distances of 100 and 250 m from nests, response distances were not measured, and experiments were conducted at all times of night from dusk to dawn, such that 13% of all tests were implemented more than ~4 h after dusk.

**Environmental measurements.** We measured factors that we suspected might influence the detection process during playback experiments at nest sites. As spatial factors, we quantified large-scale geographic gradients across the study area by determining

longitude, latitude, and elevation, and a categorical factor that classified sites as either in the western or eastern portions of our study area. As temporal factors, we considered time of season (ordinal day) and time of night (minutes since sunset) at the start of experiments based on local sunset times. To describe survey conditions, we measured wind speed in six categories (0–2, 2–5, 6–12, 13–19, 20–29, and 30–39 km/hr) with handheld Kestrel weather meters and estimated noise levels in four general categories (0-quiet-minimal interference, 1-low-minor interference, 2-medium-significant interference, or 3-high-substantial interference) based on the degree to which noise in the surrounding environment interfered with listening for Elf Owls calls. To quantify moon illumination, we considered both moon phase and moon position because they are both linked to variation in ambient light levels, and classified illumination on a scale from 0 to 5, ranging from no illumination to full or gibbous moon > 30 degrees above the horizon (Table S1). To quantify vegetation obstruction, we visually estimated total volume of vegetation in the straight-line corridor between surveyors and nests in six classes (0–5, 6–20, 21–40, 41–60, 61–80, and 81–100%). When making these measurements, tree and shrub canopies were considered to have 100% volume despite variation in foliage volume. Finally, to describe conspecific densities, we determined the number of Elf Owl pairs within ~500 m of each focal nest in four categories (0, 1–2, 2–4, and  $\geq 5$  pairs) based on results from transect surveys, experiments at nests, and nest searches.

**Analyses.** To assess responses, we estimated response times and distances based on data from transect surveys across the study area and in the eastern and western portions of our study area, and compared estimates during transect surveys with those from playback experiments at nests to assess potential differences. For data gathered during transect surveys, only information from the estimated initial detection of each individual Elf Owl was considered to improve independence. Histograms, summary statistics, and *t*-tests were used to describe distributions and compare means.

To assess factors that influenced detection probability, we used data from playback experiments at nests to fit generalized linear

mixed models (GLMMs). We fit owl response or non-response during each test trial as a binomial response variable in a logistic regression framework and included the identity of each repeatedly tested focal pair as a random intercept. As potential explanatory factors, we fit the design factor test distance as a covariate in all models together with different additive combinations of other factors to produce a set of biologically plausible models. These factors included vegetation obstruction, time of season (ordinal day), time of night (minutes since sunset), wind speed, noise levels, moon illumination, and local density of Elf Owls. To assess potential variation in detection probability across space, we also considered the four spatial factors (e.g., longitude, latitude, elevation, and region). Because continuous spatial factors were highly correlated ( $r \geq 0.92$ ), we first compared full models with each spatial factor fit separately and in interaction with test distance and used the spatial factor that best described the data in all subsequent models. We treated noise levels, moon illumination, and wind speed as continuous factors because spacing between levels was equal or approximately equal and used the mid-point of the range of each vegetation obstruction category.

To guide model selection and assess evidence for different models and explanatory factors, we used AIC<sub>c</sub> and 95% CI of parameter estimates (Burnham and Anderson 2002). Because the effects of test distance and temporal factors could vary geographically, we considered interactions between these factors during initial model building steps. All other factors were not highly correlated ( $r \leq 0.42$ ) and thus considered together in models. We considered quadratic terms for time of night and ordinal day to assess whether responsiveness was higher near dusk and dawn and lower near midnight, or during specific seasons. Before modeling, histograms of all continuous factors were plotted to assess distributions, and vegetation obstruction was natural log transformed to reduce the influence of extreme values. To evaluate models, we plotted scaled residuals against fitted values, assessed patterns in the mean and variance of values and presence of outliers, and confirmed random effect variances were greater than zero (Bolker 2015). We also assessed classification accuracy by using

predicted probabilities to calculate the proportion of cases that were correctly classified assuming values  $\geq 0.5$  represented predicted responses. We used the lme4 library in R to fit GLMMs with maximum likelihood methods and adaptive Gauss–Hermite quadrature (Bates et al. 2015, R Development Core Team 2016).

Finally, we used estimates of detection probability to assess the number of survey events ( $X$ ) needed to achieve detection of all territorial owls based on the following equation:  $(1 - (1 - p)^X)$ . Estimates of detection probability ( $p$  = number of responses/number of test trials) from all response tests in each geographic region were used in calculations, as were averages of  $p$  at each test distance. Estimates are presented as means  $\pm$  SE.

## RESULTS

**Effort.** We surveyed 121 transects (192.8 km) and 1488 stations across nine watersheds between 140 and 1250 m in elevation (Fig. S1). We detected 918 Elf Owls representing an estimated 587 unique individuals, with one or more Elf Owls detected at 33.9% of stations and 59.5% of transects. Twice as many transects were occupied in the eastern than the western portion of our study region, with  $> 78\%$  of owls detected in the eastern portion. We conducted 255 playback experiments at 49 Elf Owl nests in 10 distinct portions of our study areas that spanned a broad range of elevations (140–1140 m asl). Within years, we conducted an average of  $4.6 \pm 0.1$  experiments per focal pair. Playback experiments at nests were conducted between 9 April and 29 June, with those in the west averaging  $16.4 \pm 2.2$  d earlier than in the east due to differences in breeding phenology.

**Detection patterns.** During transect surveys, Elf Owls were typically detected close to stations; median detection distance was 80 m, averaged  $103 \pm 3$  m overall, and only 25% of detections were at distances  $> 140$  m, with none detected  $> 400$  m away (Fig. 1). Response times were rapid, and the distribution was longer-tailed than that for distance; median response time was 1.6 min and averaged  $2.0 \pm 0.08$  min, with only 25% at times  $> 3$  min and 6.8% at times after the 5-min survey period (Fig. 1). Response times

averaged  $27.3 \pm 11.5\%$  faster in the west ( $1.6 \pm 0.2$  min) than the east ( $2.1 \pm 0.1$  min;  $t_{585} = 2.4$ ,  $P = 0.009$ ), but response distances averaged  $27.0 \pm 6.9\%$  farther away in the west ( $124 \pm 8$  m) than in the east ( $98 \pm 3$  m;  $t_{585} = 3.9$ ,  $P < 0.001$ ).

