Journal of Raptor Research

Advancing the science, conservation, and understanding of birds of prey

Journal of Raptor Research 59(1):jrr2422
doi: 10.3356/jrr2422

Testing the Efficacy of Protected Areas: Use of Protected Activity Centers by GPS-Tagged Mexican Spotted Owls

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ABSTRACT.—Protected areas play an important role in wildlife conservation, yet evaluating their effectiveness can be difficult. We assessed the efficacy of protected areas for Mexican Spotted Owls (*Strix occidentalis lucida*) by examining how federally designated Protected Activity Centers (PACs) and nest cores aligned with true Mexican Spotted Owl space use for roosting and foraging. We also examined if Mexican Spotted Owls used multiple PACs—a behavior commonly observed in California Spotted Owls (*Strix occidentalis occidentalis*)—and how Mexican Spotted Owl home range size compared to PAC size. We GPS tagged 22 owls from April through August 2023 across two study areas in the southwestern United States. PAC and nest core use was high, with over half (58%) of nocturnal foraging locations and 92% of diurnal roosting locations within PACs. Mexican Spotted Owls spent little time in other PACs outside of their home PAC, with most owls using just one PAC exclusively. Breeding season 75% kernel density home range estimates closely approximated Mexican Spotted Owl PAC size; however home ranges varied greatly among individuals based on sex, study area, and breeding status. Our research adds to that of previous studies showing Spotted Owls use PACs extensively, suggesting PACs are adequately protecting critical nest, roost, and foraging habitat for this species. However, we also observed a range of individual variation, emphasizing the importance of allowing protected area boundaries to be dynamic rather than static within a rapidly changing world.

KEY WORDS: *American Southwest*; *animal tracking*; *conservation*; *home range*; *movement ecology*; *space use*.

EVALUACIÓN DE LA EFICACIA DE LAS ÁREAS PROTEGIDAS: USO DE CENTROS DE ACTIVIDAD PROTEGIDOS POR PARTE DE INDIVIDUOS DE STRIX OCCIDENTALIS LUCIDA MARCADOS CON GPS

RESUMEN.—Las áreas protegidas juegan un papel importante en la conservación de la fauna silvestre, aunque evaluar su eficacia puede ser difícil. Evaluamos la eficacia de las áreas protegidas para *Strix occidentalis lucida* examinando cómo los Centros de Actividad Protegidos (CAP) y los núcleos de nidos designados por el gobierno se alineaban con el uso real del espacio por parte de *S. o. lucida* para posarse y alimentarse. También examinamos si *S. o. lucida* usaba múltiples CAP—un comportamiento comúnmente observado en *S. o. occidentalis*—y cómo el tamaño del área de campeo de *S. o. lucida* se comparaba con el tamaño del CAP. Marcamos con GPS a 22 individuos desde abril hasta agosto de 2023 en dos áreas de estudio en el suroeste de los Estados Unidos. El uso de CAP y de núcleos de nidos fue alto, con más de la mitad (58%) de las ubicaciones de alimentación nocturna y el 92% de las ubicaciones de de posaderos durante el día dentro de los CAP. Los individuos de *S. o. lucida* pasaron poco tiempo en

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otros CAP fuera de su CAP principal, con la mayoría de los individuos usando solo un CAP de manera exclusiva. Las estimaciones de área de campeo basadas en la densidad kernel del 75% en la temporada de reproducción se aproximaron mucho al tamaño del CAP de *S. o. lucida*; sin embargo, las áreas de campeo variaron mucho entre los individuos según el sexo, el área de estudio y el estado reproductivo. Nuestra investigación se suma a la de estudios previos que muestran que *S. occidentalis* usa los CAP extensamente, lo que sugiere que los CAP están protegiendo adecuadamente los hábitats críticos de nidos, posaderos y zonas de alimentación para esta especie. Sin embargo, también observamos un rango de variaciones individuales, lo que enfatiza la importancia de permitir que los límites de las áreas protegidas sean dinámicos en lugar de estáticos en un mundo que cambia rápidamente.

[Traducción del equipo editorial]

INTRODUCTION

Protected areas play a key role in conservation and are often touted as critical to safeguard wildlife species around the globe (Gaston et al. 2008, Hannah et al. 2020), despite the inherent limitations that come with setting what are often static reserve boundaries for mobile animal species (Nightingale et al. 2023). Additionally, climate change—among other stressors such as wildfires or the introduction of invasive species—can cause shifts in resource use and habitat quality over time, creating further misalignment between protected area boundaries and true space use by a given animal (Hannah et al. 2007, Whitney et al. 2023). Assessing the continued effectiveness of such management boundaries is thus incredibly important, especially for endangered species that can be particularly vulnerable to disturbance.

Many studies seek to evaluate the effectiveness of protected areas by examining "the representation and the maintenance of key biodiversity features" within reserves (Gaston et al. 2008). In other words, one must determine if the species the protected area was initially established to protect are still present and if space use by these species still aligns with protected area boundaries. Conducting such evaluations of species presence and space use can be especially challenging for larger-scale protected areas that are meant to conserve numerous species and/or conserve ecosystem biodiversity in general. But even data on how well a single species is represented within a given protected area can be difficult to obtain, especially for ones that are endangered or otherwise cryptic or rare.

