

Differential landscape use by forest owls two years after a mixed-severity wildfire

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Abstract. Owls are important avian predators in forested systems, but little is known about landscape use by most forest-adapted owl species in environments impacted by mixed-severity wildfire. To better understand species-specific patterns of post-wildfire landscape use within an owl guild, we used passive acoustic monitoring using autonomous recording units. The technology is effective for multi-species surveys, especially if some species are rare, nocturnal, or difficult to detect by traditional means. In 2017, we surveyed the interior and adjacent unburned areas of a 10,700-ha mixed-severity wildfire that burned in 2015 in southwest Oregon. We used occupancy modeling to identify patterns of landscape use by five species of forest owls: barred owls (*Strix varia*), great horned owls (*Bubo virginianus*), western screech-owls (*Megascops kennicottii*), northern pygmy-owls (*Glaucidium gnoma*), and northern saw-whet owls (*Aegolius acadicus*). Our results showed a positive relationship between increasing fire severity and probability of use by western screech-owls and a similar but somewhat weaker relationship for northern pygmy-owls. Barred owls were rarely detected in severely burned areas and their use decreased with increased fire severity. We observed generally low landscape use for great horned owls, which decreased with increased fire severity and at higher elevations. Thus, four out of the five species appeared to use recently burned forests at different levels, with only northern saw-whet owls showing near-complete avoidance of the burned area. These findings increase our understanding of the basic ecology of each species and highlight the varied use of burned areas within this community. These previously undocumented patterns of landscape use in burned landscapes should provide insights to managers and policymakers in the Pacific Northwest as climate shifts, and fires may increase in size, frequency, and severity.

Key words: barred owl; forest owls; great horned owl; landscape use; mixed-severity wildfire; northern pygmy-owl; northern saw-whet owl; occupancy modeling; Pacific Northwest; passive acoustic monitoring; post-fire; western screech-owl.

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INTRODUCTION

The role of disturbance on wildlife and their habitats is complex and varied, and while wildfires continue to increase in the western United States, their effects on avian predators remain

poorly understood (Halofsky et al. 2011, Perry et al. 2011, Lesmeister et al. 2019). Wildfire alters the structure of avian communities (Donaghy Cannon 2011, White et al. 2016) and while changing fire regimes could result in negative impacts to some species, many forest-adapted

species in the western United States can benefit from disturbances that affect forest structure (Seavy et al. 2012, Lorenz et al. 2015, White et al. 2016). Southwest Oregon's forests historically experienced a relatively short fire return interval of mixed-severity fires (12–19 yr, Agee 1993), but in the past century, fire suppression and harvest practices have altered this cycle, which can result in increased wildfire size and severity (Perry et al. 2011, Wimberly and Liu 2014). In these systems, owls likely play a key functional role as nocturnal avian predators (Wood et al. 2019). As such, they are important to consider when investigating the relationship between wildlife and landscapes affected by mixed-severity fire. Occurrence of owls in burned forests may indicate the presence of structural components suitable for use by owls and sufficient prey populations to support these predators. However, apart from studies of northern spotted owls (*Strix occidentalis caurina*) and California spotted owls (*S. o. occidentalis*) (e.g., Clark et al. 2011, 2013, Jones et al. 2016, Rockweit et al. 2017, Jones et al. 2020a, Kramer et al. 2020), little research exists regarding territorial occupancy or landscape use by other owl species in post-fire landscapes. Here, we define landscape use as the proportion of surveyed locations being used by one or more individuals of a species throughout a survey season (MacKenzie et al. 2018). Most avian community studies in post-fire landscapes of the Pacific Northwest, USA, have focused on songbirds (e.g., Donaghy Cannon 2011, Halofsky et al. 2011, Latif et al. 2016), likely in part due to the difficulty of surveying cryptic, nocturnal species.

The varied effects that mixed-severity wildfire have on forest structure, suitable nest sites, and prey availability could affect how and when owls use burned landscapes for a range of life-history functions. Immediate structural changes from wildfire include opening of the canopy, snag creation, and reducing understory vegetation (Agee 1993, 2005). Canopy opening and suppression of understory shrubs can subsequently result in vigorous growth of the herbaceous layer shortly post-fire (Apfelbaum and Haney 1981, Smucker et al. 2005, Donato et al. 2009). Some studies have linked these novel conditions to increased abundance of prey species for owls including insects, small mammals, and birds one to five years post-fire, especially for cavity-nesting and

ground-foraging bird species (Lowe et al. 1978, Swengel 2001, Zwolak 2009, Fontaine and Kennedy 2012). Woodpeckers are the primary cavity excavators in this system and benefit from increased invertebrate prey availability, mainly wood-boring insects that colonize dead wood (Murphy and Lenhausen 1998, Smith 2000). Small owls are secondary cavity nesters and readily use cavities created by woodpeckers (e.g., Bonar 2000, Aitken and Martin 2007); thus, cavities excavated in the first post-fire year could be accessible to owls in the second breeding season after a fire. In general, very little is known about the effects of wildfire on forest owl communities, but species-specific responses are likely complex and variable because they differ in diet, habitat requirements, predation risk, and other life-history traits (Johnsgard 2002).

The five owl species included in this study, northern saw-whet owls (*Aegolius acadicus*), northern pygmy-owls (*Glaucidium gnoma*), western screech-owls (*Megascops kennicottii*), barred owls (*Strix varia*), and great horned owls (*Bubo virginianus*) co-occur but each appears to occupy a distinct niche in Pacific Northwest forests based on specific habitat and diet requirements, as well as diel activity patterns. Northern pygmy-owls, western screech-owls, and barred owls occupy a wide range of forest types and are considered habitat generalists (Giese and Forsman 2003, Sater et al. 2006, Davis and Weir 2010, Singleton et al. 2010, Jenkins et al. 2019), northern saw-whet owls typically nest in dense coniferous forests and forage in deciduous patches and openings (Hayward and Garton 1988), and great horned owls tend to occupy forests adjacent to wetlands, fields, meadows, and other openings (Johnson 1992). In terms of diet, northern saw-whet owls specialize in hunting small rodents (Holt and Leroux 1996, Marks and Doremus 2000), while barred and great horned owls consume a broader range of mammalian prey including some lagomorphs and other larger species (Marti 1974, Livezey and Bednarz 2007, Wiens et al. 2014), as well as some non-mammalian taxa. Western screech-owls and northern pygmy-owls are diet generalists; both incorporate higher proportions of insect and avian prey into their diets, especially northern pygmy-owls preying on songbirds and western screech-owls consuming nocturnal insects (Ross

1969, Holt and Leroux 1996, Rains 1997). Intraguild predation is known to occur and both barred and great horned owls have been documented taking smaller owls as prey (Marti and Kochert 1996, Elliott 2006). In British Columbia, recent declines in western screech-owl populations have been attributed to competition and predation by barred owls, which were first documented in the province in the 1960s (Elliott 2006, Acker 2012, COSEWIC 2012). Of the five species, all are primarily nocturnal except northern pygmy-owls, which are more diurnally active with a peak of activity around sunrise (Holt and Norton 1986, Sater et al. 2006).

