



Integrating Callback and Acoustic Surveys to Determine Drivers of Canyon Occupancy by Mexican Spotted Owls at Grand Canyon National Park

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ABSTRACT.—Mexican Spotted Owls (*Strix occidentalis lucida*) are a federally threatened subspecies of Spotted Owl that occupy forests and canyons across the Desert Southwest of the USA. While Mexican Spotted Owls in forest habitat are well studied, those occupying canyon habitats are underrepresented in the literature. We used data from callback surveys from 2001–2021 and autonomous recording units (ARUs) from 2019–2021 in a multi-method, multi-season occupancy model to assess long-term occupancy of 33 management units (called protected activity centers [PACs]) in Grand Canyon National Park. We assessed survey effort and determined how vegetation diversity, side-canyon topographic complexity, and shrub cover influenced occupancy. Results derived from our model suggested that populations of Mexican Spotted Owls in the Grand Canyon remained stable over the last two decades. Owls preferentially occupied PACs with higher diversity of vegetation types during the breeding season, whereas canyon complexity and shrub cover did not have a strong effect on occupancy. Callback surveys were more effective than ARUs at detecting owls on a single night (mean probability of detection = 0.74 and 0.38, respectively). However, ARUs expanded the survey season into February and allowed more PACs to be sampled over multiple nights with less field effort. Conducting surveys early in the breeding season improved detection probability regardless of method. Overall, our study highlighted PACs that have been under surveyed across the study period, identified habitat features that are consistent with long-term PAC occupancy, and demonstrated the potential to combine traditional callback survey data with ARU data to more effectively monitor Mexican Spotted Owls.

KEY WORDS: *acoustic monitoring; Arizona; integrated models; long-term monitoring; National Parks.*

INTEGRACIÓN DE CENSOS CON REPRODUCCIÓN DE LLAMADAS Y CENSOS ACÚSTICOS PARA DETERMINAR LOS FACTORES QUE INFLUYEN EN LA OCUPACIÓN DE CAÑONES POR *STRIX OCCIDENTALIS LUCIDA* EN EL PARQUE NACIONAL DEL GRAN CAÑÓN

RESUMEN.—*Strix occidentalis lucida* es una subespecie catalogada como amenazada a nivel federal que habita bosques y cañones en la región desértica del sudoeste de EUA. Si bien las poblaciones de *S. o. lucida* que habitan bosques han sido ampliamente estudiadas, aquellas que ocupan hábitats de cañón están escasamente

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representadas en la literatura científica. Utilizamos datos provenientes de censos con reproducción de reclamos realizados entre 2001 y 2021 y de unidades autónomas de grabación (UAG) obtenidos entre 2019 y 2021 en un modelo de ocupación multi-método y multi-estacional para evaluar la ocupación a largo plazo de 33 unidades de manejo (denominadas centros de actividad protegidos [CAP]) en el Parque Nacional del Gran Cañón. Evaluamos el esfuerzo de muestreo y determinamos cómo la diversidad de la vegetación, la complejidad topográfica de los cañones laterales y la cobertura de arbustos influyeron sobre la ocupación. Los resultados obtenidos con nuestro modelo sugieren que las poblaciones de *S. o. lucida* del Gran Cañón se mantuvieron estables durante las dos últimas décadas. Los búhos ocuparon preferentemente durante la temporada reproductiva los CAP con mayor diversidad de tipos de vegetación, mientras que la complejidad de los cañones y la cobertura de arbustos no ejercieron un efecto importante sobre la ocupación. Los censos con reproducción de reclamos fueron más eficaces que las UAG para detectar búhos durante una sola noche (probabilidad media de detección = 0.74 y 0.38, respectivamente). Sin embargo, las UAG ampliaron la temporada de muestreo hasta febrero y permitieron evidenciar un mayor número de CAP durante múltiples noches con un menor esfuerzo de campo. Realizar los censos al comienzo de la temporada reproductiva incrementó la probabilidad de detección, independientemente del método utilizado. En conjunto, nuestro estudio identificó CAP que habían sido inframuestreados durante el período de estudio, determinó las características del hábitat asociadas con la ocupación a largo plazo de estos sitios y demostró el potencial de combinar los datos obtenidos mediante censos tradicionales con reproducción de reclamos y UAG para monitorear con mayor eficacia a *S. o. lucida*.

[Traducción del equipo editorial]

INTRODUCTION

Rapid changes to natural landscapes in recent history have resulted in widespread declines to many wildlife species (Descamps et al. 2016, Dueñas et al. 2021). Long-term population monitoring programs have been fundamental for tracking how these changes affect local and global wildlife communities over time (Murphy and Weiss 1988, Hafner and Fasola 1997). For example, long-term raptor migration monitoring sites have been critical for monitoring and detecting changes to population sizes of American Kestrel (*Falco sparverius*), which are declining across much of North America (Farmer and Smith 2009, Bird and Smallwood 2023). Similarly, since 1966 the North American Breeding Bird Survey has worked to assess population status for more than 400 avian species (Sauer et al. 2017), and through this long-term effort identified declining trends in more than 50% of avian species in North America (Sauer et al. 2013). Management of many threatened and endangered species benefit from continuous population monitoring. For example, the decline and subsequent recovery of the Peregrine Falcon (*Falco peregrinus*) was confirmed through consistent long-term population monitoring across the globe (Cade et al. 1988, Franke et al. 2010, Baril et al. 2015, Varland et al. 2020). In some systems, continuous monitoring of species is extremely time consuming, costly, or physically laborious, which makes ongoing and consistent data collection difficult. Expanding monitoring programs to incorporate emerging modern technologies designed to be more efficient or cost-effective may relieve some of these challenges.

Advancements in remote data collection technology, such as drones, remote cameras, and acoustic monitors, allow researchers to collect data in areas that are difficult to access (Potapov et al. 2013, Bird et al. 2024), in a more time-efficient manner (Hodgson et al. 2017), or for longer periods. For example, in a study of gull and tern productivity in Italy, drones were found to be useful for estimating chick survival and identifying nest failures, while also being potentially more time-efficient than traditional ground methods (Valle and Scarton 2021). Additionally, remote camera traps have been used to estimate the density of unmarked animals (Evans and Rittenhouse 2018), and weather radar is now used to study avian migration remotely (Gauthreaux et al. 2019, Sivakumar et al. 2021, Nebuloni and Capsoni 2024). One emerging data collection tool, autonomous recording units (ARUs), are now routinely used to monitor vocal species such as birds, bats, and amphibians (Johnson et al. 2002, Acevedo and Villanueva-Rivera 2006). They may be deployed for weeks at a time (Hobson et al. 2002), potentially improving the chances of detecting a species (Colbert et al. 2015, Thompson et al. 2017), while also minimizing deleterious effects to the target species from more invasive survey methods (Rognan et al. 2012). ARUs also reduce the number of surveyors needed, which may decrease cost and potentially minimize variability associated with multiple observers (Borker et al. 2015, Darras et al. 2019). They may be especially useful in remote locations with limited access (Darras et al. 2019) where repeat visits to sites can be a challenge. These devices have also become a popular method to assess the presence and absence of cryptic species,

such as owls (Rognan et al. 2012, Clément et al. 2021), and more recently to assess species distribution (Campos-Cerqueira and Aide 2016, Stiffler et al. 2018), occupancy (Balantic and Donovan 2019, Jahn et al. 2022, Wood and Peery 2022), space use (Gomes et al. 2020), reproductive status (Upham-Mills et al. 2025), and abundance (Udell et al. 2024).

Despite the multitude of recent advances in technology, their application in long-term studies is often met with hesitancy due to the fear that the use of new technology may hinder comparisons with historical data (Pelton and van Manen 1996). Recent statistical models that incorporate multiple data types provide a pathway to alleviating these concerns (Jiménez et al. 2016). For example, multi-method models allow seamless integration of multiple data sources, including historical and modern methods, to robustly answer broad-scale research questions, including those relying on long-term timelines (Davis et al. 2019, Lesmeister and Jenkins 2022). Similarly, integrated population models combine multiple data types into one model to provide joint estimates of multiple demographic parameters such as abundance, survival, and fecundity (Arnold et al. 2018, Kéry and Schaub 2021, Van Ee et al. 2024). For example, in a long-term study of Kodiak brown bears (*Ursus arctos middendorffi*) on Kodiak Island off the coast of Alaska, mark-recapture data were integrated with adult and offspring count data to estimate adult survival probability (Bled et al. 2017).

Mexican Spotted Owls (*Strix occidentalis lucida*) are a federally threatened subspecies of Spotted Owl (*S. occidentalis*) distributed across old growth forests and rocky canyons in the Desert Southwest of the USA (Ganey and Balda 1989, Willey 1998, Willey and van Riper III 2007, US Fish and Wildlife Service [USFWS] 2012). Mexican Spotted Owls in forest habitat occupy areas with mature mixed-conifer forests, pine-oak stands, and high canopy closure (Ganey and Balda 1989, 1994, Seamans and Gutiérrez 1995, May et al. 2004). Alternatively, Mexican Spotted Owls in canyon landscapes have home ranges that include desert scrub, pinyon-juniper woodlands (single-leaf pinyon [*Pinus monophylla*] and one-seeded juniper [*Juniperus monosperma*]), and steep-walled narrow canyons (Rinkevich 1991, Willey and van Riper III 2007, 2015, Bowden et al. 2015), often including a water source (Rinkevich and Gutiérrez 1996). Compared to Mexican Spotted Owls in forest habitat, there are fewer studies on these owls in canyon landscapes, potentially due to the complex and challenging nature of accessing these remote areas (USFWS 2023).

However, some aspects of Mexican Spotted Owl ecology are well described. Nest and roost sites in

canyon habitat are typically in caves or on cliffs and ledges (Rinkevich and Gutiérrez 1996, Willey 1998, Bowden 2008, Willey and van Riper III 2015) and prey species commonly include woodrats (*Neotoma* spp.) and white-footed mice (*Peromyscus* spp.) (Wagner et al. 1982, Willey 2013, Thornburg 2018). Home ranges in the canyonlands of Utah averaged 928 ha, with non-breeding home ranges averaging larger than breeding home ranges (Willey and van Riper III 2007). The breeding period begins with courtship in March (USFWS 2012) and juveniles typically disperse in September (Willey and van Riper III 2000). One criteria for the recovery of this subspecies is that occupancy rates must be stable or increasing after 10 yr of monitoring (USFWS 2012). While some published studies and reports highlight occupancy dynamics of Mexican Spotted Owls in canyon habitat (Schelz et al. 2004, Hockenbary 2011, Willey and Zambon 2014), assessing long-term occupancy trends needs more attention (but see Thornburg et al. 2016). ARUs have the potential to improve consistency in long-term monitoring programs, but a regional protocol for monitoring occupancy status using ARUs is needed (USFWS 2023).

Agencies manage Mexican Spotted Owl areas with protected activity centers (PACs), which are management units that encompass a minimum of 242 ha around an identified Mexican Spotted Owl nest or roost location, with the aim of protecting their potential breeding areas (USFWS 2012). When nest or roost sites cannot be identified, PACs may also be designated following a set of guidelines laid out in the Mexican Spotted Owl Recovery Plan (USFWS 2012). For example, two auditory detections separated by at least 1 wk within the same area during the breeding season can be used to designate a PAC (USFWS 2012). PACs are not intended to represent an owl's entire home range, yet studies show they are being heavily used by owls. One study found that Mexican Spotted Owl PACs contained on average 58% of total nocturnal locations and 92% of diurnal roost locations (Reid et al. 2025), and another study found that PACs contained 100% of nests and 97% of roosts (Ganey et al. 2014). While the utility of PACs has been explored through studies of space use (Ganey et al. 2014, Reid et al. 2025) and occupancy (Blakesley 2015) in forest habitat, PAC occupancy in canyon habitat has yet to be assessed.