The Mexican Spotted Owl (*Strix occidentalis lucida*) offers a salient case study to this issue as it is a threatened species for which protected areas play an important role and recent advances in GPS tagging approaches allow for the collection of high-resolution space use data. Indigenous to mature forests and canyons of the southwestern United States and Mexico, the Mexican Spotted Owl was originally listed as threatened under the United States Endangered Species Act in 1993 due to logging pressure and habitat loss in particular, with conservation efforts focusing heavily on the protection of critical nest/roost habitat within designated reserves (US Fish and Wildlife Service [USFWS] 1995, 2012). Federal recovery strategies called for the establishment of Protected Activity Centers (PACs) on public lands, meant to encompass "the best possible Mexican Spotted Owl habitat ... [including] as much roost/nest habitat as is reasonable, supplemented by foraging habitat where appropriate." (USFWS 2012:317). Managers delineate Mexican Spotted Owl PAC boundaries by enclosing a minimum area of 243 ha centered around known nest sites and roosting areas, with management activities such as timber harvests, road construction, and certain fuels treatments that remove vegetation to reduce fire risk (Agee and Skinner 2005) highly limited within PAC boundaries (USFWS 2012). Additionally, 40 ha "nest cores," enclosing the specific nest and/or roost stand within the PAC, are created upon initial PAC establishment and offer an additional boundary of protection inside which management activities are even more limited (USFWS 2012). While PAC and nest core boundaries can be adjusted as new nest or roost locations are discovered or in response to changes in habitat quality, it is important to note these boundary adjustments occur at the discretion of local biologists and are not necessarily made uniformly across regions or time (USFWS 2012).

PAC size was initially determined by the median size of 75% adaptive kernel contours estimated for 14 radio-marked owls (USFWS 2012), with subsequent studies finding PACs (Peery et al. 1999, Willey and Van Riper 2007, Ganey et al. 2011) and nest cores (Bowden et al. 2015) to be an adequate size relative to core areas of use for Mexican Spotted Owls. However, whether an individual Spotted Owl actually adheres to PAC and/or nest core boundaries for nesting, roosting, and foraging is rarely

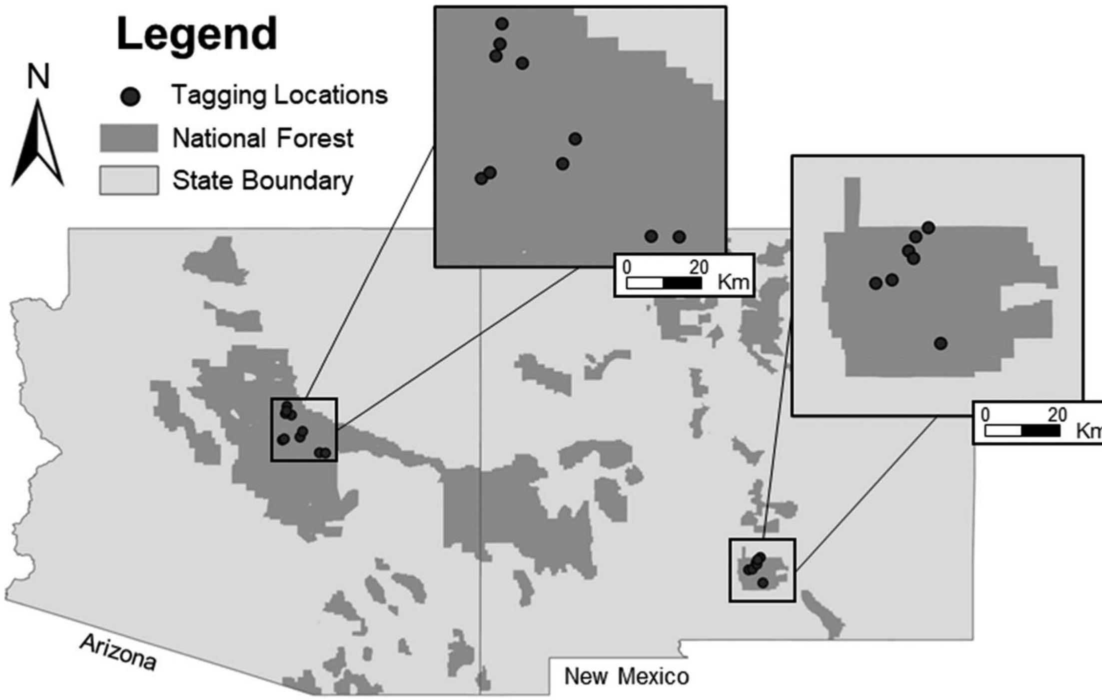

Figure 1. Map of Mexican Spotted Owl GPS tagging locations on the Coconino and Tonto National Forests, Arizona; and Lincoln National Forest, New Mexico. US National Forest land is shown in dark gray, with GPS tagging locations indicated by black dots.

assessed. One 2014 study using demographic data found PAC use by Mexican Spotted Owls to be high, with a median of 100% of nest and 97% of roost locations found within PAC boundaries (Ganey et al. 2014). However, this study did not incorporate foraging locations, nor did it assess if Mexican Spotted Owls use multiple PACs—a behavior that has been commonly observed in California Spotted Owls (*Strix occidentalis occidentalis*; Berigan et al. 2019, Blakey et al. 2019) but has yet to be studied in the Mexican Spotted Owl subspecies.