During playback experiments at nests, response distance averaged  $108 \pm 5$  m. Response distances averaged  $20.3 \pm 2.8\%$  closer than the mean distance at which tests were conducted ( $P < 0.0001$ ; paired  $t$ -test) and the distribution was somewhat less right-skewed than for transect surveys. Response time averaged  $2.9 \pm 0.13$  min across all positive tests, and the distribution was highly right-skewed, with 9.6% of responses occurring after the 5-min survey period (Fig. 1).

**Detection probability.** Across all playback experiments at nests, raw detection probability equaled  $0.67 \pm 0.03$  when averaged across the five test distances and  $0.65 \pm 0.03$  across all experiments ( $N = 165$  positive tests during 255 trials). Target owls responded only vocally during 63% of positive tests and both vocally and with observable movement, often toward broadcasts, during the remaining 37% of tests. Target owls responded with territorial vocalizations during 89% of positive tests, with single-noted “pew” or bark-type calls of much shorter duration otherwise. During negative tests, observers stationed near owls (or occupied nests) detected at least one target owl during 73% of tests. This pattern did not vary for tests in the east (72%) and west (74%), suggesting that spatial variation in detection probability was linked to the ability of surveyors to detect owls rather than differences in responsiveness.

The top-ranked model of detection probability included the effects of test distance in interaction with region (e.g., east vs. west), the temporal factors time of night and time of season, and test conditions linked to noise levels and wind speed (Table 1), and correctly classified results from 75.3% of tests. Despite relatively low weights for all models, effects of test distance in interaction with region, time of night, and noise levels were all in the 10 top-ranked models that had a cumulative weight of  $\sim 98\%$ . We also found some evidence for a model that included the effect of vegetation obstruction ( $\Delta AIC_c = 0.29$ ), and less evidence for models that included moon

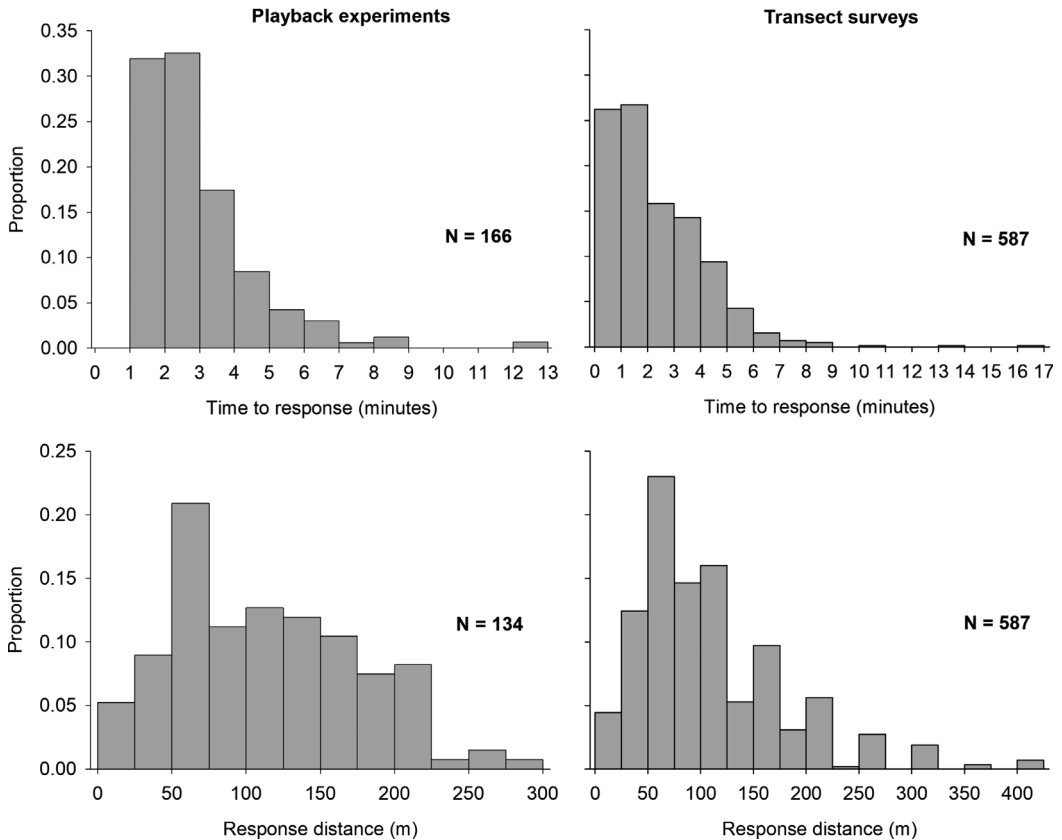


Fig. 1. Frequency histograms for response time (e.g., time between start of survey to initial response of owl) and response distance (e.g., estimated distance from surveyor to initial location of responding owl) of Elf Owls detected during playback experiments at 49 nest sites from April to June 2010–2011 and 2016–2017, and during transect surveys from March to June 2015 and 2016 in Arizona. Playback experiments at nests were conducted at distances of 50, 100, 150, 200, and 250 m from nest sites. Response distance was not estimated in 2010–2011. Only initial detections from the first survey event along transects during transect surveys were considered.

illumination ( $\Delta AIC_c = 1.39$ ) and local con-specific densities ( $\Delta AIC_c = 2.14$ ) than the best approximating model. Evidence for an interaction between test distance and region was strong based on comparing nested models with and without the interaction ( $\Delta AIC_c = 3.22$ ), but region also had a strong effect on detection probability when fit without the interaction ( $\beta \pm SE = 0.85 \pm 0.33$  for west reference level,  $P = 0.0095$ ). There was no support for a model with test distance, but without spatial differences in detection probability (Table 1).

Detection probability declined with increasing distance from target owls, but the rate of

decline varied spatially. In the west, detection probability declined with increasing distance at a much lower rate than in the east (Fig. 2). Detection probability was similar at distances up to ~100 m in both regions, but diverged widely and significantly at greater distances. Detection probability generally declined with increasing noise level and wind speed (Fig. 2). In terms of odds, each one-unit increase in noise levels decreased the odds an Elf Owl would respond by 48% after adjusting for other factors and by 26% with each one-unit increase in wind speed (Table 2). A 95% confidence interval (CI) of odds for wind speed overlapped one, however, indicating a

Table 1. Models that explained variation in detection probability of Elf Owls from April to June 2010–2011 and 2016–2017.