We sought to first assess how the combination of two survey methods, traditional callback surveys and ARU surveys, supported efforts to fulfill the primary Mexican Spotted Owl programmatic monitoring objective at Grand Canyon National Park (GCNP) of surveying all PACs over rolling 5-yr periods. Our second objective was to assess long-term PAC occupancy

during the breeding season. We defined occupancy as either a single owl or pair of Mexican Spotted Owls occurring in an established PAC during the breeding season. Our third objective was to determine how occupancy related to site-level characteristics within 33 PACs. Specific site-level characteristics included vegetation diversity, the amount of shrub cover, and canyon topographic complexity (i.e., narrow slot canyons vs. broad canyons). We predicted that PACs with more diverse vegetation types, which we calculated using a Shannon diversity metric, would have higher occupancy because Mexican Spotted Owls in similar environments were found in areas with more vegetation strata (Rinkevich and Gutiérrez 1996). We also predicted that areas with more shrub cover would have higher owl occupancy, because shrub cover benefits small mammals (Rosenstock 1996, Flinders et al. 2002), potentially including common prey items for Mexican Spotted Owls such as woodrats and white-footed mice (Willey 2013, Thornberg 2018). Mexican Spotted Owls nest in cliffs in canyon habitat across the Southwest (Swarthout and Steidl 2003) including in GCNP where home ranges included narrow canyons (Bowden et al. 2015), and nests and roosts were most often located in shaded, narrow canyons with steep cliffs (Bowden 2008). Thus, we also predicted owls were more likely to occupy PACs at GCNP that have greater topographic complexity, specifically narrow canyons with steep cliffs, described using a measure of canyon narrowness.

Our fourth objective was to determine how survey-level characteristics (variables collected on a per-survey basis) influenced Mexican Spotted Owl detection for each survey method. Specific survey-level characteristics were individual to each method, with callback surveys related to day of year and moonlight illumination, and ARU surveys related to day of year, moonlight illumination, number of ARUs used, and maximum wind speed (m/sec). Regardless of the survey method used, we predicted that detection probability would be higher earlier in the season when owls are actively defending territories (Ganey 1990) and higher on darker nights, similar to previous studies of Mexican Spotted Owls in Arizona (Ganey 1990). Additionally, we predicted that detection probability using the ARU survey method would be higher when wind speeds were low, similar to other ARU studies (Stowell et al. 2019), and when more ARUs were used to survey a PAC and thereby presumably provide greater coverage.

METHODS

Study Area. GCNP covers more than 400,000 ha of land in northern Arizona and is managed by the

National Park Service (NPS). The climate is dry and had an average of 31 cm of precipitation annually over the course of the study (Lawrimore et al. 2016). The elevation at the canyon spans more than 2000 m and supports a variety of life zones (Huisinga et al. 2006, Kearsley et al. 2015). The North and South Rims of the park are primarily pine-oak and mixed-conifer forests, including species such as ponderosa pine (*Pinus ponderosa*), douglas fir (*Pseudotsuga menziesii*), and gambel oak (*Quercus gambelii*) (Kearsley et al. 2015). Pinyon-juniper woodlands occur at the canyon edge and the upper portions of the inner canyon (Kearsley et al. 2015). The inner canyon is characterized by steep rocky cliffs, desert scrub vegetation, and tributary canyon riparian systems with perennial and ephemeral water sources (Huisinga et al. 2006). Common plant species in the dry rocky parts of the inner canyon include blackbrush (*Coleogyne ramosissima*), fourwing saltbush (*Atriplex canescens*), and *Yucca* spp., while the riparian areas include catclaw acacia (*Acacia greggii*), coyote willow (*Salix exigua*), and arrow-weed (*Pluchea sericea*) (Huisinga et al. 2006, Kearsley et al. 2015). Backcountry recreation, including hiking, backpacking, canyoneering, and river rafting, is popular at the park, with a record 350,000 visitors to the backcountry in 2018 (NPS 2022). The period of highest park visitation, March to October, overlaps with the breeding season of multiple raptor species in the canyon, including Mexican Spotted Owls.

Data Collection. Since 2001, the NPS has identified 54 Mexican Spotted Owl PACs within GCNP (Stortz et al. 2018) adhering to USFWS protocols. Despite adequate forest habitat on the plateau surrounding GCNP, all PACs occur below the rim in the inner canyon (Willey 1998, Willey and Ward 2003, Stortz et al. 2018). Owls were not limited by PAC boundaries, but the side-canyon draws that encapsulated most PACs provided sufficient topographic barriers separating one from another (Rinkevich and Gutiérrez 1996). Twenty-one PACs have an associated core area (i.e., a 40-ha area within the PAC that includes habitat features specifically used by owls for nesting and roosting) (USFWS 2012). We suspected PACs at GCNP without associated core areas were likely established around recurring auditory observations (USFWS 2012). Regardless, PACs are still assumed to contain nest/roost habitat and are expected to be important for owls at the park (USFWS 2012). Because we did not have designated core areas for all PACs, we used PAC boundaries as a proxy for an owl's potential breeding area and we extracted site-level predictor variables based

on PACs as units. GCNP wildlife staff have sought to survey all 54 PACs every 5 yr on a rolling basis; however, due to limited staff, programmatic objectives, and difficult access, the total number of PACs surveyed each year has varied widely.

Callback surveys. Biologists conducted callback surveys following protocols recommended in the Mexican Spotted Owl Recovery Plan (USFWS 2012). They used their voice or a playback device to imitate Spotted Owl calls and provoke responses (Forsman et al. 1984, USFWS 2012). Commonly used calls included four-note hoots and contact calls, which make up a large proportion of Mexican Spotted Owl vocalizations (Ganey 1990). Surveys typically occurred during either the 2 hr after sunset or 2 hr before sunrise between 1 March and 31 August (Forsman et al. 1984) from 2001–2021. Surveys occurred at stations spaced 400–800 m apart across the length of the PAC, with calls made every 60–90 sec for 15 min, followed by a 5-min listening period (USFWS 2012). Alternatively, surveyors occasionally used a version of this method in which they periodically hooted while walking a transect through the PAC using a technique called continuous calling (USFWS 2012). We defined a detection here as either a visual or auditory observation of a single or pair of owls on a single nocturnal callback survey. We included single owls or pairs as detections to bolster sample sizes, and because assessing reproductive status was an objective in our analysis.

ARU surveys. To optimize data collection during visits to remote sites, surveyors supplemented the callback method with the use of ARUs from 2019–2021. The ARUs were 8 GB AGPTEK U3 USB stick mp3 players (AGPTEK, Brooklyn, NY, USA) placed in 12 PACs to passively detect owls between 1 February and 31 August. We placed some ARUs in some remote PACs prior to the typical start of the survey season (1 March) to experimentally see if owls were hooting earlier than expected. PACs chosen for ARU deployment were usually in areas that lacked reliable water sources later in the season and were a priority to survey before temperatures became too hot in the canyon. We also deployed ARUs in PACs that were close to proposed project areas in the park, and park staff opportunistically deployed some ARUs in PACs while conducting general wildlife surveys along the Colorado River. The ARUs were structurally modified from a single internal AA battery to an external battery pack with two D-cell batteries to increase battery power and expose the microphone to a greater listening range (M. Szydlo pers. comm.). These modest mp3 players were used instead

of conventional ARUs (e.g., Wildlife Acoustics SM4 Song Meter) because of their low cost (~\$30 per unit) and their lightweight design, which was especially beneficial for remote sites requiring long-distance backpacking to access.

Whenever possible, biologists placed ARUs 1–2 m above the ground on rock ledges and under rock overhangs to protect the units from the elements (Hetzler 2022, M. Szydlo pers. comm.). They placed 1–6 ARUs (most commonly two) ~400 m apart in each PAC. This is similar to the standard distance between calling stations for callback surveys (USFWS 2012) and to the distances between ARUs and nest locations in a similar study at Walnut Canyon, AZ (Hetzler 2022). ARUs recorded for up to 26 d ($\bar{x}$ = 20 d) when the devices typically ran out of storage. Unlike typical ARUs used in wildlife studies, the AGPTEK mp3 devices could not be programmed to record during specific windows of time, therefore acoustic data were collected 24 hr/d in WAV format. We processed the recordings using AudioSplit 1.8 (McClimans 2021), which divided the data into diurnal (0600–1900 H Mountain Standard Time [MST]) and nocturnal (1900–0600 H MST) files. We then processed the nocturnal data using Raven Pro v1.6 (Yang 2021). The use of a band-limited energy detector (BLED) (Mills 2000) significantly reduced processing time by automatically recognizing owl calls. This tool has been found effective in other avian studies (Hetzler 2022) and had comparable false-positive and false-negative detection rates to other automated detectors (Brooker et al. 2020). The BLED recognizer was designed to search for four-note hoots that fell between 200–750 Hz, were 0.192–1.024 sec in duration, and had a minimum separation of 0.256 sec (M. Szydlo pers. comm.). Technicians manually reviewed the recognizer results to identify false positives (i.e., false detections) and discard them prior to analysis. False-positive results commonly included Mourning Doves (*Zenaida macroura*), canyon tree frogs (*Hyla arenicolor*), Great Horned Owls (*Bubo virginianus*), and wind. We did not identify any juvenile Mexican Spotted Owls on ARUs, as the recognizer was not designed to identify them. We defined a detection as a Mexican Spotted Owl calling session that was separated by at least 1 hr from a previous calling session. Individual detections typically included multiple owl calls, although rare examples involved only single calls. This approach allowed us to more easily organize the data first at an hourly resolution and then at a daily resolution. An owl in a PAC could potentially be detected by more than one ARU unit. Therefore, with a night defined as dusk to dawn (1900–0600 H MST; Kramer et al. 2023), we established a

nightly detection history for each PAC, where at least one detection of a Mexican Spotted Owl on any ARU in the PAC qualified as a detection for that night of the survey. Establishing a nightly history allowed us to more easily compare ARU data to callback data. It is important to note that, while we surveyed some PACs with both callback and ARU methods in the same field season, there was no temporal overlap in the data collected. For example, if a callback survey was conducted in the evening, ARUs were deployed the following day. When ARUs were collected, a callback survey may have been conducted on the retrieval visit, but ARUs were no longer recording when callback surveys were conducted.

Data Analysis. We used a multi-season, multi-method occupancy analysis to model the probability of long-term occupancy of PACs by Mexican Spotted Owls at GCNP. The model incorporated active callback surveys collected over the last two decades (2001–2021), and ARU surveys conducted from 2019–2021, as two detection submodels. To be included in this analysis, we required a PAC to be surveyed in at least 3 yr across the course of the study using either the callback method, ARU method, or both. We excluded 21 PACs from the analysis because they were either surveyed too infrequently over the course of the study or were exclusively surveyed using additional methodology with unclear protocols, such as surveying from the rim using a parabolic microphone (Rinkevich and Gutiérrez 1996, Budney and Grotke 1997). This filtering excluded all data collected from 2008–2010, when surveys were conducted either with the parabolic microphone or outside of PAC boundaries. We assessed survey effort by comparing the number of PACs surveyed over rolling 5-yr periods using callback surveys alone, to the rolling average when callback surveys were combined with ARU surveys.

We assessed the effects of site-level predictor variables on Mexican Spotted Owl occupancy probability. We derived vegetation classifications from the GCNP-Grand Canyon Parashant National Monument Vegetation Classification and Mapping Project (Kearsley et al. 2015), sampled from 2007–2008 at a minimum mapping unit of 0.5 ha. We calculated percent cover of 19 vegetation classes within each PAC and included percentages of shrub vegetation in each PAC as a predictor. We considered additional vegetation strata, such as pinyon-juniper woodland habitat, as predictor variables; however, some vegetation types occurred in small proportions within PACs and we did not expect them to have biological significance, and some vegetation types were highly correlated with one another and

were unable to be combined in our model. We also measured the diversity of vegetation types in each PAC using the Shannon diversity index, calculated using the diversity function $H = -\sum p_i \cdot \ln(p_i)$ in the *vegan* package (Oksanen et al. 2024) in R (R Core Team 2025), where p_i was the proportion of each vegetation category v in a PAC (Supplemental Material Fig. S1a, b for low vs. high Shannon diversity sites). We acknowledge that vegetation may have changed with environmental conditions over the course of our study period; however, our model was not designed to allow for year-to-year variation in site-level predictors. We obtained elevation data using the *elevatr* package in R, which aggregates data from Amazon Web Services terrain tiles into a digital elevation model (Hollister 2023), and clipped the 30-m resolution data to our study area. To describe the narrowness of canyon habitat within each PAC, we identified steep cliff areas within PACs (defined as any 30-m pixel with slope $\geq 60^\circ$) and measured the average horizontal distance between these steep cliffs and the nearest flowline (identified via National Hydrography Dataset flowlines; US Geological Survey 2023) on a two-dimensional plane. The final predictor thus captured a rough approximation of which PACs contained more narrow canyons (e.g., steep cliff faces close to a flowline) versus wide canyons (e.g., steep cliff faces far from a flowline). This predictor was called mean cliff distance and was made negative for ease of interpretation, with more positive values representing more narrow canyons. We chose this metric to describe the topographic complexity rather than other measures such as topographic ruggedness (Ganey et al. 2011), relative topographic change (Wiley and Zambon 2014), or topographic position index (Jones et al. 2023, Nayeri et al. 2024), because these variables were not adequately capturing the specific topographic features (i.e., narrow, shaded canyons with steep cliffs) known to be important to Mexican Spotted Owls at GCNP (Bowden 2008, Bowden et al. 2015).