Here, we used passive acoustic monitoring using autonomous recording units (ARUs) to examine landscape use patterns of the forest owl community in southwestern Oregon, USA, two years after a large mixed-severity wildfire. Studies in remote areas and those of nocturnal, cryptic species have benefited greatly from recent advances in ARU technology as large amounts of data can be collected over long time periods with less human effort than alternative methods (Bayne et al. 2015). Passive acoustic monitoring affords the opportunity to develop models of community-level patterns of use without the potential bias inherent in “active” survey methods (Wood et al. 2019).

We hypothesized that because of the mixed-severity nature of this fire, each species would use some areas within the fire perimeter, but patterns of landscape use for most species would differ based on burn severity around survey stations. Except for one limited study that suggested western screech-owls may move into recently burned areas (Elliott 1985), the use of burned landscapes by northern saw-whet owls, northern pygmy-owls, and western screech-owls is largely unstudied. Based on hypothesized selection of forest types, we predicted that potential canopy openings and increased prey accessibility due to fire, particularly at low and moderate severities where some live trees remained, could improve foraging conditions for all three small owl species. We predicted that barred owls would not have a discernible pattern of use relative to fire severity, due to their generalist diet and habitat requirements in the Pacific Northwest. Finally, while great horned owls use open areas for foraging, even severe wildfire

does not create the large meadow-like openings that they prefer, so we predicted that patterns of use might not reflect the effects of fire severity.

METHODS

In 2017, we used ARUs to survey for six forest owls within the fire perimeter and the surrounding area. Passive acoustic monitoring using ARUs provides a unique opportunity to identify patterns of landscape use by multiple forest owl species after a mixed-severity fire without many of the drawbacks of traditional survey methods (i.e., broadcasting species-specific calls), including eliminating interspecific conflict resulting from those surveys (Gutiérrez et al. 2007, Van Lanen et al. 2011). Over the past decade, researchers have demonstrated the effectiveness of ARUs to study rare and nocturnal avian species (Blumstein et al. 2011, Bayne and Stralberg 2015, Duchac et al. 2020). Not only are surveys non-invasive, but the method also allows for simultaneous multi-species surveys with high detection probability (Duchac et al. 2020). Additionally, advances in automated detection software employ sophisticated recognition systems and can now extract detections from very large acoustic data sets (e.g., Katz et al. 2016, Kahl et al. 2017, Stowell et al. 2019, Ruff et al. 2020, Znidarsic et al. 2020). Together, these hardware and software advances create a powerful new tool for monitoring historically understudied avian communities.

Owl species detected in the study area were northern spotted owl, barred owl, great horned owl, western screech-owl, northern saw-whet owl, and northern pygmy-owl. Species that may occur in the area but were not detected in this study included barn owls (*Tyto alba*) and great gray owls (*Strix nebulosa*). We detected northern spotted owls only rarely at a few ARU stations so were unable to include the species in analyses beyond simple counts of detections. We quantified landscape use, the proportion of stations being used by one or more owls through the survey season, for the remaining five forest owl species using single-species occupancy models.

Study area

The Stouts Creek Fire was a mixed-severity fire that burned 10,700 ha of public and private lands from July to September 2015 in southwest

Oregon, USA (Fig. 1). The fire burned approximately 18 km east of Canyonville, Oregon, in the Klamath Mountains and southwestern Cascade Range. Dominant trees on public lands included Douglas-fir (*Pseudotsuga menziesii*), Pacific madrone (*Arbutus menziesii*), ponderosa pine (*Pinus ponderosa*), western hemlock (*Tsuga heterophylla*), and white fir (*Abies concolor*), interspersed with cedars (mainly incense cedar, *Calocedrus decurrens*), pine species, and other hardwoods (Franklin and Dyrness 1973). Private timber parcels were primarily Douglas-fir plantations actively managed for lumber and softwood plywood production. Elevation in the area ranged from approximately 300–1300 m.

Sampling design and acoustic data collection

At the time of our analysis, a Monitoring Trends in Burn Severity (MTBS) fire severity map was not yet available. Therefore, we used a locally developed fire severity map of the Stouts Creek Fire that was created using Landsat 8 Land Surface Reflectance imagery to calculate normalized burn ratios (NBR) in Google Earth Engine (<https://earthengine.google.com>; <https://lemma.forestry.oregonstate.edu/data>). Landsat imagery and change in NBR are often used to quantify forest disturbance from fire and other causes (e.g., Miller and Thode 2007, Miller et al. 2009). NBR was calculated at 30 m resolution for the study area from May 1 to July 31 for the year prior to the fire (2015) and the year following the fire (2016). NBR was calculated as the normalized difference between bands five and seven for each image (Li et al. 2013). Since no single image was optimal (e.g., cloud cover over part of the area on a given date), a median image of NBR for each year was calculated (M. Gregory, *personal communication*). Fire severity was determined by finding the difference of the median NBR maps ($[dNBR] = ([NBR_{2015}] - [NBR_{2016}])$) and creating an index of dNBR (Miller and Thode 2007) for the area of the fire (Fig. 1). As such, larger values represent areas that burned at higher severity, and values close to or below zero represent areas where NBR did not change between years (i.e., not burned). In our analyses, we used dNBR as a continuous covariate to quantify fire severity, but for descriptive purposes, we also separated dNBR into three classes of relative burn severity: low/unburned (dNBR

below 0.23), moderate (dNBR 0.24–0.59), and high (dNBR 0.60 and above). Subsequent review between our fire severity map and the now available MTBS fire severity map indicates that our dNBR map is highly correlated with the MTBS dNBR ($R = 0.95$) and RdNBR ($R = 0.94$).

We deployed 50 ARUs (Wildlife Acoustics Song Meter 4 models; Wildlife Acoustics 2018) in and surrounding the perimeter of the Stouts Creek Fire (Fig. 1). We divided the area into sections using a 2.58 km² grid (~1 square mile, the size of individual sections within the federal/private ownership checkerboard), with a potential survey station at each grid centroid and a goal of deploying an ARU at every accessible station. We excluded 10 grid cells in which the potential station was not under federal ownership because of access restrictions on private lands. We also included stations outside the perimeter of the fire when the point fell within 1.61 km (1 mi) of the fire perimeter. Additional accessibility restrictions eliminated eight potential stations outside the fire perimeter, resulting in 15 stations outside and 35 stations within the fire perimeter (Fig. 1). Between fall 2015 and winter 2017, salvage logging took place in severely burned areas on private timber parcels and on some Bureau of Land Management-administered land (USDI Bureau of Land Management 2015; L. Duchac, *personal observation*). While we did not place any ARUs in areas that were logged post-fire, three stations were adjacent to private timberlands where salvage logging activities took place. However, as only three stations fit these criteria, questions regarding owl use of salvage logged areas were outside the scope of the current study.