Model	K	$\Delta AIC_c$	$w_i$
Distance + Region + Distance*Region + Noise + Time of Night + Time of Season + Wind	9	0.00	0.180
Distance + Region + Distance*Region + Noise + Time of Night + Time of Season + Wind + Obstruction	10	0.29	0.156
Distance + Region + Distance*Region + Noise + Time of Night + Time of Season	8	0.44	0.145
Distance + Region + Distance*Region + Noise + Time of Night + Time of Season + Wind + Moon	10	1.39	0.090
Distance + Region + Distance*Region + Noise + Time of Night	7	1.39	0.090
Distance + Region + Distance*Region + Noise + Time of Night + Wind	8	1.68	0.078
Distance + Region + Distance*Region + Noise + Time of Night + Time of Season <sup>2</sup> + Wind	10	1.89	0.070
Distance + Region + Distance*Region + Noise + Time of Night + Time of Season + Wind + Conspecifics	10	2.14	0.062
Distance + Region + Distance*Region + Noise + Time of Night + Time of Season <sup>2</sup> + Wind + Obstruction	11	2.27	0.058
Distance + Region + Distance*Region + Noise + Time of Night + Time of Season <sup>2</sup>	9	2.48	0.052
Distance + Region + Distance*Region + Noise	6	5.45	0.012
Distance + Region + Distance*Region + Noise + Time of Season <sup>2</sup> + Wind	9	7.87	0.004
Distance + Region + Distance*Region + Time of Night	6	8.50	0.003
Distance + Region + Distance*Region + Noise + Time of Night + Obstruction	10	9.61	0.001
Distance + Region + Distance*Region	5	12.03	0.000
Distance + Region	4	15.25	0.000
Distance	3	20.20	0.000
Null {intercepts only}	2	45.94	0.000

Models are based on mixed-effects logistic regression with location (pair identity) fit as a random intercept and factors noted below as fixed effects. A set of biologically plausible model was first compared with model selection and select fixed effects to include in model, and then, models were refined by adding, subtracting, and changing terms and evaluating support using model selection techniques and  $AIC_c$ . “Region” indicates a categorical factor denoting sites in the East-South and West-North portions of our study area, and the null model includes no fixed effects for comparison. The first model was used as the best approximating model.

statistically weak effect despite high biological significance. Additionally, detection probability declined with increasing time since sunset and time of season (Fig. 2). Again, however, a 95% CI of odds for time of season barely overlapped one indicating a weaker effect than for time since sunset (Table 2). There was little evidence that vegetation obstruction influenced detection probability (odds = 0.776, 95% CI = 0.53–1.13,  $P$  = 0.18; Fig. 2).

The estimated number of repeat survey events needed to detect all territorial Elf Owls in a season also varied spatially. In the west, > 99% of owls were present within 200 m of surveyors could be detected after three surveys,

and > 98% of owls at distances within 250 m (Appendix S1). In the east, however, estimates were > 96% and > 92%, respectively, but increased to > 99% at distances  $\geq$  150 m. In contrast, after one or two surveys, the proportion of individuals detected at distances of 50 and 100 m was 1.8–5.0% higher in the east than in the west, but switched to the opposite tendency at distances  $\geq$  150 m.

## DISCUSSION

Our results provide a strong basis for understanding response patterns and factors that influence detection probability of Elf



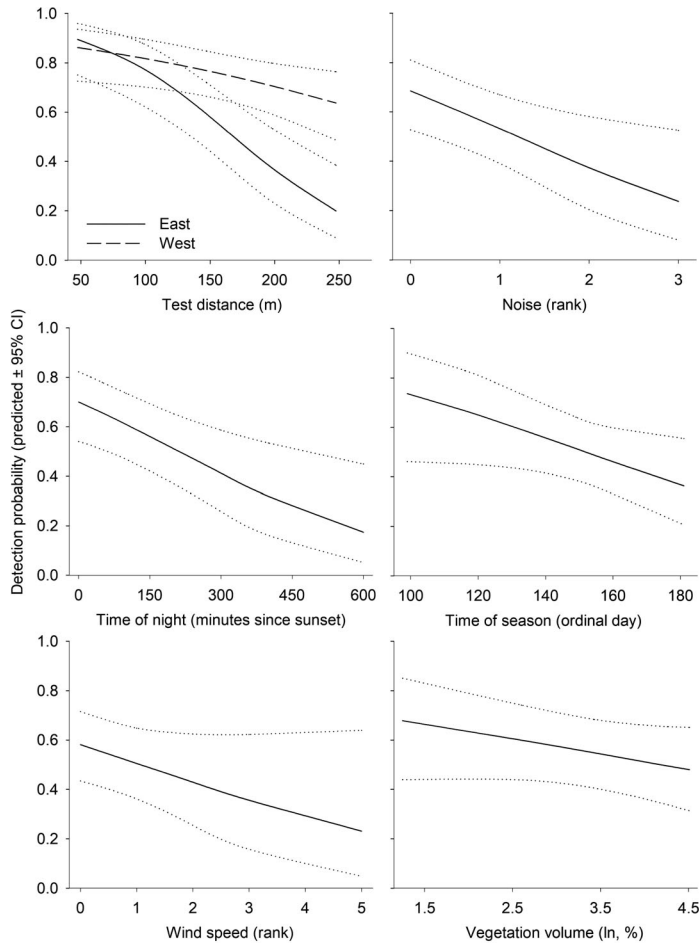


Fig. 2. Factors that explained the detection probability of Elf Owls from April to June 2010–2011 and 2016–2017. Lines (solid) are predictions  $\pm$  95% confidence intervals (dotted) based on splines connecting estimates of predicted effects from the best approximating mixed-effects logistic regression model with location (pair identify) fit as a random intercept.