We also assessed the effects of predictor variables on the detection probabilities for each survey method. For each method and survey night, we calculated the day of year and estimated mean moonlight illumination. We derived the latter metrics from the *moonlit* package in R, which described the average natural light available each night (Śmielak 2023). We obtained the maximum wind speed (m/s) for each night of an ARU survey from a weather station at GCNP Airport (Menne et al. 2012) located ~ 12 km from the rim of the canyon (35.94581°N , 112.1554°W). We also included survey effort as a variable in the ARU detection submodel, measured as the number of ARUs operating each night of the acoustic monitoring period. We removed

variables that were highly correlated (Spearman's rank correlation > 0.6) and centered and standardized all retained variables ($\bar{x}$, SD) to allow for comparison of effect sizes and improve model convergence (Schielzeth 2010).

We used a multi-season occupancy model to estimate probability of occupancy ($z_{i,k}$) for each PAC (i) during each breeding season (k), while accounting for imperfect detection (Kéry and Schaub 2012). We conservatively did not estimate occupancy for site and year combinations that we did not survey. The probability of occupancy each year (k) was related to Shannon diversity index of vegetation types, percent shrub cover, and the mean cliff distance in each PAC. We also included random site and year intercepts, ε_i and ε_k , respectively, to account for repeated sampling and annual variation in PAC occupancy:

$$\begin{aligned} \text{logit}(\psi_{i,k}) = & \beta_0 + \beta_1 * \text{Shannon diversity}_i \\ & + \beta_2 * \% \text{ shrub cover}_i \\ & + \beta_3 * \text{cliff distance}_i + \varepsilon_i + \varepsilon_k \end{aligned}$$

Occupancy was conditional on the probability of detecting an owl by either survey method, where z represented the true occupancy state, ψ represented occupancy probability modeled as a Bernoulli process, $p_{[cb]}$ represented detection probability of the callback survey method and $p_{[aru]}$ represented detection probability of the ARU survey method:

$$z_{i,k} \sim \text{Bernoulli}(\psi_{i,k} * p_{[cb]i,j,k} * p_{[aru]i,j,k})$$

The probability of detection using the callback survey method ($p_{[cb]i,j,k}$) was related to day of year and moonlight illumination via a logit link:

$$\begin{aligned} \text{logit}(p_{[cb]i,j,k}) = & \beta_{[cb]0} + \beta_{[cb]1} * \text{day of year}_{i,j,k} \\ & + \beta_{[cb]2} * \text{moonlight}_{i,j,k} \end{aligned}$$

The probability of detection using the ARU survey method ($p_{[aru]i,j,k}$) was related to day of year, maximum wind speed (m/s), number of ARUs operating each day, and moonlight illumination using a logit link:

$$\begin{aligned} \text{logit}(p_{[aru]i,j,k}) = & \beta_{[aru]0} + \beta_{[aru]1} * \text{day of year}_{i,j,k} \\ & + \beta_{[aru]2} * \text{moonlight}_{i,j,k} \\ & + \beta_{[aru]3} * \text{wind}_{i,j,k} \\ & + \beta_{[aru]4} * \text{effort}_{i,j,k} \end{aligned}$$

Priors for the random intercepts were distributed as $\varepsilon_i, \varepsilon_k \sim \text{Normal}(0, \sigma^2)$ and their standard deviations were given Student- t priors, distributed

as $\sigma[\varepsilon_i], \sigma[\varepsilon_k] \sim t(0, 2.5, 7)$ (Gelman et al. 2008). Priors for the fixed effects on occupancy, detection_[aru] and detection_[cb] were distributed as $\beta_u, \beta_a, \beta_c \sim \text{Normal}(0, 5)$ ($u = 3, a = 4, c = 2$). Priors for the occupancy and detection intercepts were set on the probability scale, so $\beta_0 = \log(\mu/1 - \mu)$, $\beta_{0[aru]} = \log(\mu_{[aru]}/1 - \mu_{[aru]})$ and $\beta_{0[cb]} = \log(\mu_{[cb]}/1 - \mu_{[cb]})$, with priors for mean occupancy and mean detection probabilities distributed as β distributions: $\mu; \mu_{[aru]}; \mu_{[cb]} \sim \beta_{(4,4)}$.

We ran all models using R v.4.5.1 (R Core Team 2025) and the *rjags* (Plummer 2024) and *jagsUI* packages (Kellner 2024). We ran five chains of 20,000 iterations, burned the first 10,000 and thinned every five. All chains converged for all models with no divergent transitions, and all $\hat{r}$ values were below the set limit of 1.02 (Gelman and Rubin 1992, McElreath 2019). We assessed model fit by comparing the deviance of the observed data to the deviance from the data predicted by the model, which we plotted at the PAC and year level (Cruz et al. 2019). We also used the deviance to calculate a Bayesian P -value, which provided a measure of how much the data predicted by the model deviated from the observed data, with values closer to 0.5 suggesting a good fit (McElreath 2019).

We evaluated long-term occupancy of PACs at GCNP by looking at changes in mean occupancy of each PAC through time. We assessed how survey effort compared to programmatic objectives by calculating the mean number of PACs surveyed over 5-yr rolling periods. Finally, when interpreting model output, we considered a predictor to have an important effect on the model if the probability of direction posterior distribution (Makowski et al. 2019) was $\geq 85\%$ (i.e., if 85% of the distribution of predictor values was either positive or negative; Arnold 2010, Jones et al. 2020). Lastly, we used marginal effect plots to visualize the relationship between strong predictors and occupancy/detection probabilities while holding other predictors in the model at their mean values.

RESULTS

Survey effort using the callback method was highly variable across the survey period (2001–2021). Effort was lowest from 2008–2010 when no PACs were surveyed using methods that met our standards for inclusion in the analysis, and was highest in 2013 when 26 PACs were surveyed ($\bar{x} = 8.5$ PACs/yr). In the 5 yr leading up to the conclusion of this study, 24 of 33 PACs (73%) were surveyed at least once; however, only 20 PACs (61%) were surveyed more than three

times across the 20-yr study using callback surveys alone. Moreover, we surveyed an average of only 7.9 PACs using the callback method across rolling 5-yr periods within the full study period (24%; range: 1.6–15.8 PACs). There was a strong bias by which method PACs were surveyed, with 53% of callback surveys related to only nine of 33 PACs. Additionally, the rolling 5-yr average was likely influenced by years 2013 and 2014, when there were significantly more PACs surveyed than in other years ($n = 26$ and 20 PACs, respectively). This spike in surveys conducted was likely a response to make up for minimal surveys in 2008–2010; it also reflected an increase in the number of surveyors. Despite this variability across the survey period, Mexican Spotted Owls were detected on 50% of individual callback surveys conducted from 2001–2021.

We collected more than 9,500 hr of acoustic data between 1900 and 0600 H from 58 ARUs in 15 Mexican Spotted Owl PACs (nine PACs in 2019, four PACs in 2020, and eight PACs in 2021). We identified 173 Mexican Spotted Owl call sessions over the survey period using ARUs. The ARU surveys recorded at least one Mexican Spotted Owl on 23% of nights, and 53% of the PACs surveyed using ARUs had at least one detection over the survey period. ARUs improved repeat sampling effort at PACs. On average, when using callback surveys alone there were 1.69 visits/PAC, whereas when using a combination of callback and ARU monitoring there was an average of 4.35 visits/PAC. There were clear improvements in survey effort for some PACs using ARUs, except during the 2020 field season, which was interrupted by the COVID-19 pandemic. Specifically, ARUs improved sampling at some of our most remote PACs that were not reasonably accessed by foot. These sites ($n = 4$) were accessed via the Colorado River, which was a faster and safer method of access during the hot summer months. Using this method, it was possible to deploy and collect ARUs by individuals on river trips that were not trained in conducting callback surveys.

The model fit from both datasets was adequate (Bayesian $p[\text{callback}] = 0.34$; Bayesian $p[\text{aru}] = 0.40$). The deviance between observed and predicted data was consistent across PACs for both survey methods (Fig. S2a, b), although the ARU method slightly underestimated observed occupancy for a few PACs (Fig. S2b). The model adequately fit estimated occupancy compared to observed occupancy from callback surveys throughout the study period (Fig. S3a). The model slightly underestimated observed occupancy from ARUs in 2019 and slightly overestimated observed occupancy from ARUs in 2021 (Fig. S3b).

Occupancy Probability. Mexican Spotted Owls occupied PACs consistently throughout the 20-yr study period (2001–2021), with a high mean probability of occupancy among sampled sites ($\psi = 0.64$, 90% CI: 0.10–0.98). Occupancy probability was lowest in the Transept Canyon PAC in 2018 ($\psi = 0.15$, 90% CI: 0.01–0.47) and highest in the Bright Angel PAC in 2011 ($\psi = 0.94$, 90% CI: 0.81–0.99) (Fig. 1). The effect of vegetation diversity was positively related to the probability that an owl occupied a PAC, with 87% of the posterior distribution falling in the positive direction (Fig. 2a). Occupancy probability was >0.75 when the Shannon vegetation diversity index in a PAC was greater than 1.6 (Fig. 3a). In contrast, the mean cliff distance and the percent shrub cover in a PAC did not exhibit meaningful effects on owl occupancy (73% positive direction and 71% negative direction, respectively) (Fig. 2b, c).

Detection Probability. Detection probability of Mexican Spotted Owls at a PAC varied by method, with callback surveys detecting owls with higher probability on average than ARU surveys on a single night ($P[\text{callback}] = 0.74$, 90% CI: 0.55–0.92, $P[\text{aru}] = 0.38$, 90% CI: 0.07–0.89). CIs around ARU detection probabilities were wide, particularly at sites with low detection. The effect of day of year was negatively associated with the probability of detecting an owl during an ARU survey, with 100% of the posterior distribution falling in the negative direction (Fig. 2d). Detection was around 0.75 at the onset of the survey period in February, which declined to around 0.10 after August (Fig. 3b). Conversely, the effect of the survey effort (number of ARUs used in a PAC) was positively associated with the probability of detecting an owl during an ARU survey, with 99% of the posterior distribution falling in the positive direction (Fig. 2e). Detection probability was more than 0.50 when five ARUs were used on a survey (Fig. 3c). The posterior distributions associated with wind speed and moon illumination were negative for the ARU method (Fig. 2f, g). Wind speed was likely to have a strong effect on detection (85%, Fig. 2f), with detection probability around 0.50 when maximum wind speed was close to 6 m/sec (Fig. 3d). Moonlight illumination offered no strong effect on detection probability using the ARU method (61%, Fig. 2g).