We conducted surveys during April–July 2017 and programmed ARUs to passively record two four-hour daily segments: two hours before and after sunrise and two hours before and after sunset. This schedule balanced the need to capture the vocalizations of multiple species, while avoiding continuous 12- or 24-h recording which was unnecessary considering the active periods of our study species. We mounted ARUs to small trees with diameter ~15–20 cm for unobstructed listening ability. We deployed ARUs at least 50 m from roads, trails, and streams to reduce vandalism and noise. ARU stations were approximately 1.6 km apart; while listening distances vary widely depending on environmental factors

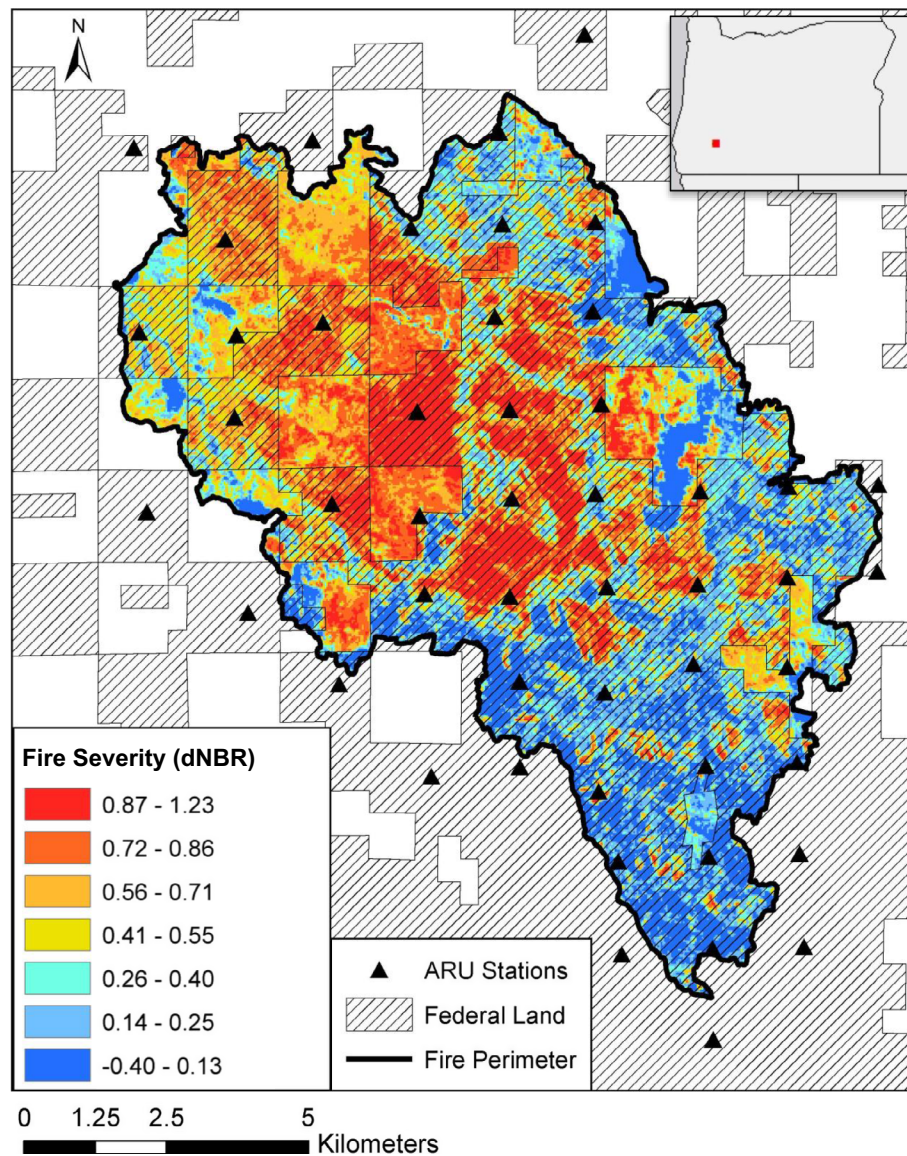


Fig. 1. Map showing fire severity using Landsat 8 dNBR (difference in Normalized Burn Ratio) and mixed ownership of lands burned during the 2015 Stouts Creek Fire. Hashed areas represent federal lands, black triangles represent autonomous recording unit (ARU) survey stations located ~1 mile apart, and black line outlines the fire's final perimeter. Larger values of dNBR indicate a greater loss of forest cover between the pre-fire and post-fire years, that is, higher severity. Severity values near or below zero indicate no change or increase in vegetation between pre- and post-fire years, that is, unburned to low severity. Inset map at upper right shows location of study area in southwest Oregon, USA.

(Yip et al. 2017, Duchac et al. 2020), we were confident this distance would eliminate concerns of overlapping recordings between ARU stations. We visited ARU stations every six weeks to replace batteries and memory cards.

Sound processing and statistical analyses

We used the Simple Clustering feature in Wildlife Acoustics Kaleidoscope Pro software to categorize similar calls into clusters (Wildlife Acoustics 2018) and manually reviewed the

software's output. Kaleidoscope uses a hidden Markov model to group sounds with similar characteristics, then produces spectrograms (visual representations of sound) which vastly improves efficiency of reviewing clips. We set the frequency range for clustering between 200 and 1200 Hz, the length of target vocalizations to 0.5 to 7.5 s, and the inter-syllable gap between individual notes of a call to 2 s. We retained default values for all other cluster settings. We reviewed the resulting clips and manually tagged each vocalization that was positively identifiable as one of the owl species of interest.

Using these detections, we generated weekly encounter histories for the five owl species, then conducted occupancy analyses for each focal species using RPresence (R Core Team 2018). We fit single-species, single-season occupancy models to evaluate landscape use using the MacKenzie et al. (2018) definition of use (ψ) as the proportion of stations that were used by each species. We interpreted ψ as the probability of use due to likely violation of the closure assumption because most species in the study had home range sizes large enough to overlap more than one ARU station (Rohner 1997, Giese and Forsman 2003, Hinam and St. Clair 2008, Davis and Weir 2010, Groce and Morrison 2010, Schilling et al. 2013, Wiens et al. 2014). We also modeled detection probability (p) for each species, defined as the probability of detecting a species given it was present at a station (MacKenzie et al. 2018).

For all species, we set a minimum threshold for what we considered a valid detection to reduce positively biased estimates of landscape use based on rare calling events. These detections could have been from non-territorial, transient individuals or from rare movements of an individual at the edge or outside of its territory (e.g., Berigan et al. 2019), and as such may not reflect ecologically relevant patterns of landscape use. We made this adjustment by removing detections from encounter histories at stations with the lowest 1% of detections for each species' overall range of detections at any given station. For example, if we detected a maximum of 1000 vocalizations at an individual station for a species, for any stations with fewer than 10 vocalizations over the survey season, we changed the encounter history for any stations from a 1 (detected) to a 0 (not detected). For northern

pygmy-owls, we excluded one outlier station with over 12,000 detections from our minimum threshold for detection calculations because it had over 5.5 times the number of detections compared to any other station (range 1–2115). These calls were verified as authentic; it is likely the station was simply very near a nest or activity center, resulting in a particularly large number of detections through the season. The station with the next highest total ($n = 2115$) was used to set the maximum for this species, but we retained the encounter history at this station for occupancy modeling.