Here, we used GPS tags to assess the efficacy of PACs for Mexican Spotted Owls at two study areas in the southwestern United States. To do so, we examined how Mexican Spotted Owl space use—both diurnal roost locations as well as nocturnal foraging locations—aligned with PAC and nest core boundaries. We also examined how often Mexican Spotted Owls used multiple PACs, an important yet understudied behavior that can complicate conservation efforts by biasing occupancy estimates in studies of unmarked Spotted Owls (Berigan et al. 2019). Finally, we examined home range size relative to PAC size to determine if PACs appeared to be of an appropriate size for owls in our study area. This study provides important insights into the use of protected areas by a threatened subspecies, and utilizes modern technology to provide managers with updated information on how Spotted Owls use PACs in the southwestern United States.

METHODS

Study Area. Our study areas were located in the Lincoln National Forest in the Sacramento Mountains, New Mexico, USA; and in the Tonto and Coconino National Forests in the Upper Gila Mountains, Arizona, USA (Fig. 1). In New Mexico, the habitat was mixed-conifer forest dominated by white fir (*Abies concolor*) and Douglas-fir (*Pseudotsuga menziesii*) along slopes and ridgetops, with montane meadows in canyon and valley bottoms (Ganey et al. 2014). Southwestern white pine (*Pinus strobiformis*), ponderosa pine (*Pinus ponderosa*), and quaking aspen (*Populus tremuloides*) were also common in the area. Rain and snowfall in this area was among the highest in the state, averaging 762 mm of precipitation annually, with average maximum temperatures at 14°C annually (Western Regional Climate Center [WRCC] 2023). Private land was prevalent near study sites in New Mexico, mainly in the form of small, private ranches and inholdings. Elevation in this area ranged from 1900 to 2900 masl.

In Arizona, the study area was topographically complex and included sites above, below, and along the Mogollon Rim, a ~610-m-tall fault scarp. Habitat included ponderosa pine forest, pinyon-juniper (*Pinus* spp.-*Juniperus* spp.) woodland, and mixed-conifer forest consisting of white fir, Douglas-fir, and ponderosa pine (Ganey et al. 2011). Two sites were located directly along the Mogollon Rim itself, where the habitat consisted of steep canyons dominated by mixed-conifer forest along the canyon bottoms and dry, ponderosa pine forest above the canyon rim. Sites below the Mogollon Rim experienced warmer temperatures and received less rainfall overall, with maximum temperatures averaging 22°C annually and precipitation averaging 533 mm annually, compared to sites above the Rim, where maximum temperatures averaged 15°C and precipitation averaged 660 mm annually (WRCC 2023). Elevation in this area ranged from 1500 to 2500 masl.

Data Collection. We GPS tagged 22 Mexican Spotted Owls (6 females and 16 males) across 17 sites from April through August of 2023, with 12 owls (3 females and 9 males) tagged in Arizona and 10 owls (3 females and 7 males) tagged in New Mexico. All tagged owls were fitted with numbered USGS bands and unique color bands so individual identity could be established without requiring recapture. We captured owls using noose poles, pan traps, and hand capture methods (Forsman 1983), with sex and breeding status determined prior to capture following standard demographic survey protocols (Franklin et al. 1996). Only non-nesting male and female owls and nesting males were tagged as part of this study so as not to disturb nesting females during incubation. Further, we weighed all owls prior to tagging to ensure smaller owls (<450 g) were not tagged. GPS tags (Pinpoint-120, SWIFT, Lotek, Ontario, Canada) weighed approximately 6 g (<2% of average Spotted Owl body weight) and were attached to the two central retrices, allowing for the tag to be molted if the owl could not be recaptured (McGinn et al. 2023). GPS locations had a median error of 28 m based on field tests conducted at four locations in different environments with varying degrees of canopy cover and vegetation. Tags were programmed to collect nocturnal locations every hour from 2100 to 0500 H MST nightly and diurnal roost locations at 1400 H MST once every 4 d to maximize battery life.