The effect of day of year was also negatively associated with the probability of detecting an owl using callback surveys, with 97% of the posterior distribution falling in the negative direction (Fig. 2h). Detection probability using the callback method was around 0.85 at the beginning of the survey season in March and declined to around 0.60 at the

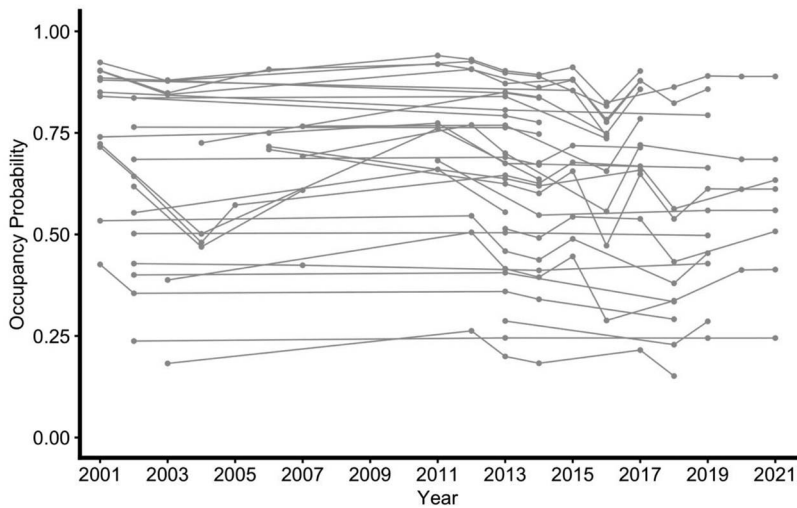


Figure 1. Estimated mean occupancy probability from a multi-season, multi-method occupancy model for Mexican Spotted Owl PACs at Grand Canyon National Park from 2001–2021. Thin grey lines represent the occupancy probability for each PAC included in the analysis and points along the lines represent years when those PACs were surveyed. There is a noticeable gap from 2008–2010 when no surveys were conducted that met our requirements for inclusion in the study.

end of the season in August (Fig. 3e). Moonlight illumination was positively associated with the probability of detecting an owl using callback surveys, with 93% of the posterior distribution falling in the positive direction (Fig. 2i). Detection probability increased from 0.60 on darkest nights to around 0.80 when moonlight illumination was more than 0.09 lux (Fig. 3f).

DISCUSSION

While a variety of factors threaten Mexican Spotted Owls across their range (Wan et al. 2018) leading to declines among some populations (Seamans et al. 1999), the results of our study of PAC occupancy over time at GCNP demonstrated that this local population of Mexican Spotted Owls appeared to be relatively stable over the 20-yr study period. Mexican Spotted Owls occupied PACs with high vegetation diversity, while the percent shrub cover and narrowness of the canyon habitat in a PAC had no meaningful effect on the probability of occupancy. Callback surveys detected Mexican Spotted Owls more consistently across the survey period than did ARU surveys; however, ARU surveys were particularly successful at detecting Mexican Spotted Owls early in the breeding period when they can be vulnerable to disturbance.

Mexican Spotted Owls were more likely to occupy PACs with higher vegetation diversity. These

PACs (with Shannon diversity indices > 1.50) had on average 9.43 primary vegetation types spanning a variety of taxa and canopy heights. Higher vegetation diversity at a site may reflect greater vertical and horizontal habitat complexity (Coverdale and Davies 2022), potentially affording cooler microclimate areas preferred by this species (Barrows 1981, Willey 1998, Ganey 2004). Mexican Spotted Owls in Zion National Park were also found in canyons with a greater number of vegetation strata (Rinkevich and Gutiérrez 1996). Additionally, while the inner canyon at GCNP is predominantly an arid desert environment, it also contains water sources that support lush vegetation in some areas (Huisinga et al. 2006). We were unable to obtain complete data of water presence at the canyon, particularly for ephemeral streams. We suspect, however, that higher vegetation diversity might be a direct reflection of water presence in PACs. Proximity to water is important for some populations of Mexican Spotted Owls. For example, in Zion National Park, 90% of Mexican Spotted Owls were found in canyons with either perennial or ephemeral water sources (Rinkevich and Gutiérrez 1996). Water is a limited resource in desert ecosystems (Rosenstock et al. 1999). Despite the physiological adaptations most desert species have to limited water availability (Schmidt-Nielsen 1964, Mares 1983), reliable water sources still attract an abundance of wildlife (Edwards et al. 2016), including small mammals (Switalski and Bateman

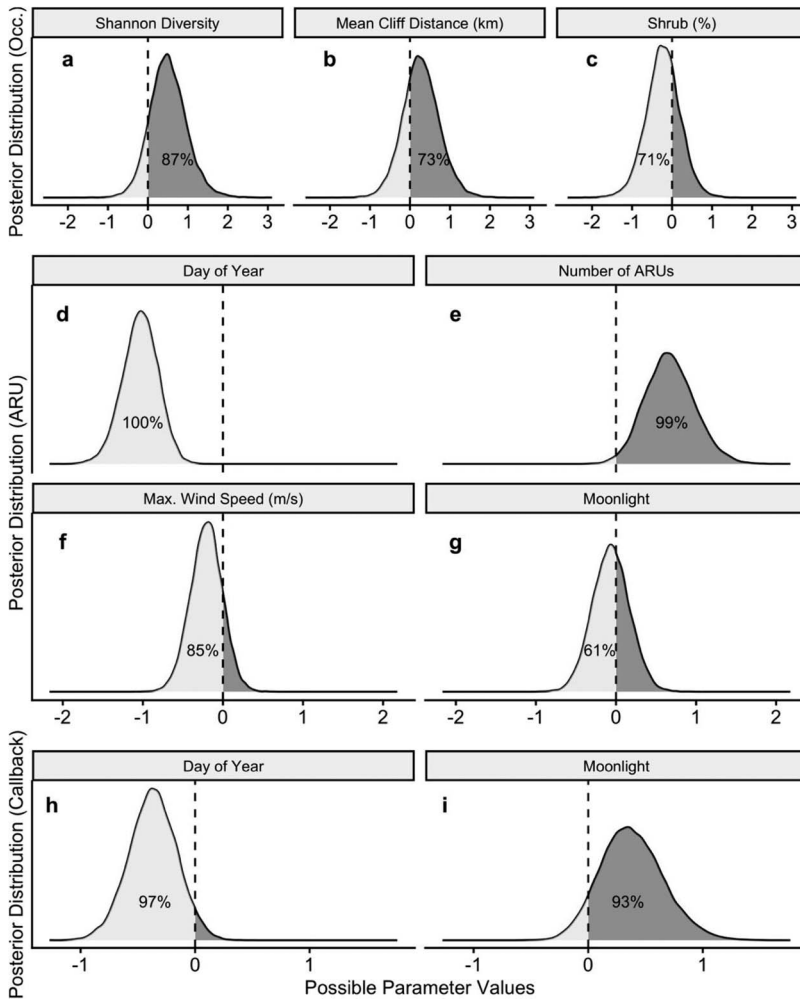


Figure 2. Posterior density distributions depicting the probability of direction for each predictor in the multi-season, multi-method occupancy (a–c), ARU detection (d–g), and callback detection (h–i) sub-models for Mexican Spotted Owls at Grand Canyon National Park (2001–2021). Predictor variables were considered to have a potentially meaningful effect on the model if 85% of their distribution was positive (shaded region) or negative (unshaded region).

2017, Rich et al. 2019). Areas that provide water in GCNP may be a hotspot for owl prey, ultimately influencing Mexican Spotted Owl occupancy.

Similarly, we hypothesized that shrub cover would support greater prey abundances and therefore predicted that owls would have higher occupancy in PACs with greater shrub cover; however, our results showed no support for this prediction. Shrublands are scattered across the geologic formations and elevations below the rim of GCNP (Kearsley et al. 2015) and are likely to be used by small mammal communities for cover and food (Parmenter and MacMahon 1983, Thornburg 2018). In particular,

we were interested in capturing vegetation strata that may reflect the presence of woodrats and white-footed mice, which are common Mexican Spotted Owl prey items (Willey 2013, Thornburg 2018). For example, there is some evidence that white-footed mice use areas with greater shrub cover in Capitol Reef National Park in southern Utah (Thornburg 2018). Furthermore, blackbrush, a common shrub species at GCNP, is known to be associated with desert woodrats (*Neotoma lepida*) in Arizona (Smith 1995). Desert woodrats are also known to consume creosote bush (*Larrea divaricate*; Cameron and Rainey 1972) and use sagebrush (*Artemisia* spp.) for structural materials in

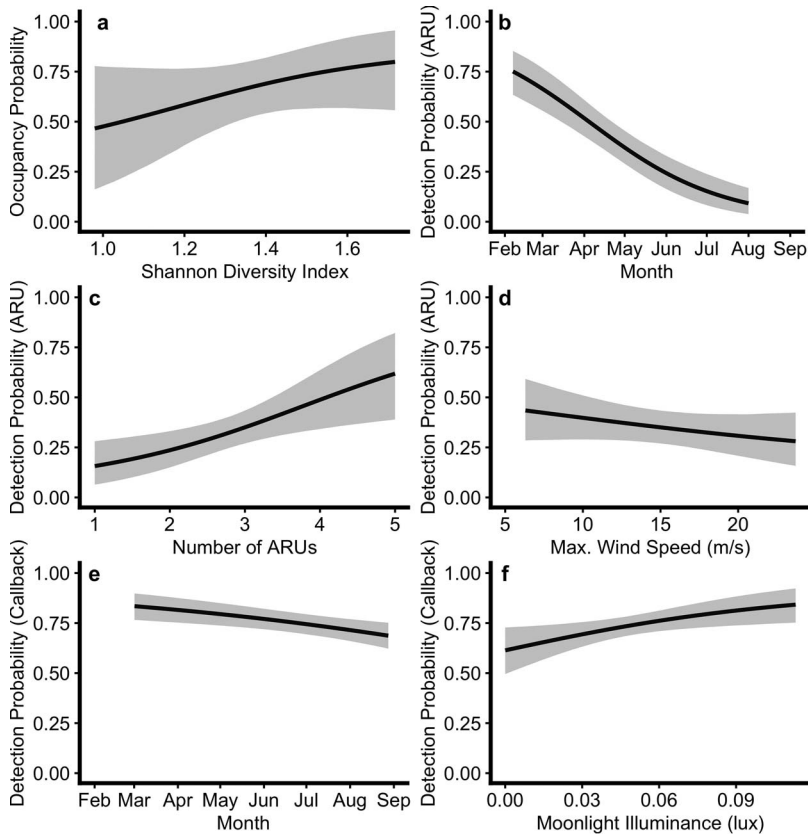


Figure 3. Marginal effect plots depicting Mexican Spotted Owl occupancy probability with changing (a) Shannon diversity index, (b) detection probability using the ARU method with changing day of year, (c) number of ARUs deployed on a survey, (d) maximum wind speed, (e) the detection probability using the callback method with changing day of year, and (f) moonlight illumination. Estimates derived from a multi-season, multi-method occupancy model using callback and ARU surveys for Mexican Spotted Owls in 33 PACs in Grand Canyon National Park monitored from 2001–2021. Shaded areas represent the 90% credible intervals.

their middens (Stones and Hayward 1968), both of which are common shrubs in GCNP. Despite this, some studies show the diet of desert woodrats consists of primarily juniper berries (Stones and Hayward 1968). While pinyon-juniper woodland habitat is prevalent at GCNP, it is not a common vegetation type within PAC boundaries. Shrub cover in PACs ranged from 25% to 95%; therefore, we suspect that even the lowest amount of shrub cover may have been enough to support an abundance of prey items for Mexican Spotted Owls. It is also possible that Mexican Spotted Owls at GCNP are simply not utilizing PACs for foraging like we expected they would. In a study of radiotracked Mexican Spotted Owls at GCNP, owls were found to forage in pinyon-juniper woodland habitat on the rim of the canyon, rather than down low on the shrub-covered benchlands

(Bowden 2008, Bowden et al. 2015). Furthermore, while the amount of shrublands varied from one PAC to another, this metric was static across the study period. The long-term change in shrub cover within PACs is unknown. Identifying this change through targeted vegetation surveys within PACs may more accurately reflect how various cover types are related to Mexican Spotted Owl occupancy. Further research relating vegetation with prey species that are important to Mexican Spotted Owls at GCNP (Willey 2013), would also help determine specific cover types that are important for owls in the inner canyon.

We predicted that owls would be more likely to occupy PACs in narrow side-canyons, which we described using a measure of mean cliff distance. We found only weak support for this prediction.