Owls during the breeding season across broad spatial, temporal, and ecological gradients in the northern Sonoran Desert. Although Elf Owls may not respond to mimicked vocalizations (Marshall 1957), broadcasting conspecific vocalizations during the breeding season results in high levels of responsiveness (Hardy and Morrison 2000, Boal and Bibles 2001). Importantly, responses to broadcasts in our study generally occurred rapidly, with response patterns suggesting some limited movement toward surveyors. Detection probability also varied with spatial and temporal factors and with some survey conditions such

as noise levels, but not with variation in moon illumination or local conspecific densities. These and other patterns suggest that Elf Owls can be efficiently surveyed across a range of contexts, but that protocols should be designed around observed responsiveness patterns and study objectives to foster accurate estimation of population parameters.

Detection probability of Elf Owls in our study was relatively high, and higher than or similar to that of other species of owls. Overall, detection probability averaged 0.67 within 250 m of occupied nests and within 4 min of the start of broadcasts. Similar detection

Table 2. Factors that explained variation in detection probability of Elf Owls in Arizona, April–June 2010–2011 and 2016–2017.

Factor	Estimate	SE	Z	P	Odds	95% CI LB	95% CI UB
Intercept	7.096	1.797	4.0	< 0.0001	1.2E+03	35.6333	4.1E+04
Distance (m)	−0.018	0.004	−4.3	< 0.0001	0.982	0.975	0.990
Region (East or West)	−0.876	0.883	−1.0	0.32	0.416	0.074	2.350
Distance × Region	0.011	0.005	2.3	0.022	1.011	1.002	1.021
Time of night (min. since sunset)	−0.004	0.001	−2.9	0.0037	0.996	0.993	0.999
Time of season (ordinal day)	−0.019	0.010	−1.9	0.058	0.981	0.961	1.001
Noise (rank: 0–3)	−0.649	0.257	−2.5	0.012	0.523	0.316	0.865
Wind (rank: 0–5)	−0.306	0.191	−1.6	0.11	0.736	0.506	1.071

Models are based on mixed-effects logistic regression with locality (pair identity) as a random intercept and factors noted below as fixed effects. Estimates are from the best approximating model with random effects variance equaled to 0.183 based on 255 observations at 49 locations.

probabilities have been reported for Burrowing Owls (*Athene cunicularia*, 0.64; Conway and Simon 2003), Northern Spotted Owls (*Strix occidentalis caurina*, 0.53–0.85; Olson et al. 2005, Bailey et al. 2009), and Tawny Owls (*Strix aluco*, 0.71; Vrezec and Bertoneclj 2018) during or just before the breeding season. In contrast, detection probability of Elf Owls in our study was lower than that for Flammulated Owls (*Psilosops flammeolus*, ~0.80 within 200–300 m; Barnes and Belthoff 2008) and Ferruginous Pygmy-Owls (*Glaucidium brasilianum*, > 0.99 within 100 m, 0.93 within 300 m; Flesch and Steidl 2007) during and just before the breeding season and based largely on the same methods. In contrast, detection probability of Elf Owls in our study was much higher than that for Barred Owls in the Pacific Northwest (0.09–0.43; Bailey et al. 2009) and for four species of Australian owls (0.13–0.26; Debus 1995, Wintle et al. 2005). Although different methods complicate these comparisons, such variation among species and populations is likely due to differences in factors such as home-range size, resource densities, body size, and seasonal differences in territorial defense.

Systematic variation in detection probability across space and time can complicate efforts to survey and monitor wildlife populations (Yoccoz et al. 2001, Williams et al. 2002). If the ratio of a raw index and true parameter value varies spatially or temporally, inferences on population processes based on indices can be biased in complex ways (Bart

et al. 2004). Although many investigators have described variation in detection probability or response rates across temporal gradients (McLeod and Anderson 1998, Flesch and Steidl 2007, Conway et al. 2008), fewer find variation across large-scale spatial gradients (Conway and Gibbs 2011). Across broad environmental gradients in the Sonoran Desert along which rainfall increased ~four-fold and elevation increased ~eightfold, detection probability estimated during playback experiments at occupied nests in our study declined with increasing distances between surveyors and owls, and at greater rates at lower latitudes and higher elevation in the eastern portion of our study area. In the more arid west, detection probability also declined with increasing distance from owls, but at lower rates. Moreover, across more than 500 Elf Owls detected during our efforts, owls in the west responded faster and from greater distances than those in the east, indicating similar differences in response behavior. Spatial differences in responsiveness we observed could be due to failure of surveyors to detect owls that were in fact responding, or to differences in the actual number of owls that responded to broadcasts. By positioning an observer near nests or the locations of target owls during playback experiments at nests, we confirmed the former mechanism. Such patterns are likely not driven by greater vigilance required to maintain larger territories in the western portion of our study area, given results from telemetry and territory mapping

suggest low spatial variation in home-range size (Boone and Flesch, unpubl. data). Rather, these patterns were likely linked to greater resource levels that provide more habitat and foster higher densities in the more mesic eastern Sonoran Desert, where higher quantities of critical limiting resource such as saguaro cacti that provide nest sites and trees that provide cover and hunting perches are found. Where owl densities were high, additional territories were sometimes located between surveyors and target owls, reducing our ability to detect focal pairs and distinguish them from intervening respondents. Although such patterns may be common in regions that span broad resource gradients, the limited spatial scope and similarity in environmental conditions often considered in many studies could explain why these patterns are rarely documented. Interestingly, variation in local conspecific densities around focal pairs had no influence on detection probability despite evidence that it is important in some systems (Penteriani et al. 2002, Conway and Gibbs 2011).

With regard to temporal variation, we found evidence of seasonal and, especially, nightly variation in detection probability, which declined with increasing time since sunset and later in the breeding season. These patterns are likely driven by seasonal changes in territorial behavior and nightly changes in feeding and other activities, although spatial differences in breeding phenology across the study may have also influenced our results. Whereas the overall effect size of seasonal changes was similar to that for time since sunset, precision was much lower for seasonal effects, possibly because nesting was initiated ~2–4 weeks earlier in the western portion of our study area. Future studies should attempt to parse these effects and assess the biological significance of patterns. Regardless, observed seasonal variation in detection probability is likely biologically significant in this system, conforms generally to other studies of owls, and has important implications for survey timing. For temperate-zone owls, detection probability or response rates often peak just before and early during the nesting season (Ganey 1990, Morrell et al. 1991, Clark and Anderson 1997, Barnes and Belthoff 2008) or during natal dispersal (Lundberg 1980, Ritchison et al. 1988), but declines later in the

breeding season and during the period of fledgling dependency (Flesch and Steidl 2007).