We used a suite of site and survey covariates derived from field observations and remotely sensed data to model landscape use and probability of detection for each focal species (Table 1). We derived site-specific covariates for each station from remotely sensed data in ArcGIS (Esri 2015) including terrain ruggedness (RUGGED; the standard deviation of elevation in a 250 m buffer), and topographic position (TOPO; continuous value representing relative position on the slope). We calculated TOPO from the topographic position index, which was the difference in elevation of the station compared to the mean elevation within a 450-m radius (Glenn et al. 2017). Negative values represented lower slope locations, and positive values indicated higher slope (nearer to ridgetops). We also calculated distance in meters to the nearest stream (STREAM) from each station. We used average dNBR to quantify fire severity within 250 and 500 m buffers at each station (SEV250 and SEV500; Fig. 1; Table 1). PERIM was the distance from each station to the fire's perimeter, with zero value at the fire perimeter, positive values inside, and negative values outside the fire perimeter (Table 1).

We compiled mean weekly precipitation (PRECIP) in millimeters for each ARU station from daily PRISM precipitation data, which were generated using a combination of modeling and interpolation methods (Daly et al. 2008) and are available nationally at 63-ha resolution (Prism Climate Group 2018). We summarized mean weekly temperature data (TEMP) from HOBO data loggers (Onset 2017) that we deployed at ten ARU stations distributed around the study area. HOBO loggers collected temperature data every two hours over the survey season.

Table 1. Site and survey covariates used to model single-species landscape use and probability of detection using ARU (autonomous recording unit) data for five owl species.

Variable	Description	Barred owl	Great horned owl	Northern saw-whet owl	Northern pygmy-owl	Western screech-owl
STREAM†	Distance in meters from ARU station to nearest stream. Derived from GIS	0	+	0	0	0
PERIM†	Measurement in meters from each ARU station to the fire's perimeter. Values inside the perimeter are positive, values outside the perimeter are negative	0	0	0	0	0
SEV250†	Average severity index value derived from dNBR map using GIS software within 250-m buffer around each ARU station	0	0	–	0	0
SEV500†	Average severity index value derived from dNBR map using GIS software within 500-m buffer around each ARU station	0	0	–	0	0
TOPO†	Topographic position within 450-m radius; continuous variable of relative position on slope, with the mid-slope as zero, upper slope values positive, and lower slope values negative. Derived from GIS data	–	–	0	0	0
RUGGED†	Terrain ruggedness; standard deviation of elevation in a 250-m buffer around each ARU station	–	–	0	0	0
ELEV†	Elevation in meters, measured by handheld GPS device at each ARU station	–	–	0	0	0
WEEK‡	Numbered week of the survey season (1–15)	–	–	–	–	–
TEMP‡	Mean weekly temperature recordings obtained from HOBO loggers (Onset 2017) at 10 ARU stations throughout the study area	0	0	0	0	0
PRECIP‡	Daily precipitation in millimeters derived from PRISM climate data (Prism Climate Group 2018) averaged weekly per ARU station. PRISM precipitation data are reported in a grid with units of 0.63 km ² or 63 ha	0	–	–	–	–
NOISE‡	Measure of average weekly background noise in decibels below full scale (dBFS, 0 is maximum possible digital volume) from each ARU station between 220 and 1000 Hz. Calculated by Kaleidoscope Pro software	–	–	–	–	–

Notes: Data were collected during 2017 in and surrounding the 2015 Stouts Creek Fire in southwest Oregon, USA. Included are species-specific predictions for the effect of covariates (+ positive, – negative, 0 no effect) on use or detection probability.

† Site covariates varied between ARU stations but static throughout season.

‡ Survey covariates varied between ARU stations and by week.

Precipitation and temperature (PRECIP and TEMP) were negatively correlated especially in weeks 5–12 (average r over full survey season = -0.66 ; average r in weeks 5–12 = -0.85), so were not included together in models of detection probability. We used Kaleidoscope Pro software's noise analysis feature (Wildlife Acoustics 2018) to estimate weekly background noise levels (NOISE) directly from recordings at each station. We calculated mean decibel levels of NOISE in the frequency range of 0.2–1 KHz (i.e., frequency range of owl vocalizations) for each hour of

recording and averaged to weekly values for each ARU station. Finally, we used a WEEK covariate to allow for probability of detection to vary by survey week throughout the season. We z-transformed all continuous covariate values before use in analyses for consistency and to improve model convergence.

We used a stage-based approach to model development, beginning with univariate models of p . Following Morin et al. (2020), we moved forward with competitive models of p within five AIC_c (Akaike's information criterion adjusted for

small sample size) when modeling ψ , in order to capture more of the variation in the model set rankings. We then created multivariate ψ models combining covariates from univariate models within five AIC_c . We ranked models based on AIC_c values and evaluated model support using differences between a model's AIC_c and the model with the lowest AIC_c (ΔAIC_c) and Akaike's model weights (w_i) (Burnham and Anderson 2002). We examined model coefficients ($\hat{\beta}$) and 95% confidence intervals (CI) on coefficients in competitive models to determine direction of effect and the strength of evidence for specific covariate effects (similar to Forsman et al. [2011] and Dugger et al. [2016]). We considered covariates with coefficient CIs that do not overlap zero to have the strongest support, while those with CIs that slightly overlapped zero (<10%) were considered to have weak support, and coefficients with CIs that widely overlapped were considered to have no support.

RESULTS

Over the 15-week survey season, we detected ≥ 1 owl species at 46 of 50 ARU stations and ≥ 2 species at 39 of 50 stations. After eliminating 271 individual vocalizations that fell below our 1% threshold as described above, we retained 38,761 vocalizations: 425 northern saw-whet owl vocalizations at seven stations (Fig. 2a), 24,202 northern pygmy-owl vocalizations (23 stations, Fig. 2b), 6,059 western screech-owl vocalizations (20 stations; Fig. 2c), 6025 barred owl vocalizations (25 stations; Fig. 2d), and 2050 great horned owl vocalizations (six stations; Fig. 2e). Estimates of landscape use (the proportion of stations being used by one or more owls through the survey season) from the intercept-only model [$\psi(\cdot)$] for the five owl species (with CIs) were as follows: 0.141 (northern saw-whet owl; CI 0.069–0.269), 0.400 (western screech-owl; CI 0.275–0.540), 0.460 (northern pygmy-owl; CI 0.328–0.598), 0.120 (great horned owl; CI 0.055–0.243), and 0.500 (barred owl; CI 0.365–0.635). We detected northern spotted owls on one occasion at three stations over the survey season. One station was outside the fire perimeter, a second burned at very low severity (dNBR 0.058), and the third burned at moderate severity (dNBR 0.372). All three stations were on lands managed by the US

Forest Service on the Umpqua National Forest. At the three stations adjacent to private parcels that appeared to have post-fire logging activity, ARUs only detected western screech-owls. The four stations without any owl detections had among the highest average seasonal NOISE levels and varied in burn severity from low (dNBR 0.157) to high (dNBR 0.816).