Steep-walled canyons have previously been linked with Mexican Spotted Owl habitat preferences across the Desert Southwest (Rinkevich and Gutiérrez 1996, Willey and van Riper III 2007, Bowden 2008, Willey and Zambon 2014). Narrow canyons offer owls a cooler, shaded reprieve from direct sunlight during the day (Rinkevich and Gutiérrez 1996, Willey 1998). Mexican Spotted Owls used narrow canyons with a mean width of 85 m in Zion National Park (Rinkevich and Gutiérrez 1996) and 68 m across the canyonlands of Utah (Willey and van Riper III 2015). Canyon width at roost sites at GCNP averaged 46.2 m (Bowden 2008), and nest and roost sites in the Guadalupe Mountains of southern New Mexico and western Texas occurred in canyons that averaged only 9.5 m wide at canyon bottoms (Mullet and Ward 2010). Although their use of narrow canyons in some environments is consistent, there are some outliers. For example, Mexican Spotted Owls in Texas used a canyon that exceeded 500 m wide at the roost location (Willey and van Riper III 2015). Similarly, Mexican Spotted Owls at GCNP were also observed to forage on the rim above wide canyons (Bowden 2008, Bowden et al. 2015). While we believe that our measure of canyon narrowness accurately distinguished narrow canyons from broad canyons, there may not have been a large enough spread of values in owl PACs at our study site to have a strong effect on occupancy. Additionally, our metric estimated the narrowness of owl PACs as a whole, which may have been less informative than measuring the narrowness of the canyon at specific roost locations like other studies have achieved (Willey and van Riper III 2015). Further research is needed to fully understand and describe the nuance in the topographic microhabitat preferences of Mexican Spotted Owls at GCNP.

Moonlight illumination had a positive effect on Mexican Spotted Owl detection when using callback surveys. Across owl species, the relationship between vocal activity and lunar conditions varies. While vocal activity increases around the full moon among Burrowing Owls (*Athene cunicularia*), Eagle Owls (*Bubo bubo*), and Eurasian Scops Owls (*Otus scops*) (Braga and Motta-Junior 2009, Penteriani et al. 2010, Mori et al. 2014), vocal activity of Mexican Spotted Owls in Arizona was previously linked to the last quarter and new moon phases (Ganey 1990). In our study, detection probability was high (0.6) during nights when moonlight illumination was 0 lux, but detection probability was even higher (0.8) when moon illumination reached 0.12 lux. Our results are consistent with studies that suggest brighter nights are advantageous for some owl species (Pérez-Granados et al. 2021).

Moonlight illumination likely affords more ambient light for foraging at night. Short-eared Owls (*Asio flammeus*) were found to be more efficient hunters under brighter moon conditions (Clarke 1983). Moonlight may also have provided more light for surveyors to detect owls visually. At our study site, Mexican Spotted Owls were rarely visually observed on nocturnal surveys due to the height of the canyon walls. However, small amounts of light may have improved surveyors' ability to visually detect birds enough to influence detection probability. This may help explain why moonlight illumination was considered a strong predictor for the callback survey but had no strong effect on ARU detections. While our results align with other studies, more research needs to be conducted to understand the specific mechanisms driving associations between moonlight illumination and nocturnal owl activity.

ARU detection probabilities increased with the number of acoustic monitors used in the survey. This effect likely can be attributed to recording distance limitations for each individual device. Although the number of ARUs used to survey a PAC was intended to increase with the size of the PAC and provide complete coverage, ARU failure at some stations led to some PACs being under surveyed and consequently owls were likely under detected in these areas. The reason for ARU failure could not be identified in many cases (i.e., simple device malfunction), but in some instances was attributed to animals chewing through device wires, an issue that has been identified in other ARU studies (Rognan et al. 2012). We recommend that at least four ARUs be used on PAC surveys in GCNP to improve detection probability. ARU detection probabilities were also affected by wind, with higher detection on nights with lower maximum wind speeds. Other ARU studies reported similar findings (Turgeon et al. 2017, Bobay et al. 2018, Stowell et al. 2019), including other studies of owls specifically (Takats and Holroyd 1997). Callback survey protocols restrict surveys to nights when wind conditions are less than a level 4 on the Beaufort wind strength scale (13 - 18 mph; USFWS 2012); however, there is no standard for omitting data collected by acoustic monitors on windy evenings. Our results suggest that detection is highest when maximum wind speeds are at 6 m/s, or a level 3 on the Beaufort scale (8–12 mph). While detection was likely even higher when wind speed was below 6 m/s, we were only able to predict across the maximum wind speeds observed in our dataset.

We were more likely to detect Mexican Spotted Owls earlier in the breeding season, regardless of survey method. As the season progressed, the probability of detection with ARUs declined steeply, while detection with callback surveys declined slightly but

remained high. Thus, callback surveys likely elicited responses even when owls were naturally less vocal later in the season (Ganey 1990, Morrell et al. 1991). Since ARU surveys rely on non-elicited vocalizations, the decline in detection with ARUs as the season progressed probably reflected owls becoming less territorial later in the breeding season when they either no longer needed to staunchly defend their territories (Ganey 1990) or they were caring for young (Reid et al. 2022). Mexican Spotted Owls and other Spotted Owl subspecies are sensitive to higher temperatures (Barrows and Barrows 1978, Barrows 1981, Ganey 2004), which also might have contributed to low calling rates throughout the hottest summer months. ARUs were more likely to detect Mexican Spotted Owls in February, prior to the official start of the callback survey period on 1 March (USFWS 2012). Thus, ARUs implemented in February are unlikely to disrupt wildlife (Digby et al. 2013) and can extend the official survey season, increasing the number of PACs surveyed each year. When surveyed passively with ARUs, the probability of detecting Barred Owls (*Strix varia*) also was higher earlier in the breeding season and declined as the season progressed (Clément et al. 2019).

Using the callback method alone to reach the prescribed objective of surveying all of the PACs over rolling 5-yr periods proved to be a challenge with allocated resources. As a result, PAC surveys over the last 20 yr were largely opportunistic. All of the identified Mexican Spotted Owl PACs at GCNP were below the rim of the canyon (Willey 1998, Willey and Ward 2003), limiting the modes of access to travel on foot or by river raft, and creating a challenging environment for repeated sampling. As a result, three PACs were heavily monitored over the years ($n = 11\text{--}12$ yrs each), while the remaining 30 PACs were surveyed on average in only 6 yr of the study period. Additional surveys were conducted at GCNP across the study period using a parabolic microphone (Budney and Grotke 1997, Bowditch et al. 2018) to amplify sounds from within the canyon and aid surveyors in detecting Mexican Spotted Owls from the rim (Rinkevich and Gutiérrez 1996). However, the survey methods used were ambiguous and therefore we did not use these data for analysis. Specifically, it was unclear whether these data were collected passively by simply listening from the rim or if surveyors hooted for owls while listening with the microphone.

Removing data gathered with a parabolic microphone greatly reduced the number of total sites included in our final analysis, as well as the mean number of repeat visits to sites. The clear exception was from 2013 to 2014, when roughly double the

number of callback surveys were conducted in comparison with other years. This result can partly be attributed to having a greater number of field technicians (6–9) assisting in those years, whereas the overall average number of observers for callback surveys across the full survey period was approximately four.

ARUs improved survey effort without increasing the number of specialized technicians, and increased the average number of repeat samples per year at PACs ($n = 1.7$ repeat visits using callback alone, and $n = 4.4$ repeat visits when using both methods). ARUs could also be deployed and collected by any individual, rather than exclusively owl surveyors, which increased the personnel allocated to this research. Additionally, ARUs were particularly useful for targeting PACs that were extremely remote (PACs most accessible from the Colorado River) and subsequently seldom sampled. ARUs could also be deployed earlier in the field season, effectively extending the survey period.

Despite the benefits of ARUs, we acknowledge that callback surveys and ARUs are not completely interchangeable. Callback surveys continue to be the most suitable method for sites that can be easily revisited, or when identifying a nest location is the priority. Developing a two-method approach that maximizes survey effort and detection rates is likely to result in the most accurate estimates of occupancy probability (Rognan et al. 2012). Other studies also report benefits of multi-method approaches. For example, wolf detection in Canada was highest when using ARUs and cameras (Garland et al. 2020), while estimates of wolf reproductive states in Spain were more accurate at sites with low detection and high occupancy when sign surveys and howling sessions were used (Jiménez et al. 2016). In another example, detection probability of Barred Owls was as high as 0.9 when using callback and ARU surveys combined (Clément et al. 2021).

By complementing callback surveys with ARU surveys in a rugged and remote landscape, we demonstrated that more sites could be surveyed each year without increased resources. We recommend deploying ARUs early in the breeding season at sites that are difficult to access. If the survey crew is understaffed, easily accessible sites should be sampled later in the breeding season with callback surveys, which maintain high detection throughout the survey period. We recommend increasing survey effort in PACs that have been under surveyed and that future monitoring efforts also identify whether PACs with high occupancy probability also produce young. We also demonstrated how data from multiple survey methods could be coupled with multi-method, multi-season occupancy models to estimate variation in long-term occupancy and determine habitat relationships. We advocate for

greater consideration of multi-method approaches to complement long-term monitoring programs.

SUPPLEMENTAL MATERIAL (available on-line). Figure S1. Mexican Spotted Owl PACs in Grand Canyon National Park with the lowest Shannon diversity of vegetation (a) and with the highest Shannon diversity of vegetation (b). Figure S2. Deviance estimated as the differences between the observed data at each protected activity center (PAC) using callback surveys (a) and ARU surveys (b) from the data predicted by a multi-season occupancy model of Mexican Spotted Owls surveyed using call-back surveys at Grand Canyon National Park from 2001–2021. Figure S3. Deviance estimates calculated by comparing annual differences between the observed data and the data predicted by a multi-season occupancy model of Mexican Spotted Owls surveyed using callback surveys (a) and ARU surveys (b) at Grand Canyon National Park from 2001–2021.

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LITERATURE CITED

- Acevedo, M. A., and L. J. Villanueva-Rivera (2006). Using automated digital recording systems as effective tools for the monitoring of birds and amphibians. *Wildlife Society Bulletin* 34:211–214. <https://www.jstor.org/stable/3784958>.
- Arnold, T. D. (2010). Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178. doi:10.2193/2009-367.
- Arnold, T. D., R. G. Clark, D. N. Koons, and M. Schaub (2018). Integrated population models facilitate ecological understanding and improved management decisions. *Journal of Wildlife Management* 82:266–274. doi:10.1002/jwmg.21404.
- Balantic, C., and T. Donovan (2019). Dynamic occupancy modeling using automated acoustic monitoring data. *Ecological Applications* 29:e01854. doi:10.1002/eap.1854.
- Baril, L. M., D. B. Haines, and D. W. Smith (2015). Long-term reproduction (1984–2013), nestling diet, and eggshell thickness of Peregrine Falcons (*Falco peregrinus*) in Yellowstone National Park. *Journal of Raptor Research* 49:347–358. doi:10.3356/rapt-49-04-347-358.1.
- Barrows, C. W. (1981). Roost selection by Spotted Owls: An adaptation to heat stress. *The Condor* 83:302–309. doi:10.2307/1367496.
- Barrows, C., and K. Barrows (1978). Roost characteristics and behavioral thermoregulation in the Spotted Owl. *Western Bird* 9:1–8. https://digitalcommons.usf.edu/western_birds/vol9/iss1/1.
- Bird, D. M., C. Petalas, P. Pace, and K. H. Elliott (2024). Using drones to measure the status of cavity-nesting raptors. *Drone Systems and Applications* 12:1–7. doi:10.1139/dsa-2023-0121.
- Bird, D. M., and J. A. Smallwood (2023). Evidence of continuing downward trends in American Kestrel populations and recommendations for research into causal factors. *Journal of Raptor Research* 57:131–145. doi:10.3356/JRR-22-35.
- Blakesley, J. A. (2015). Site Occupancy by Mexican Spotted Owls (*Strix occidentalis lucida*) in the US Forest Service Southwest Region, 2014. Technical Report SC-MSO-USFS-01. Rocky Mountain Bird Observatory, Brighton, CO, USA. <https://www.birdconservancy.org/wp-content/uploads/2025/01/MSO-Site-Occupancy-USFS-Region-3-2014.pdf>.
- Bled, F., J. L. Belant, L. J. Van Daele, N. Svoboda, D. Gustine, G. Hilderbrand, and V. G. Barnes Jr. (2017). Using multiple data types and integrated population models to improve our knowledge of apex predator population dynamics. *Ecology and Evolution* 7:9531–9543. doi:10.1002/ece3.3469.
- Bobay, L. R., P. J. Taillie, and C. E. Moorman (2018). Use of autonomous recording units increased detection of a secretive marsh bird. *Journal of Field Ornithology* 89:384–392. <https://www.jstor.org/stable/44994136>.
- Borker, A. L., P. Halbert, M. W. McKown, B. R. Tershy, and D. A. Croll (2015). A comparison of automated and traditional monitoring techniques for Marbled Murrelets using passive acoustic sensors. *Wildlife Society Bulletin* 39:813–818. doi:10.1002/wsb.608.
- Bowden, T. S. (2008). Mexican Spotted Owl Reproduction, Home Range, and Habitat Associations in Grand Canyon National Park. MS Thesis. Montana State University, Bozeman, MT, USA.
- Bowden, T. S., J. M. Ferguson, R. V. Ward, M. L. Taper, and D. W. Willey (2015). Breeding season home range and habitat use of Mexican Spotted Owls (*Strix occidentalis lucida*) below the South Rim of Grand Canyon National Park. *Wilson Journal of Ornithology* 127:678–689. doi:10.1676/15-004.1.
- Bowditch, N. L., S. K. Searing, J. A. Thomas, P. K. Thompson, J. N. Tubis, and S. P. Bowditch (2018). Use of a parabolic microphone to detect hidden subjects in search and rescue. *Wilderness and Environmental Medicine* 29:11–17. doi:10.1016/j.wem.2017.09.002.