Vegetation screening can influence the detection process during surveys and hence is an important consideration when designing surveys for species that occur in dense vegetation (Emlen 1971, Oelke 1981, Kery 2002, Buckland et al. 2005, Anderson et al. 2015, Flesch et al. 2019). Detection probability of Elf Owls in our study, however, did not vary markedly across broad gradients in vegetation obstruction from short open shrub-dominated desert scrub to tall dense riparian gallery forests with  $\geq 60\%$  vegetation volume between owls and surveyors. Such patterns are likely due to the acoustic properties of Elf Owl calls, which are not appreciably attenuated to the point of being inaudible, at least in the lowland environments we considered. However, detection probability declined somewhat with increasing vegetation obstruction despite the relative rarity of these conditions, suggesting a biologically relevant effect. Had a broader range of test distances been considered (e.g.,  $> 250$  m), denser vegetation been available, or point-specific survey time more constrained, observed effects would likely have been greater. Regardless, provided surveyors allow ample time following broadcasts to detect owls and space stations at recommended distances, vegetation screening is not likely to influence results.

During both transect surveys and playback experiments at nests, Elf Owls that responded to conspecific calls generally did so rapidly, with  $> 90\%$  detected in  $\leq 5$  min. The few owls that responded later often did so less aggressively with calls of shorter duration, or in places with higher than average noise or wind. During playback experiments at nests, however, response times averaged almost a minute longer than those during transect surveys, likely because some responses were triggered by broadcasts at prior stations. This resulted in some owls already calling when surveyors arrived at stations, which likely biased estimates of response time from transect surveys low. During playback experiments at nests, no target owls were detected before broadcasts because this was an explicit design element to assure responses were induced by broadcasts. Regardless, these patterns suggest that one or two additional

minutes of survey time per station may be warranted, especially at the first station along transects.

**Implications for surveys.** The best survey techniques have a high and consistent probability of detecting the target species and low sampling error (Thompson et al. 1998). For Elf Owls, broadcasting territorial calls is a reliable and efficient means of estimating occupancy and abundance during the breeding season because detection probability is high, especially within 100 m of occupied nests, and because owls respond rapidly and predictably across a wide range of distances, vegetation conditions, and times of night and season. Regardless, given relationships we observed, several design considerations will maximize the precision and efficiency of broadcast surveys for Elf Owls (Appendix S2). First, constraining surveys to periods when detection probability is fairly constant is advantageous (Yoccoz et al. 2001, Bart et al. 2004, MacKenzie et al. 2006) and can be accomplished by surveying within ~4 h of local sunset time during the early courtship, pairing, and nesting phases of the breeding season. Timing surveys just before nesting will also foster detection of individuals that fail to nest or establish breeding territories that may not be available for sampling later in the season, although such owls may be of less significance to populations. To allow Elf Owls sufficient time to respond, we recommend surveying stations for 5–6 min or longer if stations are widely spaced, as may be desired for some study objectives.

Marked differences in detection probability that we observed between owls in two ecologically distinct geographic regions of our study area have important implications for survey design, even for investigators planning localized efforts. Because detection probability declined less with increasing distance in the more arid western portion of our study area, spacing survey stations at greater distances in this region can augment efficiency without increasing false absence rates. In the eastern portion of our study area, spacing stations ~100 m apart can foster detecting most territorial individuals during single-occasion surveys, but, for optimal efficiency, this distance could be increased from 150 to 200 m in the more arid western portion of the study area without marked increases in false absence

rates. To promote independence, spacing stations at greater distances may also be useful where occupancy is the focus, whereas spacing stations at 100- to 150-m intervals seems best for estimating abundance, especially where densities are high. Given high overall detection probability that increased from 0.77 to 0.94 from one to two survey occasions at distances of 150 m from active nests (Appendix S1), single-occasion surveys may be adequate to reach many study objectives, especially when resources are limited and large areas need to be covered. Ultimately, selecting optimal station spacing, number of survey occasions, and other design details should be based on study objectives and available resources.

#### ACKNOWLEDGMENTS

We thank A. Arcidiacono, K. Brennan, C. Sanchez Gonzalez, V. Murphy, R. Villa, G. Bland, and K. Urban for help with field work. U.S. Bureau of Reclamation provided funding and C. Ronning, M. Reilly, S. Farinella, T. Baribault, J. Knowles, S. Kokos, and N. Rudd contributed essential support. For access, we thank K. Knight and S. Wolf, S. Dollarhide, P. Else, B. Magill, and owners of the Lincoln Ranch. We are grateful to The Nature Conservancy of Arizona, especially M. Haberstich of Aravaipa Canyon Preserve, T. Bommarito and H. English in the San Pedro Valley, K. Baldwin, B. Powell, and D. Carter on Pima County lands, A. Springer, D. Swann, and N. Kline on National Park Service lands, C. Bell, K. Blair, J. Fernandez, S. Culling, and S. Flatland of the U.S. Fish and Wildlife Service, and R. Peck, J. Conn, and M. Radke of the Bureau of Land Management for providing access to preserves across Arizona.

#### LITERATURE CITED

- ANDERSON, A. S., T. A. MARQUES, L. P. SHOO, AND S. E. WILLIAMS. 2015. Detectability in audio-visual surveys of tropical rainforest birds: The influence of species, weather and habitat characteristics. *PLoS ONE* 10: e0128464.
- BAILEY, L. L., J. A. REID, E. D. FORSMAN, AND J. D. NICHOLS. 2009. Modeling co-occurrence of Northern Spotted and Barred owls: Accounting for detection probability differences. *Biological Conservation* 142: 2983–2989.
- BARNES, K. P., AND J. R. BELTHOFF. 2008. Probability of detection of Flammulated Owls using nocturnal broadcast surveys. *Journal of Field Ornithology* 79: 321–328.
- BART, J., S. DROEGE, P. GEISSLER, B. PETERJOHN, AND C. J. RALPH. 2004. Density estimation in wildlife surveys. *Wildlife Society Bulletin* 34: 1242–1247.
- BATES, D., M. MAECHLER, B. BOLKER, AND S. WALKER. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–48.