Analysis. We assessed Mexican Spotted Owl space use through several key measures. First, we examined the proportion of nocturnal and diurnal locations found within PAC boundaries, as well as within the smaller 40-ha nest cores. Second, we evaluated the proportion of nocturnal and diurnal locations within (1) the owl's home PAC (where the tagged owl's nest or main roosting area was located), (2) in other PACs, and (3) outside of any PAC. Finally, we estimated home range size for tagged birds over the breeding season tracking period. Given the high temporal resolution of our GPS-tracking data, we used 95% autocorrelated-Gaussian kernel density estimators (AKDE) using the *amt* package (Singer et al. 2019) in Program R (Version 4.3.1, R Core Team 2023). Importantly, AKDE does not assume data to be independent and identically distributed, making it an effective home range estimator for high-resolution tracking data (Noonan et al. 2019). Autocorrelation in the data was estimated by fitting continuous-time movement models, with best-fit models selected using the corrected Akaike information criterion for each individual (Noonan et al. 2019). As Mexican Spotted Owl PAC size was originally estimated based on 75% adaptive kernel contours, we also generated 75% AKDE to directly compare to PAC size, as well as 95% minimum convex polygon (MCP) home range estimates for comparison to previous radio telemetry studies.

For each measure of owl space use—the proportion of nocturnal and diurnal locations within PAC and nest core boundaries; the proportion of locations within the owl's home PAC, in other PACs, and outside of PACs; and home range size—we tested whether these features differed among sexes, nesting status, or study areas using a three-way unbalanced analysis of variance (ANOVA) in Program R. Pairwise comparisons were assessed with Tukey's post hoc test as needed (Zar 2010). One male owl from our New Mexico study site had unknown nesting status, and was thus excluded from all ANOVA analyses.

RESULTS

PAC Usage. In total, our GPS tags collected 7898 locations, averaging 349 nocturnal locations (range: 48–625) and 10 diurnal roost locations (range: 1–19) per owl. Tags recorded an average of 42 nights of data (range: 5–76) per owl, with four individuals

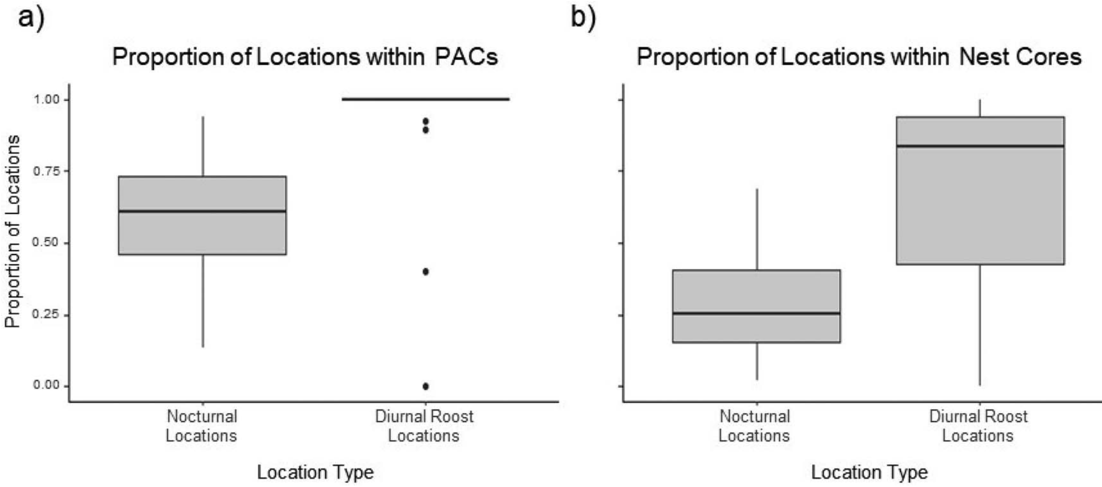

Figure 2. Boxplots showing the proportion of nocturnal locations and diurnal roost locations of GPS-tagged Mexican Spotted Owls (n = 22) within (a) PACs, and (b) nest cores. The vertical lines represent minimum and maximum values, gray boxes represent the lower and upper quartiles, and the black horizontal line represents the median. Black dots represent outliers. Diurnal roost locations were highly concentrated within PACs and nest cores, while on average over half of nocturnal locations occurred within PACs and over a quarter occurred within nest cores.

tracked for <20 nights due to tag malfunctions and early molting of tail feathers. On average, 58% of an individual owl's nocturnal locations (range: 14–94%) occurred within PACs, with 28% (range: 2–69%) occurring within nest cores (Fig. 2). Diurnal roost locations occurred within PACs 92% of the time on average (range: 0–100%) and occurred within nest cores 66% of the time (range: 0–100%). Overall, 18 of 22 owls had 100% of their roost locations occurring within PACs, and 11 owls had >80% of their roosts within nest cores. There was no difference in the proportion of locations occurring within PACs by study area (df = 1, $F = 0.01$, $P = 0.91$), breeding status (df = 1, $F = 2.09$, $P = 0.17$), or sex (df = 1, $F = 0.06$, $P = 0.81$), nor were there differences observed within nest cores (study area: df = 1, $F = 0.01$, $P = 0.92$; breeding status: df = 1, $F = 0.78$, $P = 0.39$; sex: df = 1, $F = 1.01$, $P = 0.33$).