Detectability

The covariates with the strongest support for an effect on the probability of detection for these five owl species were background noise (NOISE), terrain ruggedness (RUGGED), temperature (TEMP), precipitation (PRECIP), and distance to streams (STREAM) (Table 2). For northern saw-whet owls, the most-supported detection probability model included only background noise (NOISE) with lower probability of detection at ARU stations having the highest background noise (Table 2; Appendix S1: Table S1). The terrain ruggedness (RUGGED) model for probability of detection had the most support for northern pygmy-owls, with decreased detection probability as ruggedness increased (Table 2; Appendix S1: Table S2). The most-supported detection probability models for western screech-owls had either an additive negative effect of background noise (NOISE; $\hat{\beta} = -0.479$, CI -0.848 to -0.111 ; Table 2; Appendix S1: Table S3) and positive effect of temperature (TEMP, p increased as TEMP increased; $\hat{\beta} = 0.404$, CI 0.103 – 0.704 ; Table 2; Appendix S1: Table S3), or the additive negative effects of background noise (NOISE) and precipitation (PRECIP, p decreased as PRECIP increased; $\hat{\beta} = -0.304$, CI -0.601 to -0.007 ; Table 2; Appendix S1: Table S3). Temperature and precipitation (TEMP and PRECIP) were negatively correlated so not included together in the same model. For barred owls, detection probabilities were negatively associated with increased precipitation (PRECIP, Table 2; Appendix S1: Table S4) and in separate models, with decreased temperature (TEMP). For great horned owls, a model including the negative effect of background noise (NOISE) plus the positive effect of distance to streams (STREAM, Table 2; Appendix S1: Table S5) received the most support.

Landscape use

Landscape use differed by species with respect to various combinations of fire severity within

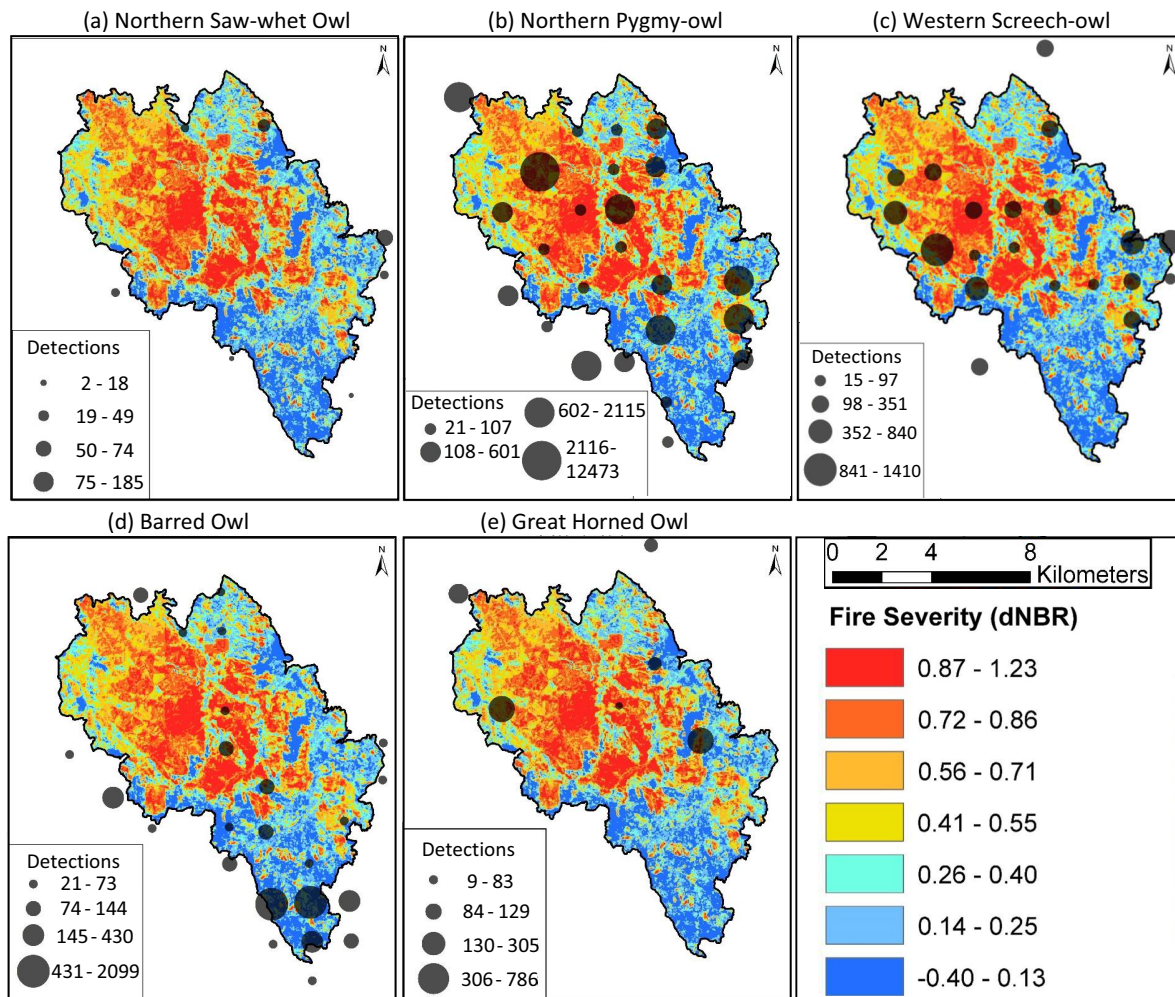


Fig. 2. (a–e) Fire severity map and counts of detections at each autonomous recording unit (ARU) station for (a) northern saw-whet owls, (b) northern pygmy-owls, (c) western screech-owls, (d) barred owls, and (e) great horned owls in and around the area burned by the Stouts Creek Fire, Oregon, USA. Map colors represent fire severity categories using dNBR (difference in Normalized Burn Ratio), with red indicating highest severity and blue indicating unburned areas. Filled circles represent stations where ARUs detected vocalizations of each species and relative size of each circle represents the number of detections for the species at each station. For each species, we excluded stations with the lowest 1% of the range of detections; lowest number of detections for each species reflects this exclusion (e.g., for great horned owls in Fig. 2e, stations with eight or fewer detections were excluded). Due to wide variation in overall detections between species, scales of circle sizes differ and are indicated on each individual map. Black line indicates the fire's perimeter.

250 m of the survey station (SEV250), severity within 500 m (SEV500), distance to the fire's perimeter (PERIM), topographic position (TOPO), and elevation (ELEV). We observed a scale-dependent relationship between estimates of landscape use and fire severity for all five species, with

all species but great horned owls showing an effect at the 250-m scale (SEV250, Fig. 3). Northern pygmy-owl and western screech-owl landscape use increased as fire severity increased, while use by northern saw-whet owls, great horned owls, and barred owls decreased with fire severity.

Table 2. Model coefficient estimates ($\hat{\beta}$) and upper and lower 95% confidence limits (UCL; LCL), difference in AIC_c between each candidate model and the model with the lowest AIC_c value (ΔAIC_c ; adjusted for small sample size), and Akaike weights (w) from models estimating use (ψ) and probability of detection (p) for northern saw-whet, western screech, northern pygmy, barred, and great horned owls.