- Braga, A. C. R., and J. C. Motta-Junior (2009). Weather conditions and moon phase influence on Tropical Screech Owl and Burrowing Owl detection by playback in southeast Brazil. *Ardea* 97:395–401. doi:[10.5253/078.097.0401](https://doi.org/10.5253/078.097.0401).
- Brooker, S. A., P. A. Stephens, M. J. Whittingham, and S. G. Willis (2020). Automated detection and classification of birdsong: An ensemble approach. *Ecological Indicators* 117:106609. doi:[10.1016/j.ecolind.2020.106609](https://doi.org/10.1016/j.ecolind.2020.106609).
- Budney, G. F., and R. W. Grotke (1997). Techniques for audio recording vocalizations of tropical birds. *Ornithological Monographs* 48:147–163. doi:[10.2307/40157532](https://doi.org/10.2307/40157532).
- Cade, T. J., J. H. Enderson, C. G. Thelander, and C. M. White (1988). *Peregrine Falcon Populations: Their Management and Recovery*. (T. J. Cade, J. H. Enderson, C. G. Thelander, and C. M. White, Editors). The Peregrine Fund, Inc., Boise, ID, USA.
- Cameron, G. N., and D. G. Rainey (1972). Habitat utilization by *Neotoma lepida* in the Mohave Desert. *Journal of Mammalogy* 53:251–266.
- Campos-Cerqueira, M. and T. M. Aide (2016). Improving distribution data of threatened species by combining acoustic monitoring and occupancy modelling. *Methods in Ecology and Evolution* 7:1340–1348. doi:[10.1111/2041-210X.12599](https://doi.org/10.1111/2041-210X.12599).
- Clarke, J. A. (1983). Moonlight's influence on predator/prey interactions between Short-eared Owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology* 13:205–209. <https://www.jstor.org/stable/4599626>.
- Clément, M. A., K. Barrett, and R. F. Baldwin (2019). Key habitat features facilitate the presence of Barred Owls in developed landscapes. *Avian Conservation and Ecology* 14:12. doi:[10.5751/ACE-01427-140212](https://doi.org/10.5751/ACE-01427-140212).
- Clément, M., J. Shonfield, E. M. Bayne, R. Baldwin, and K. Barrett (2021). Quantifying vocal activity and detection probability to inform survey methods for Barred Owls (*Strix varia*). *Journal of Raptor Research* 55:45–55. doi:[10.3356/0892-1016-55.1.45](https://doi.org/10.3356/0892-1016-55.1.45).
- Colbert, D. S., J. A. Rutinger, M. Streich, M. Chamberlain, L. M. Conner, and R. J. Warren (2015). Application of autonomous recording units to monitor gobbling activity by Wild Turkey. *Wildlife Society Bulletin* 39: 757–763. doi:[10.1002/wsb.577](https://doi.org/10.1002/wsb.577).
- Coverdale, T. C., and A. B. Davies (2022). Unravelling the relationship between plant diversity and vegetation structural complexity: A review and theoretical framework. *Journal of Ecology* 111:1378–1395. doi:[10.1111/1365-2745.14068](https://doi.org/10.1111/1365-2745.14068).
- Cruz, J., S. K. Windels, W. E. Thogmartin, S. M. Crimmins, L. H. Grim, J. H. Larson, and B. Zuckerburg (2019). Top-down effects of repatriating Bald Eagles hinder jointly recovering competitors. *Journal of Animal Ecology* 88:1054–1065. doi:[10.1111/1365-2656.12990](https://doi.org/10.1111/1365-2656.12990).
- Darras, K., P. Batáry, B. J. Furnas, I. Grass, Y. A. Mulyani, and T. Tscharrntke (2019). Autonomous sound recording outperforms human observation for sampling birds. *Ecological Applications* 29:1247–1265. doi:[10.1002/eap.1954](https://doi.org/10.1002/eap.1954).
- Davis, A. J., J. D. Kirby, R. B. Chipman, K. M. Nelson, T. Xifara, C. T. Webb, R. Wallace, A. T. Gilbert, and K. M. Pepin (2019). Not all surveillance data are created equal—A multi-method dynamic occupancy approach to determine rabies elimination from wildlife. *Journal of Applied Ecology* 56:2551–2561. doi:[10.1111/1365-2664.13477](https://doi.org/10.1111/1365-2664.13477).
- Descamps, S., J. Aars, E. Fuglei, K. M. Kovacs, C. Lydersen, O. Pavlova, A. Pedersen, V. Ravolainen, and H. Strom (2016). Climate change impacts on wildlife in a high Arctic archipelago – Svalbard, Norway. *Global Change Biology* 23:490–502. doi:[10.1111/gcb.13381](https://doi.org/10.1111/gcb.13381).
- Digby, A., T. Michael, B. D. Bell, and P. D. Teal (2013). A practical comparison of manual and autonomous methods for acoustic monitoring. *Methods in Ecology and Evolution* 4:675–683. doi:[10.1111/2041-210X.12060](https://doi.org/10.1111/2041-210X.12060).
- Dueñas, A., G. Jimenez-Uzcategui, and T. Bosker (2021). The effects of climate change on wildlife biodiversity of the Galapagos Islands. *Climate Change Ecology* 2:100026. doi:[10.1016/j.ecochg.2021.100026](https://doi.org/10.1016/j.ecochg.2021.100026).
- Edwards, S., A. C. Gange, I. Wiesel (2016). An oasis in the desert: The potential of water sources as camera trap sites in arid environments for surveying a carnivore guild. *Journal of Arid Environments* 124:304–309. doi:[10.1016/j.jaridenv.2015.09.009](https://doi.org/10.1016/j.jaridenv.2015.09.009).
- Evans, M. J. and T. A. G. Rittenhouse (2018). Evaluating spatially explicit density estimates of unmarked wildlife detected by remote cameras. *Journal of Applied Ecology* 55:2565–2574. doi:[10.1111/1365-2664.13194](https://doi.org/10.1111/1365-2664.13194).
- Farmer, C. J., and J. P. Smith (2009). Migration monitoring indicates widespread declines of American Kestrels (*Falco sparverius*) in North America. *Journal of Raptor Research* 43:263–273. doi:[10.3356/JRR-08-14.1](https://doi.org/10.3356/JRR-08-14.1).
- Flinders, J. T., D. S. Rogers, J. L. Webber-Alston, and H. A. Barber (2002). Mammals of the Grand Staircase-Escalante National Monument: A literature and museum survey. *Monographs of the Western North American Naturalist* 1:1–64. doi:[10.3398/1545-0228-1.1.1](https://doi.org/10.3398/1545-0228-1.1.1).
- Forsman, E. D., E. C. Meslow, and H. M. Wight (1984). Distribution and biology of the Spotted Owl in Oregon. *Wildlife Monographs* 87:1–64. <https://www.jstor.org/stable/3830695>.
- Franke, A., M. Settingington, G. Court, and D. Birkholz (2010). Long-term trends of persistent organochlorine pollutants, occupancy and reproductive success in Peregrine Falcons (*Falco peregrinus tundrius*) breeding near Rankin Inlet, Nunavut, Canada. *Arctic* 63:442–450. <https://www.jstor.org/stable/20799624>.
- Ganey, J. L. (1990). Calling behavior of Spotted Owls in Northern Arizona. *The Condor* 92:485–490. doi:[10.2307/1368245](https://doi.org/10.2307/1368245).
- Ganey, J. L. (2004). Thermal regimes of Mexican Spotted Owl nest stands. *The Southwestern Naturalist* 49: 478–486.
- Ganey, J. L., and R. P. Balda (1989). Distribution and habitat use of Mexican Spotted Owls in Arizona. *The Condor* 91:355–361. doi:[10.2307/1368314](https://doi.org/10.2307/1368314).