- BOAL, C. W., AND B. D. BIBLES. 2001. Responsiveness of Elf Owls to conspecific and Great Horned Owl calls. *Journal of Field Ornithology* 72: 66–71.
- BOLKER, B. M. 2015. Linear and generalized linear mixed models. In: *Ecological statistics: contemporary theory and application* (G. A. Fox, S. Negrete-Yankelevich, and V. J. Sosa, eds.), pp. 309–333. Oxford University Press, Oxford, UK.
- BROWN, D. E. (ed.). 1982. *Biotic communities of the American Southwest: United States and Mexico*. Desert Plants 4: 1–342.
- BUCKLAND, S. T., D. R. ANDERSON, K. P. BURNHAM, AND J. L. LAAKE. 2005. *Distance sampling*. John Wiley & Sons, New York, NY.
- BURNHAM, K. P., AND D. R. ANDERSON. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York, NY.
- CLARK, K. A., AND S. H. ANDERSON. 1997. Temporal, climatic, and lunar affecting owl vocalizations of western Wyoming. *Journal of Raptor Research* 31: 358–363.
- CONWAY, C. J., V. GARCIA, M. D. SMITH, AND K. HUGHES. 2008. Factors affecting detection of Burrowing Owl nests during standardized surveys. *Journal of Wildlife Management* 72: 688–696.
- CONWAY, C. J., AND J. P. GIBBS. 2005. Effectiveness of call-broadcast surveys for monitoring marsh birds. *Auk* 122: 26–35.
- CONWAY, C. J., AND J. P. GIBBS. 2011. Summary of intrinsic and extrinsic factors affecting detection probability of marsh birds. *Wetlands* 31: 403–411.
- CONWAY, C. J., AND J. C. SIMON. 2003. Comparison of detection probability associated with Burrowing Owl survey methods. *Journal of Wildlife Management* 67: 501–511.
- DEBUS, S. J. S. 1995. Surveys of large forest owls in northern New South Wales: methodology, calling behavior and owl responses. *Corella* 19: 38–50.
- EMLEN, J. T. 1971. Population densities of birds derived from transect counts. *Auk* 88: 323–342.
- FLESCH, A. D., I. W. MURRAY, J. M. GICKLHORN, AND B. F. POWELL. 2019. Application of distance sampling for assessing abundance and habitat relationships of a rare Sonoran Desert cactus. *Plant Ecology* 220: 1029–1042.
- FLESCH, A. D., AND R. J. STEIDL. 2007. Detectability and response rates of Ferruginous Pygmy-Owls. *Journal of Wildlife Management* 71: 981–990.
- FLESCH, A. D., AND R. J. STEIDL. 2010. Importance of environmental and spatial gradients on patterns and consequences of resource selection. *Ecological Applications* 20: 1021–1039.
- FULLER, M. R., AND J. A. MOSHER. 1981. Methods of detecting and counting raptors: a review. *Studies in Avian Biology* 6: 235–246.
- FULLER, M. R., AND J. A. MOSHER. 1987. Raptor survey techniques. In: *Raptor management techniques manual* (B. G. Pendleton, B. A. Millsap, K. W. Cline, and D. M. Bird, eds.), pp. 37–65. National Wildlife Federation, Washington, D.C.
- GANEY, J. L. 1990. Calling behavior of Spotted Owls in northern Arizona. *Condor* 92: 485–490.
- GERHARDT, R. P. 1991. Response of Mottled Owls to broadcast of conspecific call. *Journal of Field Ornithology* 62: 239–244.
- GLINSKI, R. L. (ed.). 1998. *Raptors of Arizona*. University of Arizona Press, Tucson, AZ.
- HAGIHARA, R., R. E. JONES, S. SOBTZICK, C. CLEGUER, C. GARRIGUE, AND H. MARSH. 2018. Compensating for geographic variation in detection probability with water depth improves abundance estimates of coastal marine megafauna. *PLoS ONE* 13: e0191476.
- HALTERMAN, M. D., S. A. LAYMON, AND M. J. WHITFIELD. 1989. Status and distribution of the Elf Owl in California. *Western Birds* 20: 71–80.
- HARDY, P. C., AND M. L. MORRISON. 2000. Factors affecting the detection of Elf Owls and Western Screech Owls. *Wildlife Society Bulletin* 28: 333–342.
- HENRY, S. G., F. R. GEHLBACH, D. MOLFETTO, AND P. HOWARD. 2020. Elf Owl (*Micrathene whitneyi*), version 1.0. In: *Birds of the World* (S. M. Billerman, ed.). Cornell Lab of Ornithology, Ithaca, NY.
- KENNEDY, P. L., AND D. W. STAHLER. 1993. Responsiveness of nesting Northern Goshawks to taped broadcasts of 3 conspecific calls. *Journal of Wildlife Management* 57: 249–257.
- KERY, M. 2002. Inferring the absence of a species—a case study of snakes. *Journal of Wildlife Management* 66: 330–338.
- LIGON, J. D. 1968. The biology of the Elf Owl, *Micrathene whitneyi*. University of Michigan Museum of Zoology Miscellaneous Publications 136: 1–70.
- LOWER COLORADO RIVER MULTI-SPECIES CONSERVATION PROGRAM. 2004. Lower Colorado River Multi-Species Conservation Program, Volume II: Habitat Conservation Plan, Final. Sacramento, CA. <http://www.lcrmscp.gov>.
- LUNDBERG, A. 1980. Vocalizations and courtship feeding of the Ural Owl *Strix uralensis*. *Ornis Scandinavica* 11: 65–70.
- MACKENZIE, D. I., J. D. NICHOLS, J. A. ROYLE, K. H. POLLOCK, L. BAILEY, AND J. E. HINES. 2006. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Academic Press, New York, NY.
- MARSHALL, J. T. 1957. Birds of pine-oak woodland in southern Arizona and adjacent Mexico. *Pacific Coast Avifauna* 32: 1–125.
- MCGARIGAL, K., AND J. D. FRASER. 1985. Barred Owl responses to recorded vocalizations. *Condor* 87: 552–553.
- MCLEOD, M. A., AND D. E. ANDERSEN. 1998. Red-shouldered Hawk broadcast surveys: factors affecting detection of responses and population trends. *Journal of Wildlife Management* 62: 1385–1397.
- MORRELL, T. E., R. H. YAHNER, AND W. L. HARKNESS. 1991. Factors affecting detection of Great Horned Owls by using broadcast vocalizations. *Wildlife Society Bulletin* 19: 481–488.
- MOSHER, J. A., M. R. FULLER, AND M. KOPENY. 1990. Surveying woodland raptors by broadcast conspecific vocalizations. *Journal of Field Ornithology* 61: 453–461.