Species	Model structure	ΔAIC_c	w	Covariate†	($\hat{\beta}$)	UCL	LCL
Northern saw-whet owl	ψ (PERIM), p (NOISE)	0	0.347	PERIM (ψ)	-1.156	0.020	-2.331
				NOISE (p)	-0.913	-0.155	-1.670
	ψ (SEV250), p (NOISE)	0.96	0.215	SEV250 (ψ)	-1.088	0.189	-2.364
				NOISE (p)	-0.925	-0.171	-1.678
	ψ (.), p (NOISE)	2.72	0.089	NULL (ψ)	-1.652	-0.815	-2.489
Northern pygmy-owl	ψ (SEV250 + RUGGED), p (RUGGED)	0	0.139	SEV250 (ψ)	0.585	1.223	-0.053
				RUGGED (ψ)	-0.609	0.045	-1.264
				RUGGED (p)	-0.536	-0.117	-0.956
	ψ (SEV250 + TOPO), p (RUGGED)	0.04	0.136	SEV250 (ψ)	0.513	1.124	-0.099
				TOPO (ψ)	0.585	1.222	-0.051
				RUGGED (p)	-0.572	-0.123	-1.020
	ψ (TOPO), p (RUGGED)	0.43	0.112	TOPO (ψ)	0.557	1.179	-0.065
				RUGGED (p)	-0.562	-0.120	-1.005
	ψ (SEV250), p (RUGGED)	1.02	0.083	SEV250 (ψ)	0.491	1.094	-0.113
				RUGGED (p)	-0.619	-0.153	-1.085
	ψ (RUGGED), p (RUGGED)	1.09	0.080	RUGGED (ψ)	-0.509	0.125	-1.144
				RUGGED (p)	-0.534	-0.116	-0.951
	ψ (PERIM + TOPO), p (RUGGED)	1.37	0.078	PERIM (ψ)	0.401	1.008	-0.206
				TOPO (ψ)	0.541	1.167	-0.085
				RUGGED (p)	-0.557	-0.119	-0.995
Western screech-owl	ψ (SEV250 + RUGGED), p (NOISE + TEMP)	0	0.684	NULL (ψ)	-0.166	0.166	-0.419
				RUGGED (p)	-0.588	-0.130	-1.046
				SEV250 (ψ)	1.657	2.738	0.576
				RUGGED (ψ)	-0.996	-0.160	-1.832
	ψ (SEV250 + RUGGED), p (NOISE + PRECIP)	3.10	0.145	NOISE (p)	-0.479	-0.111	-0.848
				TEMP (p)	0.404	0.704	0.103
				SEV250 (ψ)	1.606	2.601	0.611
				RUGGED (ψ)	-0.973	-0.164	-1.782
				NOISE (p)	-0.439	-0.080	-0.798
				PRECIP (p)	-0.304	-0.007	-0.601
Barred owl	ψ (SEV250), p (NOISE + TEMP)	4.40	0.076	SEV250 (ψ)	1.213	1.955	0.471
				NOISE (p)	-0.453	-0.113	-0.794
				TEMP (p)	0.404	0.705	0.102
	ψ (SEV250 + ELEV), p (PRECIP)	0	0.346	SEV250 (ψ)	-0.943	-0.219	-1.667
				ELEV (ψ)	0.672	1.399	-0.055
				PRECIP (p)	-0.575	-0.325	-0.825
	ψ (SEV250 + ELEV), p (TEMP)	0.88	0.223	SEV250 (ψ)	-0.943	-0.219	-1.667
				ELEV (ψ)	0.672	1.400	-0.055
				TEMP (p)	0.589	0.848	-0.330
	ψ (SEV250), p (PRECIP)	1.16	0.194	SEV250 (ψ)	-1.052	-0.352	-1.751
				PRECIP (p)	-0.575	-0.328	-0.821
Great horned owl	ψ (SEV250), p (TEMP)	2.03	0.125	SEV250 (ψ)	-1.052	-0.352	-1.751
				TEMP (p)	0.589	0.848	0.330
	ψ (ELEV), p (PRECIP)	5.29	0.025	ELEV (ψ)	0.809	1.470	0.147
				PRECIP (p)	-0.575	-0.329	-0.821
	ψ (SEV500 + ELEV), p (NOISE + STREAM)	0	0.656	SEV500 (ψ)	-1.662	0.073	-3.397
				ELEV (ψ)	-1.726	0.068	-3.520
				NOISE (p)	-1.131	-0.288	-1.975
				STREAM (p)	0.598	1.066	0.130

(Table 2. Continued.)

Species	Model structure	ΔAIC_c	w	Covariate [†]	($\hat{\beta}$)	UCL	LCL
	$\psi(\text{ELEV}), p(\text{NOISE} + \text{STREAM})$	3.07	0.142	ELEV (ψ)	−1.335	0.131	−2.801
				NOISE (p)	−1.214	−0.384	−2.043
				STREAM (p)	0.639	1.113	0.166
	$\psi(\text{SEV500}), p(\text{NOISE} + \text{STREAM})$	4.54	0.068	SEV500 (ψ)	−1.061	0.249	−2.371
				NOISE (p)	−1.054	0.256	−1.851
				STREAM (p)	0.587	1.053	0.122
	$\psi(\cdot), p(\text{NOISE} + \text{STREAM})$	5.59	0.040	NULL (ψ)	−1.92	−1.050	−2.783
				NOISE (p)	−1.079	−0.283	−1.874
				STREAM (p)	0.596	1.063	0.130

Notes: Models listed for each species are those with 90% of model weight unless the null ($\cdot$) model for ψ appears before reaching 90% of weight, in which case models up to the null are included. Data were collected using autonomous recording units from April to July of 2017 in and surrounding the area burned in summer 2015 by the Stouts Creek Fire in southwest Oregon.

[†] PERIM, distance from fire's perimeter; SEV250, average fire severity within a 250-m radius around each station; SEV500, average fire severity within a 500-m radius around each station; RUGGED, terrain ruggedness measured as the standard deviation of elevation in a 250-m radius around each station; TOPO, topographic position relative to a 450-m radius around each station; STREAM, distance in meters to the nearest stream; ELEV, elevation in meters at each station; PRECIP, daily precipitation in mm averaged weekly at each station; TEMP, temperature measured hourly and averaged weekly at each station; NOISE, measure of average weekly background noise between 200 and 1000 Hz.

Nearly all northern saw-whet owl detections were outside the fire's perimeter (Fig. 2a), and landscape use was negatively associated with distance to the fire's perimeter (PERIM) (95% CIs barely overlapped zero; Table 2). A model including a negative effect of fire severity within 250 m (SEV250) on landscape use was competitive for northern saw-whet owls ($\Delta AIC_c = 0.96$), with CIs overlapping zero by <10%, suggesting weak support for this covariate (Fig. 3).