- Ganey J. L., and R. P. Balda (1994). Habitat selection by Mexican Spotted Owls in Northern Arizona. *The Auk* 111:162–169. doi:[10.2307/4088514](https://doi.org/10.2307/4088514).
- Ganey, J. L., J. P. Ward Jr., J. S. Jenness, W. M. Block, S. Hedwall, R. S. Jonnes, D. L. Apprill, T. A. Rawlinson, S. C. Kyle, and S. L. Spangle (2014). Use of protected activity centers by Mexican Spotted Owls in the Sacramento Mountains, New Mexico. *Journal of Raptor Research* 48:210–218. doi:[10.3356/JRR-13-18.1](https://doi.org/10.3356/JRR-13-18.1).
- Ganey, J. L., J. P. Ward Jr., and D. W. Willey (2011). Status and Ecology of Mexican Spotted Owls in the Upper Gila Mountains Recovery Unit, Arizona and New Mexico. General Technical Report RMRS-GTR-256WWW. US Department of Agriculture, US Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA. doi:[10.2737/RMRS-GTR-256](https://doi.org/10.2737/RMRS-GTR-256).
- Garland, L., A. Crosby, R. Hedley, S. Boutin, and E. Bayne (2020). Acoustic vs. photographic monitoring of gray wolves (*Canis lupus*): A methodological comparison of two passive monitoring techniques. *Canadian Journal of Zoology* 98:219–228. doi:[10.1139/cjz-2019-0081](https://doi.org/10.1139/cjz-2019-0081).
- Gauthreaux, S. A., A. Shapiro, D. Mayer, B. L. Clark, and E. E. Herricks (2019). Detecting bird movements with L-band avian radar and S-band dual-polarization Doppler weather radar. *Remote Sensing in Ecology and Conservation* 5:237–246. doi:[10.1002/rse2.101](https://doi.org/10.1002/rse2.101).
- Gelman, A., A. Jakulin, M. G. Pittau, and Y. Su (2008). A weakly informative default prior distribution for logistic and other regression models. *Annals of Applied Statistics* 2:1360–1383. doi:[10.1214/08-AOAS191](https://doi.org/10.1214/08-AOAS191).
- Gelman, A., and D. B. Rubin (1992). Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–511. doi:[10.1214/ss/1177011136](https://doi.org/10.1214/ss/1177011136).
- Gomes, D. G. E., G. Appel, and J. R. Barber (2020). Time of night and moonlight structure vertical space use by insectivorous bats in a Neotropical rainforest: An acoustic monitoring study. *PeerJ* 8:e10591. doi:[10.7717/peerj.10591](https://doi.org/10.7717/peerj.10591).
- Hafner, H., and M. Fasola (1997). Long-term monitoring and conservation of herons in France and Italy. *Colonial Waterbirds* 20:298–305. doi:[10.2307/1521697](https://doi.org/10.2307/1521697).
- Hetzler, B. C. (2022). Winter surveys for Mexican Spotted Owls with audio recorders. *Western Birds* 53:327–334. doi:[10.21199/WB53.4.3](https://doi.org/10.21199/WB53.4.3).
- Hobson, K. A., R. S. Rempel, H. Greenwood, B. Turnbull, and S. L. van Wilgenburg (2002). Acoustic surveys of birds using electronic recordings: New potential from an omnidirectional microphone system. *Wildlife Society Bulletin* 30:709–720. <https://www.jstor.org/stable/3784223>.
- Hockenbary, C. (2011). Exploring Relationships Among Recreation, Habitat Type, and Mexican Spotted Owls on the Colorado Plateau in Southern Utah. PhD Dissertation. Montana State University, Bozeman, MT, USA.
- Hodgson, J. C., R. Mott, S. M. Baylis, T. T. Pham, S. Wotherspoon, A. D. Kilpatrick, R. R. Segaran, I. Reid, A. Terauds, and L. P. Koh (2017). Drones count wildlife more accurately and precisely than humans. *Methods in Ecology and Evolution* 9:1160–1167. doi:[10.1111/2041-210X.12974](https://doi.org/10.1111/2041-210X.12974).
- Hollister, J. W. (2023). *elevatr*. Access elevation data from various APIs. Version 0.99.0. <https://CRAN.R-project.org/package=elevatr>.
- Huisinga, K., L. Makarick, and K. Watters (2006). *River and Desert Plants of the Grand Canyon*. Mountain Press Publishing Company, Missoula, MT, USA.
- Jahn, P., J. G. Ross, D. I. MacKenzie, and L. E. Molles (2022). Acoustic monitoring and occupancy analysis: Cost-effective tools in reintroduction programmes for Roroax-Great Spotted Kiwi. *New Zealand Journal of Ecology* 46:3466. doi:[10.20417/nzj ecol.46.21](https://doi.org/10.20417/nzj ecol.46.21).
- Jiménez, J., E. J. García, L. Llana, V. Palacios, L. M. González, F. García-Domínguez, J. Muñoz-Igualada, and J. V. López-Bao (2016). Multimethod, multistate Bayesian hierarchical modeling approach for use in regional monitoring of wolves. *Conservation Biology* 30:883–893. doi:[10.1111/cobi.12685](https://doi.org/10.1111/cobi.12685).
- Johnson, J. B., M. A. Menzel, J. W. Edwards, and W. M. Ford (2002). A comparison of 2 acoustical bat survey techniques. *Wildlife Society Bulletin* 30:931–936. <https://www.jstor.org/stable/3784249>.
- Jones, G. M., A. J. Shirk, Z. Yang, R. J. Davis, J. L. Ganey, R. J. Gutiérrez, S. P. Healey, S. J. Hedwall, S. J. Hoagland, R. Maes, K. Malcom, K. S. McKelvey, J. S. Sanderlin, M. K. Schwartz, M. E. Seamans, H. Y. Wan, and S. A. Cushman (2023). Spatial and temporal dynamics of Mexican Spotted Owl habitat in the southwestern US. *Landscape Ecology* 38:23–37. doi:[10.1007/s10980-022-01418-8](https://doi.org/10.1007/s10980-022-01418-8).
- Jones, G. M., L. Smith, I. G. W. Gottlieb, H. K. Ober, B. Brosi, and R. J. Fletcher Jr. (2020). Herpetofaunal responses to intensification of woody bioenergy production in a global biodiversity hotspot. *Forest Ecology and Management* 477:118493. doi:[10.1016/j.foreco.2020.118493](https://doi.org/10.1016/j.foreco.2020.118493).
- Kearsley, M. J., K. Green, M. Turkman, M. Reid, M. Hall, T. Ayers, and K. Christie (2015). Grand Canyon National Park–Grand Canyon/Parashant National Monument Vegetation Classification and Mapping Project. National Park Service Natural Resource Report NPS/GRCA/NRR—2015/913. Fort Collins, CO, USA. <https://irma.nps.gov/DataStore/Reference/Profile/2221240>.
- Kellner, K. (2024). *jagsUI*: A wrapper around ‘rjags’ to Streamline ‘JAGS’ Analyses. Version 1.6.2. <https://CRAN.R-project.org/package=jagsUI>.
- Kéry, M., and M. Schaub (2012). *Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*, First edition. Academic Press. doi:[10.1016/B978-0-12-387020-9.00005-5](https://doi.org/10.1016/B978-0-12-387020-9.00005-5).
- Kéry, M., and M. Schaub (2021). *Integrated Population Models: Theory and Ecological Applications with R and JAGS*. Academic Press. doi:[10.1016/C2019-0-02015-8](https://doi.org/10.1016/C2019-0-02015-8).
- Kramer, H. A., K. G. Kelly, S. A. Whitmore, W. J. Berigan, D. S. Reid, C. M. Wood, H. Klinck, S. Kahl, P. N. Manley, S. C. Sawyer, and M. Z. Peery (2023). Using bioacoustics to enhance the efficiency of Spotted Owl

- surveys and facilitate forest restoration. *Journal of Wildlife Management* 88:e22533. doi:[10.1002/jwmg.22533](https://doi.org/10.1002/jwmg.22533).
- Lawrimore, J. H., R. Ray, S. Applequist, B. Korzeniewski, and M. J. Menne (2016). Global Summary of the Year (GSOY), Version 1. NOAA National Centers for Environmental Information. doi:[10.7289/JWPF-Y430](https://doi.org/10.7289/JWPF-Y430).
- Lesmeister, D. B., and J. M. A. Jenkins (2022). Integrating new technologies to broaden the scope of Northern Spotted Owl monitoring and linkage with USDA forest inventory data. *Frontiers in Forests and Global Change* 5:966978. doi:[10.3389/ffgc.2022.966978](https://doi.org/10.3389/ffgc.2022.966978).
- Makowski, D., M. S. Ben-Shachar, S. H. Annabel Chen, D. Lüdtke (2019). Indices of effect existence and significance in the Bayesian framework. *Frontiers in Psychology* 10:2767. doi:[10.3389/fpsyg.2019.02767](https://doi.org/10.3389/fpsyg.2019.02767).
- Mares, M. A. (1983). Desert rodent adaptation and community structure. *Great Basin Naturalist Memoirs* 7: 30–43. <https://www.jstor.org/stable/23378266>.
- May, C. A., M. L. Petersburg, and R. J. Gutiérrez (2004). Mexican Spotted Owl nest and roost site habitat in Northern Arizona. *Journal of Wildlife Management* 68: 1054–1064. <https://www.jstor.org/stable/3803661>.
- McClimans, D. (2021). AudioSplit, Version 1.8. <https://github.com/dmcclimans/AudioSplit.git>.
- McElreath, R. (2019). *Statistical Rethinking: A Bayesian Course with Examples in R and Stan*, Second edition. CRC Press, Boca Raton, FL, USA.
- Menne, M. J., I. Durre, B. Korzeniewski, S. McNeal, K. Thomas, X. Yin, S. Anthony, R. Ray, R. S. Vose, B. E. Gleason, and T. G. Houston (2012). Global Historical Climatology Network – Daily (GHCN– Daily), Version 3. NOAA National Climatic Data Center. doi:[10.7289/V5D21VHZ](https://doi.org/10.7289/V5D21VHZ).
- Mills, H. (2000). Geographically distributed acoustical monitoring of migrating birds. *Journal of the Acoustical Society of America* 108:2582. doi:[10.1121/1.4743594](https://doi.org/10.1121/1.4743594).
- Mori, E., M. Menchetti, and F. Ferretti (2014). Seasonal and environmental influences on the calling behaviour of Eurasian Scops Owls. *Bird Study* 61:277–281. doi:[10.1080/00063657.2014.897303](https://doi.org/10.1080/00063657.2014.897303).
- 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. <https://www.jstor.org/stable/3782162>.
- Mullet, T. C., and J. P. Ward (2010). Microhabitat features of Mexican Spotted Owl nest and roost sites in the Guadalupe Mountains. *Journal of Raptor Research* 44: 277–285. doi:[10.3356/JRR-10-22.1](https://doi.org/10.3356/JRR-10-22.1).
- Murphy, D. D., and S. B. Weiss (1988). A long-term monitoring plan for a threatened butterfly. *Conservation Biology* 2(4):367–374. doi:[10.1111/j.1523-1739.1988.tb00201.x](https://doi.org/10.1111/j.1523-1739.1988.tb00201.x).
- National Park Service (2022). Integrated Resource Management Applications (IRMA) Portal: Overnight Stays. [https://irmadev.nps.gov/Stats/SSRSReports/National%20Reports/Overnight%20Stays%20\(1979%20-%20Last%20Calendar%20Year\)](https://irmadev.nps.gov/Stats/SSRSReports/National%20Reports/Overnight%20Stays%20(1979%20-%20Last%20Calendar%20Year)).
- Nayeri, D., S. Cushman, J. Ganey, L. Hysen, M. S. Gunther, D. Willey, and H. Y. Wan (2024). Multiscale habitat suitability modeling for a threatened raptor offers insight into ecological model transferability. *Ecological Modelling* 496:110845. doi:[10.1016/j.ecolmodel.2024.110845](https://doi.org/10.1016/j.ecolmodel.2024.110845).
- Nebuloni, R., and C. Capsoni (2024). The weather radar as a tool for collecting quantitative data on migrating birds. *IEEE Journal of Microwaves* 4:906–918. doi:[10.1109/JMW.2024.3492150](https://doi.org/10.1109/JMW.2024.3492150).
- Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, H. Wagner, et al. (2024). *vegan*: Community Ecology Package, Version 2.6-8. <https://CRAN.R-project.org/package=vegan>.
- Parmenter, R. R., and J. A. MacMahon (1983). Factors determining the abundance and distribution of rodents in a shrub-steppe ecosystem: The role of shrubs. *Oecologia* 59:145–156. doi:[10.1007/BF00378831](https://doi.org/10.1007/BF00378831).
- Pelton, M. R., and F. T. van Manen (1996). Benefits and pitfalls of long-term research: A case study of black bears in Great Smoky Mountains National Park. *Wildlife Society Bulletin* 24:443–450. <https://www.jstor.org/stable/3783325>.
- Penteriani, V., M. del Mar Delgado, L. Campioni, and R. Lourenço (2010). Moonlight makes owls more chatty. *PLoS ONE* 5:e8696. doi:[10.1371/journal.pone.0008696](https://doi.org/10.1371/journal.pone.0008696).
- Pérez-Granados, C., K. Schuchmann, and M. I. Marques (2021). Vocal activity of the Ferruginous Pygmy-owl (*Glaucidium brasilianum*) is strongly correlated with moon phase and nocturnal temperature. *Ethology Ecology & Evolution* 33:62–72. doi:[10.1080/03949370.2020.1820582](https://doi.org/10.1080/03949370.2020.1820582).
- Plummer, M. (2024). *rjags*: Bayesian Graphical Models using MCMC. Version 4-16. <https://CRAN.R-project.org/package=rjags>.
- Potapov, E. R., I. G. Utekhina, and D. Rimlinger (2013). Usage of UAV for surveying Steller's Sea Eagle nests. *Raptors Conservation* 27:253–260.
- R Core Team (2025). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Reid, D. S., C. M. Wood, S. A. Whitmore, W. J. Berigan, H. A. Kramer, N. F. Kryshak, J. J. Keane, S. C. Sawyer, R. J. Gutiérrez, H. Klinck, and M. Z. Peery (2022). Breeding status shapes territoriality and vocalization patterns in Spotted Owls. *Journal of Avian Biology* 8: e02952. doi:[10.1111/jav.02952](https://doi.org/10.1111/jav.02952).
- Reid, D. S., C. J. Zulla, N. F. Kryshak, J. Williams, S. J. Hedwall, R. Kirby, and G. M. Jones (2025). Testing the efficacy of protected areas: Use of protected activity centers by GPS-tagged Mexican Spotted Owls. *Journal of Raptor Research* 59:1–11. doi:[10.3356/jr2422](https://doi.org/10.3356/jr2422).
- Rich, L. N., S. R. Beissinger, J. S. Brashares, B. J. Furnas (2019). Artificial water catchments influence wildlife distribution in the Mojave Desert. *Journal of Wildlife Management* 83:885–865. doi:[10.1002/jwmg.21654](https://doi.org/10.1002/jwmg.21654).
- Rinkevich, S. E. (1991). *Distribution and Habitat Characteristics of Mexican Spotted Owls in Zion National Park, Utah*. MS Thesis. Humboldt State University, Arcata, CA, USA.