- OELKE, H. 1981. Limitations of estimating bird populations because of vegetation structure and composition. *Studies in Avian Biology* 6: 316–321.
- OLSON, G. S., R. G. ANTHONY, E. D. FORSMAN, S. H. ACKERS, P. J. LOSCHL, J. A. REID, K. M. DUGGER, E. M. GLENN, AND W. J. RIPPLE. 2005. Modeling of site occupancy dynamics for Northern Spotted Owls, with emphasis on the effects of Barred Owls. *Journal of Wildlife Management* 69: 918–932.
- PENTERIANI, V., M. GALLARDO, AND H. CAZASSUS. 2002. Conspecific density biases passive auditory surveys. *Journal of Field Ornithology* 73: 387–391.
- POLLOCK, K. H., J. D. NICHOLS, T. R. SIMONS, G. L. FARNSWORTH, L. L. BAILEY, AND J. R. SAUER. 2002. Large scale wildlife monitoring studies: statistical methods for design and analysis. *Environmetrics* 13: 105–119.
- R DEVELOPMENT CORE TEAM. 2016. R: A language and environment for statistical computing. Version 3.3.1. R Foundation for Statistical Computing, Vienna, Austria.
- RITCHISON, G., P. M. CAVANAGH, J. R. BELTHOFF, AND E. J. SPARKS. 1988. The singing behavior of Eastern Screech-Owls: seasonal timing and response to playback of conspecific song. *Condor* 90: 648–652.
- ROSENBERG, K. V., R. D. OHMART, W. C. HUNTER, AND B. W. ANDERSON. 1991. *Birds of the Lower Colorado River Valley*. University of Arizona Press, Tucson, AZ.
- SEAVY, N. E. 2004. Environmental correlates of African Wood Owl calling activity in Kinbale National Park, Uganda. *Journal of Raptor Research* 38: 208–213.
- SHREVE, F. 1951. *Vegetation of the Sonoran Desert*. Carnegie Institute of Washington, Publication Number 591, Washington, D.C.
- SUTHERLAND, W. J., I. NEWTON, AND R. GREEN. 2004. *Bird ecology and conservation: a handbook of techniques*. Oxford University Press, Oxford, UK.
- THOMPSON, W. L., G. C. WHITE, AND C. GOWAN. 1998. *Monitoring vertebrate populations*. Academic Press, San Diego, CA.
- TYRE, A. J., B. TENHUMBERG, S. A. FIELD, H. P. POSSINGHAM, D. NIEJALKE, AND K. PARRIS. 2003. Improving precision and reducing bias in biological surveys by estimating false negative error rates in presence-absence data. *Ecological Applications* 13: 1790–1801.
- VREZEC, A., AND I. BERTONCELJ. 2018. Territory monitoring of Tawny Owls *Strix aluco* using playback calls is a reliable population monitoring method. *Bird Study* 65(S1): S52–S62.
- WILLIAMS, B. K., J. D. NICHOLS, AND M. J. CONROY. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, CA.
- WINTLE, B. A., R. P. KAVANAGH, M. A. MCCARTHY, AND M. A. BURGMAN. 2005. The magnitude and management consequences of false negative observation error in surveys of arboreal marsupials and large forest owls. *Journal of Wildlife Management* 69: 905–917.
- YOCOZ, N. G., J. D. NICHOLS, AND T. BOULINIER. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution* 16: 446–453.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

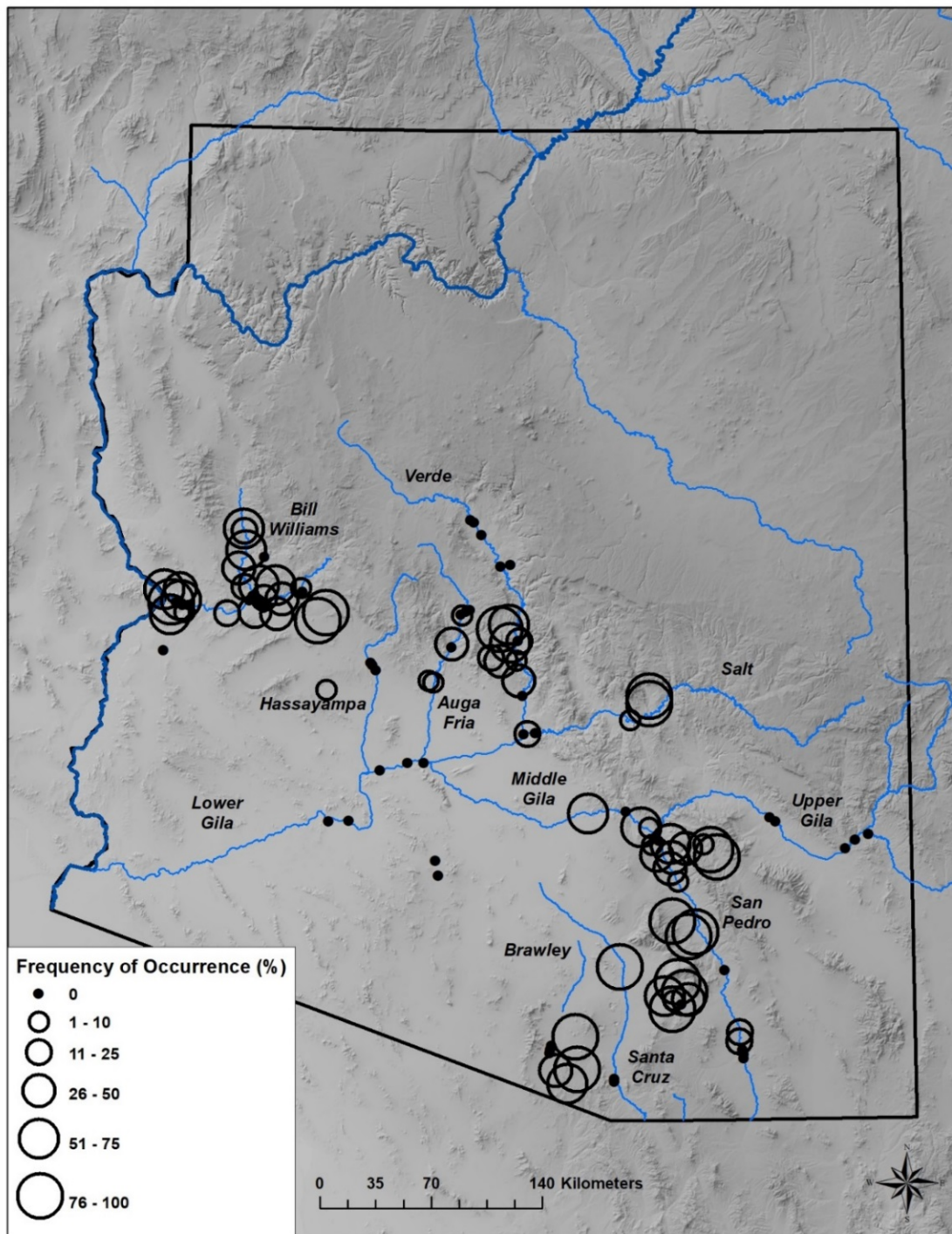
**Table S1.** Index of ambient moon illumination with values from 0–5. Moon phase was assigned to the closest category.