Western screech-owl landscape use increased with increasing fire severity within 250 m (SEV250, Fig. 4) and decreased with increasing terrain ruggedness (RUGGED), with the most-supported model carrying 68.4% of the model weight (Table 2). A competitive model for western screech-owls differed only in detection probability (effect of precipitation rather than temperature), while the landscape use effects remained the same (fire severity within 250 m and terrain ruggedness). Use by northern pygmy-owls was positively associated with increasing fire severity within 250 m (SEV250) and topographic position (TOPO, Table 2; Fig. 4). The fire severity within 250 m + terrain ruggedness (SEV250 + RUGGED) model for northern pygmy-owls was also well-supported, with landscape use decreasing with increasing terrain ruggedness (RUGGED, Table 2). Univariate fire severity within 250 m (SEV250), TOPO, and RUGGED models were also within 2 ΔAIC_c

of the most-supported model, as well as a PERIM + TOPO model with landscape use increasing further inside the burned area (Table 2).

The most-supported models for the two large owl species (barred and great horned owls) suggested landscape use patterns decreased as fire severity increased (SEV250 and SEV500) and varied with elevation (ELEV). We observed a negative relationship between barred owl landscape use and fire severity within 250 m (SEV250; Figs. 3, 4), and higher probability of use with increasing elevation (ELEV) in the two most-supported models, again differing only in detection probability (Table 2). Univariate models of fire severity within 250 m (SEV250) had similar support (Table 2). The most-supported landscape use model for great horned owls includes the additive negative effects of higher fire severity within 500 m (SEV500) and higher elevation (ELEV), with 95% CIs for both covariates very slightly overlapping zero (Table 2; Fig. 4). Competitive models for great horned owl use included univariate elevation (ELEV) and fire severity within 500 m (SEV500) models.

DISCUSSION

This is the first study to report on differences in use of a recently burned landscape within an owl guild, and the patterns we observed suggest

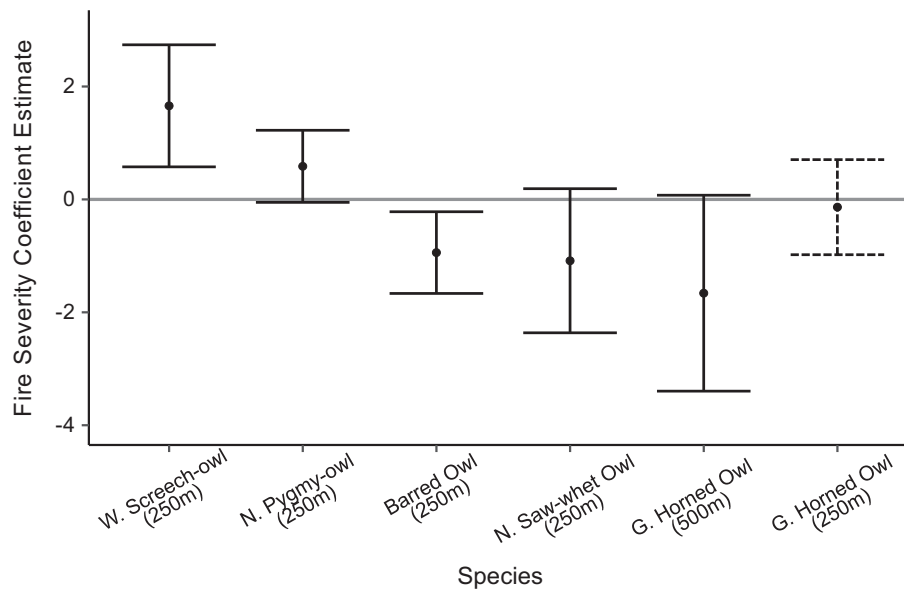


Fig. 3. Fire severity coefficient estimates with 95% confidence intervals from best-supported models of landscape use for five owl species. Positive coefficient estimates (y -axis) represent a positive effect of fire severity on landscape use, while negative values suggest decreased use as severity increases. More strongly positive or negative values indicate stronger effects. For western screech-owls, northern pygmy-owls, barred owls, and northern saw-whet owls, the severity scale with the most support was within a 250-m radius of the survey station (SEV250), while for great horned owls the 500-m scale (SEV500) had more support. At right, we have included the great horned owl coefficient estimate from models containing SEV500 (most-supported model) and SEV250 (hashed line) for comparison. Data were collected in 2017, two years post-fire using autonomous recording units in the area of a 2015 mixed-severity wildfire in southwest Oregon, USA.

the owl species we studied differ markedly in landscape use. Northern pygmy-owls and especially western screech-owls showed high use of high-severity burned areas, whereas northern saw-whet owls appeared to avoid nearly all burned areas. Both larger owls (barred and great horned owls) were more likely to use unburned and low-severity areas compared to areas that burned more severely, though great horned owls had low overall use of the study area. We detected northern spotted owls very rarely in the study area and not at all in severely burned forests, a finding similar to other studies on northern spotted owls and other spotted owl subspecies (Rockweit et al. 2017, Lesmeister et al. 2018, Jones et al. 2020b, Schofield et al. 2020). Post-fire vegetation characteristics and, by extension, resource availability, change from year to year; thus, the landscape use relationships observed here over a single breeding season may

change with time since fire (Smucker et al. 2005, Sitters et al. 2016). For example, woodpecker populations tend to peak within the first decade post-fire then decrease (Finch et al. 1997), changing cavity availability for owls as time since fire increases. Similarly, woody shrubs do not establish immediately, but 5–20 yr after wildfire can become extremely dense (Shatford et al. 2007), and prey composition and availability likely shift accordingly.

Compared to northern saw-whet or northern pygmy-owls, western screech-owl diets tend to include a larger proportion of insects (Ross 1969, Rains 1997). For this species, burned areas may create favorable conditions with increased prey and cavity availability (Hutto 1995, Murphy and Lenhausen 1998, Smith 2000, Kotliar et al. 2002). Western screech-owl numbers increased after a wildfire in California (Elliott 1985), suggesting this pattern of increased use post-fire may also