Multiple PAC Use. Overall, an average of 53% (range: 0–89%) of nocturnal locations occurred within an owl's home PAC, with 5% (range: 0–39%) occurring within other PACs and 42% (range: 6–86%) occurring outside of PACs (Fig. 3). Diurnal roost locations were almost exclusively located within an owl's home PAC, with only a single roost location (0.05%) observed in another PAC. On average, owls used 1.91 PACs (range: 1–5) and 1.32 nest cores (range: 1–4) per individual, with 13 of 22 owls (59%) using only one PAC (Fig. 4). Nesting owls used significantly more PACs (mean: 2.6, range: 1–5) than non-nesting owls (mean: 1.17, range: 1–3; df = 2, $F = 6.53$, $P = 0.02$), with no significant difference observed based on study area (df = 1, $F = 0.02$, $P = 0.89$) or sex (df = 1, $F = 0.3$, $P = 0.59$).

Home Range Size. The 95% AKDE home ranges estimated over the breeding season tracking period averaged 583 ha (range: 204–1184 ha). Males (mean: 640 ha, range: 268–1184 ha) had significantly larger home ranges than females (mean: 312 ha, range: 204–804 ha; df = 1, $F = 6.66$, $P = 0.02$), and a significant interaction was also observed between study area and breeding status (df = 1, $F = 10.14$, $P < 0.01$; Fig. 5). In our New Mexico study area, non-nesting owls (mean: 790 ha, range: 393–1184 ha) had significantly larger home ranges than nesting owls (mean: 341 ha, range: 268–612 ha; df = 16, t-ratio = −3.26, $P = 0.02$). Non-nesting owls in New Mexico also had significantly larger home ranges than non-nesting owls in Arizona (mean: 391 ha, range: 204–676 ha; df = 16, t-ratio = −3.14, $P = 0.03$). Meanwhile, in our Arizona study area, non-nesting owls did not have significantly different homes ranges from nesting owls (mean: 482 ha, range: 378–1119 ha; df = 16, t-ratio = 0.64, $P = 0.92$).

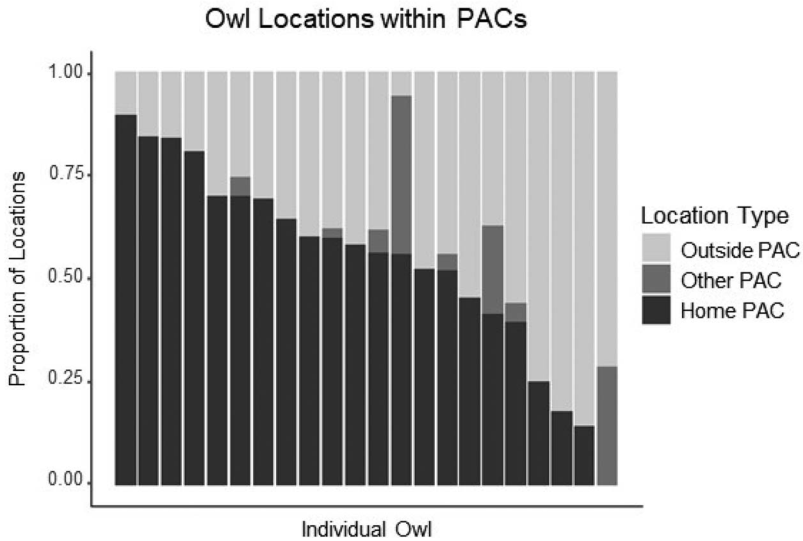

Figure 3. Proportion of all nocturnal and diurnal Mexican Spotted Owl ($n = 22$) GPS locations within an individual's home PAC (black), other PACs (dark gray), and outside PACs (light gray). Most owls had a high proportion of locations within their home PAC and spent little time in other PACs, although this varied by individual.

As Mexican Spotted Owl PAC size was originally estimated based on 75% adaptive kernel contours, we also estimated 75% AKDE home ranges for comparison. Our 75% AKDE home ranges averaged 259 ha (range: 61–573 ha). Additionally, we estimated 95% MCP home ranges to compare with previous radio telemetry studies. MCP estimates averaged 505 ha (range: 140–1103 ha). All statistical trends observed with 95% AKDE home ranges were likewise observed with 75% AKDE and MCP estimates.

DISCUSSION

We used GPS tags to assess the efficacy of Mexican Spotted Owl PACs by examining how owl space use aligned with PAC boundaries. We found that