**Fig. S1.** Distribution and frequency of occurrence of Elf Owls along 121 transects surveyed in Arizona, March–June 2015–2017. Names of nine watershed regions are illustrated with the Hassayampa River dividing the eastern and western portions of the study area.

**Appendix S1.** Estimates of detection probability ( $p$  = number of detections/number of trials) of Elf Owls in southern and western Arizona across variable levels of effort and five tests distance for the entire study area and the eastern and western portions based on test trials in April–June 2010–2011 and 2016–2017. Estimates are based on the equation  $(1 - (1 - p)^X)$  where  $X$  is the number of repeated surveys within a season. Confidence intervals are based on binomial standard error and the number of test trials done at each distance and region.

**Appendix S2.** Suggested survey design details for broadcast surveys of Elf Owls in southern and western Arizona based on observed patterns of detection probability and response patterns.

## Supplementary Material



**Figure S1: Distribution and frequency of occurrence of elf owls along 121 transects surveyed in Arizona, March-June 2015-2017. Names of 9 watershed regions are illustrated with the Hassayampa River dividing the eastern and western portions of the study area.**

**Table S1.—Index of ambient moon illumination with values from 0–5. Moon phase was assigned to the closest category.**

<b>Moon Phase</b>	<b>Low (just above horizon – 30° above horizon)</b>	<b>Intermediate (30–60° above horizon)</b>	<b>High (60–90° above horizon)</b>
New	0	0	0
Quarter	1	2	3
Half	2	3	4
Full / Gibbous	4	5	5



**Appendix A.--Estimates of detection probability ( $p$  = number of detections/number of trials) of elf owls in southern and western Arizona across variable levels of effort and five tests distance for the entire study area and the eastern and western portions based on test trials in April-June 2010-11 and 2016-17. Estimates are based on the equation  $(1 - (1 - p)^X)$  where  $X$  is the number of repeated surveys within a season. Confidence intervals are based on binomial standard error and the number of test trials done at each distance and region.**

Region	Distance (m)	Trials	One Survey			Two Surveys			Three Surveys			Four Surveys		
			$p$	95% LB	95% UB	$p$	95% LB	95% UB	$p$	95% LB	95% UB	$p$	95% LB	95% UB
All	50	40	0.825	0.707	0.943	0.969	0.916	1.023	0.995	0.972	1.017	0.999	0.990	1.009
All	100	101	0.814	0.738	0.890	0.965	0.930	1.001	0.994	0.978	1.009	0.999	0.992	1.006
All	150	139	0.771	0.701	0.841	0.947	0.910	0.985	0.988	0.970	1.006	0.997	0.989	1.006
All	200	181	0.727	0.662	0.792	0.925	0.887	0.964	0.980	0.959	1.000	0.994	0.984	1.005
All	250	255	0.668	0.610	0.726	0.890	0.851	0.928	0.963	0.940	0.986	0.988	0.974	1.001
East	50	20	0.850	0.694	1.006	0.978	0.913	1.042	0.997	0.971	1.022	0.999	0.990	1.009
East	100	42	0.834	0.722	0.947	0.972	0.923	1.022	0.995	0.975	1.016	0.999	0.991	1.008
East	150	60	0.760	0.652	0.868	0.942	0.883	1.001	0.986	0.957	1.016	0.997	0.982	1.011
East	200	82	0.661	0.558	0.763	0.885	0.816	0.954	0.961	0.919	1.003	0.987	0.962	1.011
East	250	101	0.571	0.474	0.667	0.816	0.740	0.891	0.921	0.868	0.974	0.966	0.931	1.001
West	50	20	0.800	0.625	0.975	0.960	0.874	1.046	0.992	0.953	1.031	0.998	0.981	1.016
West	100	59	0.797	0.695	0.900	0.959	0.908	1.010	0.992	0.969	1.015	0.998	0.988	1.009
West	150	79	0.782	0.691	0.873	0.952	0.905	0.999	0.990	0.967	1.012	0.998	0.987	1.008
West	200	99	0.799	0.720	0.878	0.959	0.921	0.998	0.992	0.974	1.010	0.998	0.990	1.006
West	250	154	0.741	0.672	0.810	0.933	0.893	0.972	0.983	0.962	1.003	0.995	0.985	1.006

**Appendix B.—Suggested survey design details for broadcast surveys of elf owls in southern and western Arizona based on observed patterns of detection probability and response patterns.**

<b>Parameter</b>	<b>Suggested design</b>
Distance between survey points	100-200 m depending on objectives and local densities
Playback	Male territorial calls for 30 sec., followed by 30 sec. of listening
Silence before playback	1 minute
Playback duration	3-5 minutes of alternating 30 sec. of calls and 30 sec. of listening
Silence after playback	1 minute
Number of visits	1 to 3 depending on objectives
Time Period	March-June; early courtship, pairing, and nesting phases of breeding season
Time of night	Within four hours of dusk
Weather conditions	Calm nights without rain and significant wind