- Rinkevich, S. E. and R. J. Gutiérrez (1996). Mexican Spotted Owl habitat characteristics in Zion National Park. *Journal of Raptor Research* 30:74–78. <https://digitalcommons.usf.edu/jrr/vol30/iss2/4>.
- Rognan, C. B., J. M. Szewczak, and M. L. Morrison (2012). Autonomous recording of Great Gray Owls in the Sierra Nevada. *Northwestern Naturalist* 93:138–144. doi:10.1898/nwn11-02.1.
- Rosenstock, S. S. (1996). Shrub-grassland small mammal and vegetation responses to rest from grazing. *Journal of Range Management* 49:199–203. <http://www.jstor.org/stable/4002878?origin=JSTOR-pdf>.
- Rosenstock, S. S., W. B. Ballard, and J. C. Devos Jr. (1999). Viewpoint: Benefits and impacts of wildlife water developments. *Journal of Range Management* 52:302–311. doi:10.2307/4003538.
- Sauer, J. R., W. A. Link, J. E. Fallon, K. L. Pardieck, and D. J. Ziolkowski Jr. (2013). The North American Breeding Bird Survey 1966–2011: Summary analysis and species accounts. *North American Fauna* 79:2–32. doi:10.3996/nafa.79.0001.
- Sauer, J. R., K. L. Pardieck, D. J. Ziolkowski Jr., A. C. Smith, M. R. Hudson, V. Rodriguez, H. Berlanga, D. K. Niven, and W. A. Link (2017). The first 50 years of the North American Breeding Bird Survey. *The Condor* 119:576–593. doi:10.1650/CONDOR-17-83.1.
- Scheltz, C., D. Kent, D. Chalmers, and D. Svendsen (2004). Mexican Spotted Owl Inventory in Canyonlands National Park 2002–2003. General Technical Report SEUG-002-2003. USDI National Park Service, Southeast Utah Group Resource Management Division, Moab, UT, USA.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113. doi:10.1111/j.2041-210X.2010.00012.x.
- Schmidt-Nielsen, K. (1964). *Desert Animals: Physiological Problems of Heat and Water*. Oxford University Press, London, UK.
- Seamans, M. E., and R. J. Gutiérrez (1995). Breeding habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. *The Condor* 97:944–952. doi:10.2307/1369533.
- Seamans, M. E., R. J. Gutiérrez, C. A. May, and M. Zachariah Peery (1999). Demography of two Mexican Spotted Owl populations. *Conservation Biology* 13: 744–754. <https://www.jstor.org/stable/2641689>.
- Sivakumar, A. H., D. Sheldon, K. Winner, C. S. Burt, and K. G. Horton (2021). A weather surveillance radar view of Alaskan avian migration. *Proceedings: Biological Sciences* 288:1–10. doi:10.1098/rspb.2021.0232.
- Śmielak, M. K. (2023). Biologically meaningful moonlight measures and their application in ecological research. *Behavioral Ecology and Sociobiology* 77:21. doi:10.1007/s00265-022-03287-2.
- Smith, F. A. (1995). Den characteristics and survivorship of woodrats (*Neotoma lepida*) in the eastern Mojave Desert. *The Southwestern Naturalist* 40:366–372. <http://www.jstor.org/stable/30055143?origin=JSTOR-pdf>.
- Stiffler, L. L., J. T. Anderson, and T. E. Katzner (2018). Occupancy modeling of autonomously recorded vocalizations to predict distribution of *rallids* in tidal wetlands. *Wetlands* 38:605–612. doi:10.1007/s13157-018-1003-z.
- Stones, R. C., and C. L. Hayward (1968). Natural history of the Desert Woodrat, *Neotoma lepida*. *American Midland Naturalist* 80:458–476. doi:10.2307/2423539.
- Stortz, S., C. Aslan, T. Sisk, T. Chaudhry, J. Rundall, J. Palumbo, L. Zachmann, and B. Dickson (2018). Natural Resource Condition Assessment: Greater Grand Canyon Landscape Assessment. Natural Resource Report NPS/GRCA/NRR—2018/1645. National Park Service, Fort Collins, CO, USA. <https://irma.nps.gov/DataStore/Reference/Profile/2253268>.
- Stowell, D., M. D. Wood, H. Pamula, Y. Stylianou, and H. Glotin (2019). Automatic acoustic detection of birds through deep learning: The first bird audio detection challenge. *Methods in Ecology and Evolution* 10: 368–380. doi:10.1111/2041-210X.13103.
- Swarthout, E. C. H. and R. Steidl (2003). Experimental effects of hiking on breeding Mexican Spotted Owls. *Conservation Biology* 17:307–315. doi:10.1046/j.1523-1739.2003.01420.x.
- Switalski, A. B., and H. L. Bateman (2017). Anthropogenic water sources and the effects on Sonoran Desert small mammal communities. *PeerJ* 5:e4003. doi:10.7717/peerj.4003.
- Takats, D. L., and G. L. Holroyd (1997). Owl broadcast surveys in the foothills model forest, Alberta, Canada. In *Biology and Conservation of Owls of the Northern Hemisphere: 2nd International Symposium* (J. R. Duncan, D. H. Johnson, and T. H. Nicholls, Editors). General Technical Report NC-190. US Department of Agriculture, US Forest Service, North Central Forest Experiment Station, St. Paul, MN, USA. pp. 421–431. doi:10.2737/NC-GTR-190.
- Thompson, S. J., C. M. Handel, and L. B. McNew (2017). Autonomous acoustic recorders reveal complex patterns in avian detection probability. *Journal of Wildlife Management* 81:1228–1241. doi:10.1002/jwmg.21285.
- Thornburg, J. R. (2018). Effects of seasonal precipitation and habitat associations on the demographics of Mexican Spotted Owl prey in the canyonlands region of southern Utah. MS Thesis. Montana State University, Bozeman, MT, USA.
- Thornburg, J. R., D. Willey, and R. A. Garrott (2016). Mexican Spotted Owl site occupancy trends and small mammal abundance in the canyonlands of Utah. Abstract. *Intermountain Journal of Sciences* 22: 124–125.
- Turgeon, P. J., S. L. Van Wilgenburg, and K. L. Drake (2017). Microphone variability and degradation: Implications for monitoring programs employing autonomous recording units. *Avian Conservation and Ecology* 12:9. doi:10.5751/ACE-00958-120109.
- Udell, B. J., B. R. Straw, S. C. Loeb, K. M. Irvine, W. E. Thogmartin, C. L. Lausen, J. D. Reichard, J. T. H. Coleman, P. M. Cryan, W. F. Frick, and B. E. Reichert

- (2024). Using mobile acoustic monitoring and false-positive N-mixture models to estimate bat abundance and population trends. *Ecological Monographs* 94: e1617. doi:10.1002/ecm.1617.
- Upham-Mills, E. J., A. D. Crosby, J. R. Reimer, S. Haché, and T. Stehelin (2025). Accurate prediction of Olive-sided Flycatcher breeding status using song rate measured with autonomous recording units. *Journal of Wildlife Management* 89:e70026. doi:10.1002/jwmg.70026.
- US Fish and Wildlife Service (USFWS) (2012). Recovery Plan for the Mexican Spotted Owl (*Strix occidentalis lucida*), First Revision. Southwest Regional Office, Albuquerque, NM, USA.
- US Fish and Wildlife Service (USFWS) (2023). Mexican Spotted Owl (*Strix occidentalis lucida*) 5-year Review: Summary and Evaluation. Arizona Ecological Services Office, Flagstaff, AZ, USA. https://ecosphere-documents-production-public.s3.amazonaws.com/sams/public_docs/species_nonpublish/5226.pdf.
- US Geological Survey (2023). National Hydrography Dataset Best Resolution for Hydrologic Unit 4-1501. <https://www.usgs.gov/national-hydrography/access-national-hydrography-products>.
- Valle, R. G., and F. Scarton (2021). Monitoring the hatching success of gulls Laridae and terns Sternidae: A comparison of ground and drone methods. *Acta Ornithologica* 56:241–254. doi:10.3161/00016454AO2021.56.2.010.
- Van Ee, J. J., C. A. Hagen, D. C. Pavlacky Jr., D. A. Haukos, A. J. Lawrence, A. M. Tanner, B. A. Grisham, K. A. Fricke, L. G. Rossi, G. M. Beauprez, K. E. Kuklinski, et al. (2024). Melded integrated population models. *Journal of Agricultural, Biological, and Environmental Statistics* 30:769–799. doi:10.1007/s13253-024-00620-2.
- Varland, D. E., L. A. Powell, J. B. Buchanan, T. L. Fleming, and C. Vanier (2020). Peregrine Falcon survival rates derived from a long-term study at a migratory and overwintering area in coastal Washington, USA. *Journal of Raptor Research* 54:207–221. doi:10.3356/0892-1016-54.3.207.
- Wagner, P. W., C. D. Marti, and T. C. Boner (1982). Food of the Spotted Owl in Utah. *Journal of Raptor Research* 16: 27–28. <https://digitalcommons.usf.edu/jrr/vol16/iss1/8>.
- Wan, H. Y., J. L. Ganey, C. D. Vojta, and S. A. Cushman (2018). Managing emerging threats to Spotted Owls. *Journal of Wildlife Management* 82:682–697. doi:10.1002/jwmg.21423.
- Willey, D. W. (1998). Movements and habitat utilization by Mexican Spotted Owls in the Canyonlands of Utah. PhD Dissertation. Northern Arizona University, Flagstaff, AZ USA.
- Willey, D. W. (2013). Diet of Mexican Spotted Owls in Utah and Arizona. *The Wilson Journal of Ornithology* 125:775–781. <https://www.jstor.org/stable/24640491>.
- Willey, D. W., and C. van Riper III (2000). First-year movements by juvenile Mexican Spotted Owls in the canyonlands of Utah. *Journal of Raptor Research* 34:1–7. https://digitalcommons.usu.edu/crc_research/73.
- Willey, D. W., and C. van Riper III (2007). Home range characteristics of Mexican Spotted Owls in the canyonlands of Utah. *Journal of Raptor Research* 41:10–15. doi:10.3356/0892-1016(2007)41[10:HRCOMS]2.0.CO;2.
- Willey, D. W., and C. van Riper III (2015). Roost habitat of Mexican Spotted Owls (*Strix occidentalis lucida*) in the canyonlands of Utah. *The Wilson Journal of Ornithology* 127:690–696. doi:10.1676/14-021.1.
- Willey, D. W., and R. V. Ward (2003). Mexican Spotted Owl distribution and habitat within Grand Canyon National Park. In *Protecting our Diverse Heritage: The Role of Parks, Protected Areas, and Cultural Sites* (D. Harmon, B. M. Kilgore, and G. E. Vietzke, Editors). Proceedings of the 2003 George Wright Society/National Park Service joint conference. George Wright Society, Hancock, MI, USA. pp.328–334.
- Willey, D. W., and M. Zambon (2014). Predicting the occurrence of Mexican Spotted Owls in arid canyonlands of Southern Utah. *Journal of Raptor Research* 48:118–127. doi:10.3356/JRR-13-19.1.
- Wood, C. M., and M. Z. Peery (2022). What does ‘occupancy’ mean in passive acoustic surveys? *Ibis* 164: 1295–1300. doi:10.1111/ibi.13092.
- Yang, K. L. (2021). Raven Pro: Interactive Sound Analysis Software, Version 1.6. K. Lisa Yang Center for Conservation Bioacoustics, The Cornell Lab of Ornithology, Ithaca, NY, USA. <https://www.ravensoundsoftware.com/>.

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