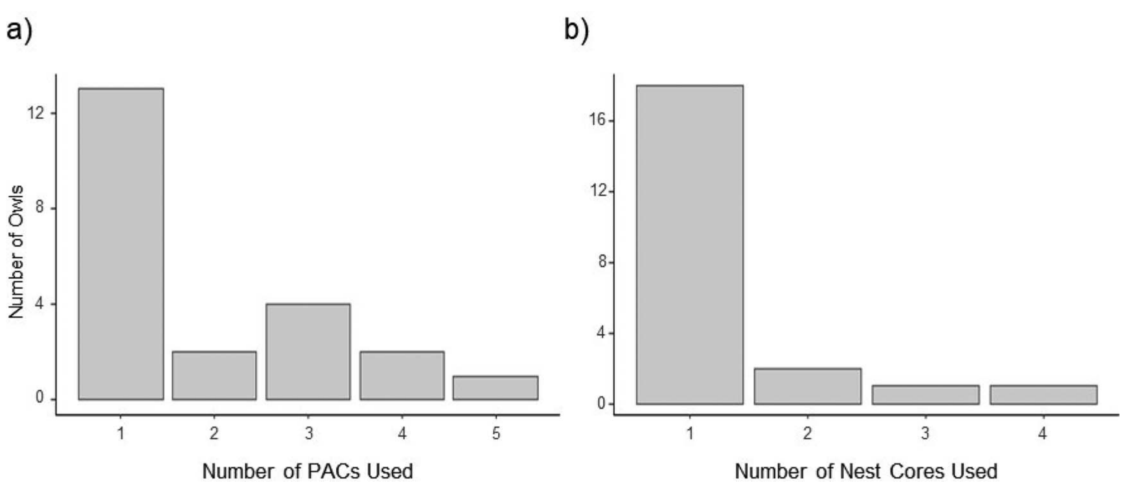

Figure 4. Bar charts summarizing (a) the number of PACs used by an individual Mexican Spotted Owl over the tracking period, and (b) the number of nest cores used. The majority of GPS-tagged owls used only one PAC and one nest core.

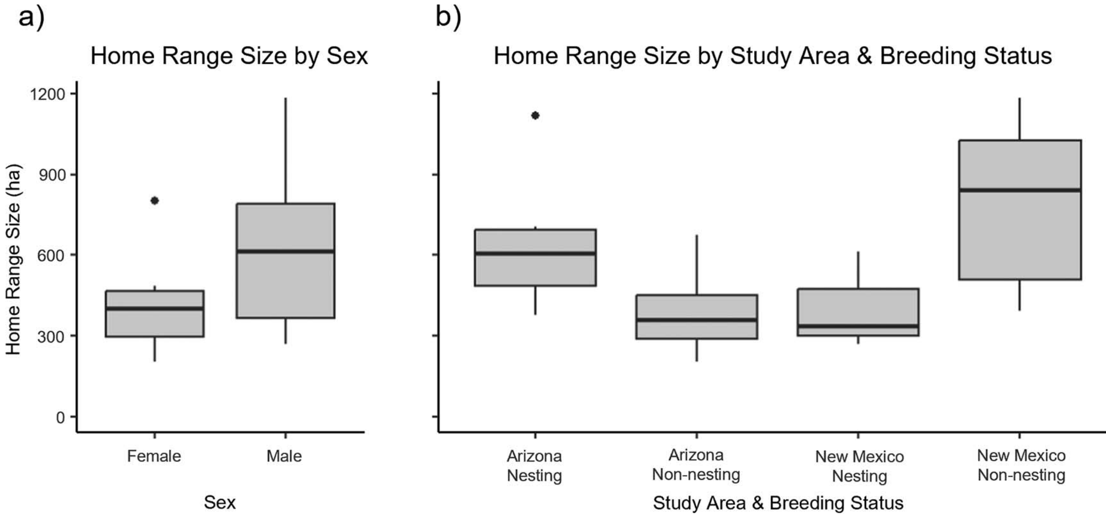

Figure 5. Boxplots of breeding season home range sizes for GPS-tagged Mexican Spotted Owls ($n = 21$) estimated using 95% kernel density estimates with autocorrelated-Gaussian bandwidth optimizers (AKDE). The vertical lines represent minimum and maximum values, gray boxes represent the lower and upper quartiles, and the black horizontal line represents the median. Black dots represent outliers. (a) Boxplot showing home range size variation by sex, with males having significantly larger home ranges than females; (b) Boxplot showing home range size variation by study area and breeding status, with non-nesting owls in our New Mexico study area having significantly larger home ranges than nesting owls in the area, and also significantly larger home ranges than non-nesting owls in our Arizona study area.

Mexican Spotted Owl space use overlapped considerably with PAC boundaries for both diurnal roosting as well as nocturnal foraging locations (Fig. 2a), consistent with previous literature examining only nests and roosts (Ganey et al. 2014). Nest core use was also high, especially for diurnal roosts (Fig. 2b) as well as nests. There were 11 nests associated with our tagged owls during this study, nine of which were successful and two of which failed prior to tagging; all nests except for one were located within PACs, either within or just outside of the nest core boundary. One owl, a nesting male, was an outlier here as his nest and roosting locations were located completely outside of any PAC boundaries; all other individuals, however, showed relatively high use of PACs, especially for nesting and roosting.

We observed Mexican Spotted Owls using multiple PACs outside of their home PAC where the nest/main roosting area was located. However, owls in our study did so at a lower rate compared to previous studies of California Spotted Owls (Berigan et al. 2019, Blakey et al. 2019). Owls in our study used an average of 1.91 PACs (range: 1–5), with 13 of 22 owls using only one PAC (Fig. 4a). Furthermore, on average only 5% of an individual owl's locations occurred within other PACs, demonstrating that spotted owls in our study spent very little time in other PACs (Fig. 3). By comparison, one study of California Spotted Owls in the Sierra Nevada found an average of 21% of owl locations occurring within other PACs, with owls using 2.33 PACs on average (Berigan et al. 2019), and a second study found California Spotted Owls using 2.7 PACs on average (Blakey et al. 2019). The lower average number of PACs used by owls in our study likely reflects the larger 243-ha PAC size used for Mexican Spotted Owls, which are double the size of PACs used for California Spotted Owls (121 ha; US Forest Service 2019). Additionally, a higher density of Spotted Owls could be present in our study areas relative to California, resulting in owls carefully partitioning their space use and leading to fewer intrusions into neighboring PACs. Nevertheless, we observed that Mexican Spotted Owls do sometimes use multiple PACs. This information is particularly salient for land managers and biologists because nocturnal surveys across multiple PACs could potentially detect the same owl and inflate occupancy estimates if not accounted for (Berigan et al. 2019).

We observed differences in the number of PACs used by Mexican Spotted Owls based on breeding status, with nesting owls using more PACs than non-

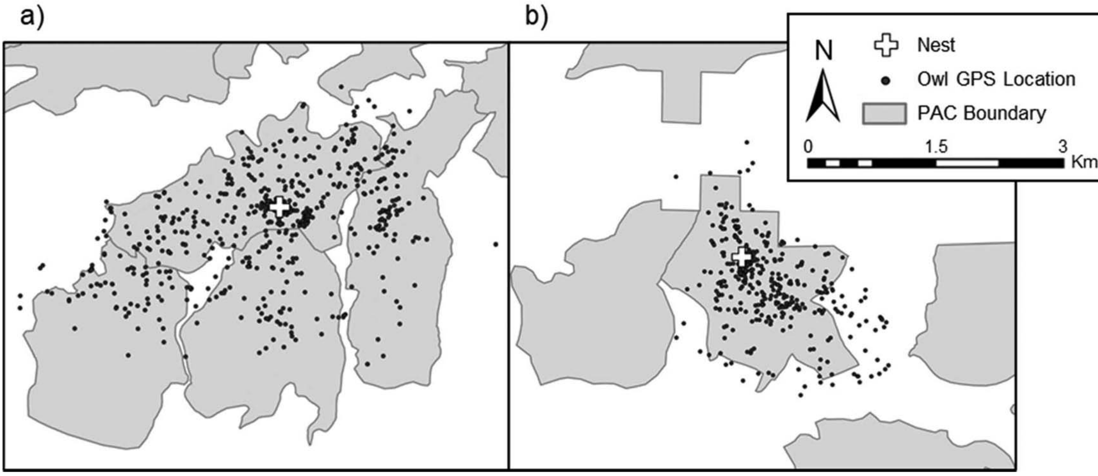

Figure 6. Example of two GPS-tagged nesting male Mexican Spotted Owls and their nearby PACs. PACs are shown in gray with GPS locations indicated by black dots and nest locations shown by white crosses. (a) For this nesting male, PAC density in the area was high with many PACs directly adjacent to each other. This male often ventured into neighboring PACs outside of his home PAC where the nest was located. (b) For this owl, PAC density was less extreme and this male also carefully partitioned his space use, never intruding into other PACs even though there were multiple PACs nearby. The sharp edges on the PACs in this map represent the presence of private land in the area, impacting PAC shape and alignment.

nesting owls. This observation could be due to differences in foraging behavior, in which nesting male owls provisioning females and young are targeting high-quality habitat patches within other nearby PACs. Provisioning young Spotted Owls requires a significant foraging investment, with breeding Northern Spotted Owls (*Strix occidentalis caurina*) shown to target areas of high prey abundance (Ward et al. 1998). Additionally, PAC establishment is shaped by many factors in the southwestern United States, with different ecological and management histories resulting in different PAC alignments and densities on the landscape. This causes the use of multiple PACs to be more likely in some areas than others—for example, in areas where neighboring PAC boundaries are directly adjacent to each other (Fig. 6a). The presence of private and non-federal land can also create artificial gaps and edges in PAC boundaries (Fig. 6b), resulting in PACs spaced farther apart than they would otherwise be. Consequently, many factors may be at play in the trends observed here of multiple PAC use by Mexican Spotted Owls, requiring further study.

The 75% AKDE breeding season home ranges (mean: 259 ha) closely approximated Mexican Spotted Owl PAC size (243 ha). However, home range estimates varied greatly among individuals. Male owls had larger breeding season home ranges than females, with non-nesting owls in our New Mexico study area having the largest home ranges (Fig. 5). Interestingly, we observed differences in home range size based on breeding status in our New Mexico study area, but not in Arizona. In New Mexico, non-nesting birds had significantly larger home ranges—more than double the size of nesting birds. Meanwhile, there was no significant difference in the home range size of nesting and non-nesting owls in Arizona. Few studies examine differences in home range size between nesting and non-nesting Spotted Owls during the breeding season; however, one study of Mexican Spotted Owls in the Rincon Mountains of Arizona did observe larger breeding season home ranges in non-nesting owls (Willey and Van Riper 2014).

The differences we observed in home range size based on breeding status in New Mexico, but not in Arizona, may be due to differences in habitat quality between the two study areas. Habitat quality is known to affect the home range size of Mexican Spotted Owls throughout their range, with greater amounts of mixed-conifer forest in particular associated with smaller home range sizes (Ganey et al. 2005). In New Mexico on the Lincoln National Forest, mixed-conifer forest was more prevalent within PACs but also more variably dispersed between PACs (mean mixed-conifer forest coverage: 17%, SD: 19%), while in Arizona mixed-conifer forest was rarer and more evenly dispersed across PACs on both the Coconino National Forest (mean: 8%, SD: 11%) and the Tonto National Forest (mean: 2%, SD: 4%; LANDFIRE 2022). The greater variability in amount of mixed-conifer forest available to owls on the Lincoln National Forest may have led to greater variation in home range size, compared to Arizona where the lower amount and variability of high-quality habitat may have resulted in more consistent home range sizes across sites. Importantly, we did not examine any habitat associations as part of this study. Future studies would benefit from examining the relationship between habitat variables and home range size to further elucidate the patterns observed here.

Home range size estimates for Mexican Spotted Owls are highly variable between studies and depend greatly on the exact study areas and methods used, making direct comparisons to other studies difficult (Ganey et al. 2011, USFWS 2012). However, the original 1995 Recovery Plan for the species cites three radio telemetry studies of Mexican Spotted Owls that resulted in 95% MCP home range estimates between 261 and 1487 ha (USFWS 1995:27). Our 95% MCP home range mean estimate of 505 ha (range: 140–1103 ha) falls well within these bounds, showing consistency between our study and previous radio telemetry-based estimations.

Conclusions. Overall, PACs appear to be meeting their goal of protecting important nest, roost, and foraging habitat for Mexican Spotted Owls. However, we also observed a range of individual variation, with some owls having near perfect overlap between their space use and home PAC boundaries while others had more obvious misalignment (Fig. 6). Ganey et al. (2014) observed similar misalignment between PAC boundaries and owl nest/roost locations obtained through demographic surveys, suggesting potential shifts in resource use over time since initial PAC establishment. In the southwestern United States, climate change and uncharacteristically severe wildfires and droughts are rapidly changing the distribution of forests (Guiterman et al. 2022). In particular, frequent large and severe wildfires represent a primary threat to Spotted Owls across the species' range (Jones et al. 2016, Wan et al. 2019). It is thus even more important that PACs and PAC boundaries are able to shift through time within such increasingly dynamic landscapes, to ensure that PACs are adaptive to changing conditions.

Certain forest management activities can help facilitate increased resistance and resilience to rapid disturbance-induced landscape changes. Fuels treatments that remove smaller-diameter trees, surface, and ladder fuels (e.g., by thinning or prescribed fire) can be used inside PACs in some instances to reduce the risk of a stand-replacing fire, helping to reduce some disturbance risk to existing owl habitat (USFWS 2012). Additionally, an important component of owl recovery planning involves the creation of suitable "recovery habitat" outside of PACs, meant to provide additional nest/roost habitat for Spotted Owls into the future (USFWS 2012). The ability to maintain and create suitable habitat that is well distributed across both space and time—both within and outside of PACs—would ideally remove the need for PACs altogether, resulting in a recovery strategy far more robust to landscape dynamics and disturbance (USFWS 2012). However, the feasibility of this approach has yet to be validated and must be considered carefully as current rates of environmental change continue to diverge from historical norms.

For protected areas to be successful, species and their associated resources must be monitored through time and boundaries updated as ranges and distributions shift (Hannah et al. 2007). Additionally, many protected areas across the globe now incorporate models of climate change directly into their initial planning in order to protect areas that may provide suitable habitat in the future (Hannah et al. 2007, Whitney et al. 2023). Our research adds to that of previous studies showing consistent use of PACs by Spotted Owls, which suggests PACs are currently and adequately protecting critical nest, roost, and foraging habitat for this species (Berigan et al. 2012, Ganey et al. 2014). However, as climate change and fire continue to threaten the American West at unprecedented rates (Guiterman et al. 2022), the success of protected areas for Spotted Owls and other threatened species will likely require even greater adaptability, consistent monitoring, and foresight in order to meet changing needs in a dynamic world.

ACKNOWLEDGMENTS

We thank S. Pederson and M. Gustafson for their invaluable assistance with data collection. We thank K. Norman, J. Goldberg, and the Jones Lab for their assistance in editing an early version of this manuscript. All research was conducted under USFWS permit #ESPER0036384, USGS bird banding permit #24395, and approved Arizona and New Mexico state permits. All animal handling was conducted in accordance with approved IACUC protocols from the US Department of Agriculture (USDA) Forest Service; and University of New

Mexico. Funding was provided by the USDA Forest Service Southwestern Region.

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Received 16 March 2024; accepted 5 September 2024
Associate Editor: Sean S. Walls