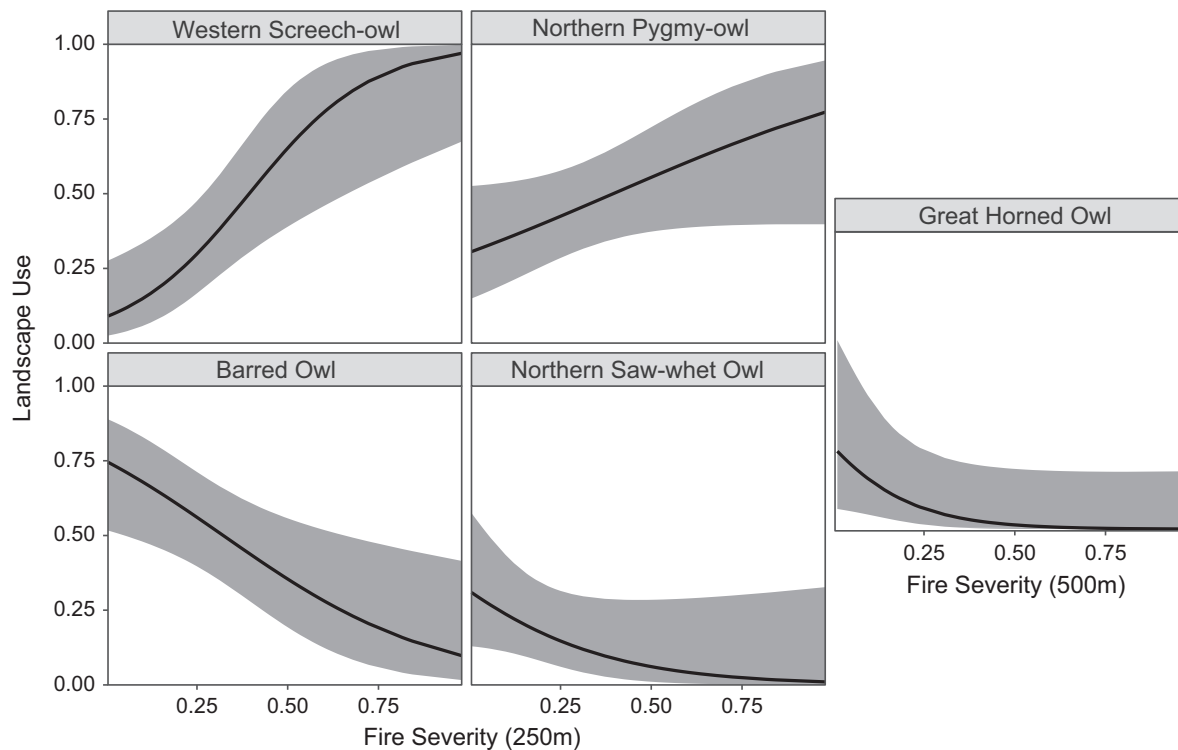


Fig. 4. Landscape use (*y*-axis) relative to fire severity (*x*-axis) from most-supported models for five owl species. In great horned owl models (right), fire severity within a 500-m radius had most support, whereas for the four remaining species fire severity within a 250-m radius had most support. For each figure, if the most-supported models contained more than one covariate, other covariates were held at the mean value when generating use estimates. Data were collected in 2017, two years post-fire using autonomous recording units in the area of the Stouts Creek Fire, a 2015 mixed-severity wildfire in southwest Oregon, USA.

occur in other areas of their range. This was also the only species detected at three stations adjacent to private parcels with post-fire salvage logging activity, all of which burned at high severity. However, not only are three observations insufficient for making statistical inference with regard to the effects of post-fire logging on western screech-owls, we were unable to determine whether these owls were detected within the adjacent logged areas or in the unlogged burned forest.

Northern pygmy-owls are generally common in the region, occur in a range of forest types, are more active in the day compared to other owls, and their diets tend to contain more songbird prey (Holt and Norton 1986, Holt and Leroux 1996, Sater et al. 2006). Therefore, increases in ground-foraging birds shortly post-fire (e.g.,

Lowe et al. 1978) could be particularly beneficial to northern pygmy-owls, which are active during the same period as most songbirds and typically ambush prey from elevated perches. Together, these behaviors could facilitate this species' use of multiple types of post-disturbance forest, including recently burned areas. Two years after this fire, western screech-owls and northern pygmy-owls may have been taking advantage of cavities excavated by woodpeckers the previous year and abundant insect and avian prey in the severely burned areas (Lowe et al. 1978, Apfelbaum and Haney 1981, Huff et al. 1985, Hutto 1995, Swengel 2001, Kotliar et al. 2002).

Unlike the other two small owls, northern saw-whet owls mostly prey on rodents (Holt and Leroux 1996), which may affect how this species uses post-fire landscapes. In this system, as in

others, herbaceous plant cover in moderately and severely burned areas was abundant and dense two years post-fire (Apfelbaum and Haney 1981, Agee 2005, Smucker et al. 2005, Donato et al. 2009; L. Duchac, *personal observation*). Small mammal response to wildfire and other disturbance appears to vary, with one meta-analysis showing decreased red-backed vole (*Myodes gapperi*) abundance post-fire, but increased deer mouse (*Peromyscus maniculatus*) abundance (Zwolak 2009). In the Pacific Northwest, deer mice and several vole species are major components of northern saw-whet owl diets (Grove 1985, Marks et al. 2015), so appropriate prey may be present in these post-fire forests, but more difficult to acquire. Rather than creating openings for foraging, abundant herbaceous plant growth two years post-fire may provide more cover for small mammals and effectively decrease prey accessibility for rodent specialists.

Alternatively, northern saw-whet owls could be limited by a lack of suitable nesting and roosting cavities within the fire's perimeter. However, this is unlikely as all three small owl species in this study are known to use similarly sized cavities for nesting and roosting (Bonar 2000, Aubry and Raley 2002, Aitken and Martin 2007). Given that northern pygmy-owls and western screech-owls were present in burned areas, suitable cavities were likely available for northern saw-whet owls as well. Their apparent absence from burned areas suggests that in this case it is a scarcity of prey, not cavities, that prevents this species from using forests affected by wildfire. Contrary to our expectations, post-fire forest conditions may not provide suitable foraging conditions for northern saw-whet owls. Since overall use by northern saw-whet owl was low throughout the study area (estimated use from intercept-only model = 0.16) further study of this species at a larger spatial scale may clarify the strength of support for this potential avoidance of burned areas.

The most-supported great horned owl and barred owl models both reflected negative associations with severely burned areas, as well as variation in landscape use based on elevation. Great horned owls were detected at low levels overall (estimated use from intercept-only model = 0.13), and there was only weak support for the negative effect of fire severity (Fig. 3).

Considering their large home ranges (~5.5 km²; Rohner 1997), the Stouts Creek Fire may not have been large enough to detect strong patterns in great horned owl landscape use. Additionally, because this was a mixed-severity fire, individual great horned owls could have access to lands burned at a range of severities. In contrast, barred owls showed a negative relationship between fire severity and landscape use. While barred owls are considered diet generalists, small terrestrial mammals, and cursorial insects make up a large part of their prey base in this region (Wiens et al. 2014; R. Baumbusch, *personal communication*). As a result, like northern saw-whet owls, a reduction in prey accessibility may decrease barred owl use of these severely burned areas. This pattern of landscape use by barred owls has not been documented previously and may further inform efforts to understand barred owl space use dynamics in Pacific Northwest forests.

In our study area, land ownership patterns changed with elevation, which may partially explain patterns of use related to elevation for barred and great horned owls. Lower elevation areas, mostly in the northwest of the study area, were a mixed ownership of land parcels managed by the U.S. Bureau of Land Management and private landowners, which created a more fragmented landscape at lower elevation relative to a mainly contiguous forest at higher elevations in the Umpqua National Forest (Fig. 1). Thus, relationships between elevation and use for these two species could also reflect use preferences for proportionately more edge habitat and open areas (preferable for great horned owls) vs. denser, more contiguous forest (more typical barred owl habitat). Our findings of increased barred owl landscape use at higher elevations is contradictory to previous observations of barred owls preferring lower elevation areas (Hamer et al. 2007, Singleton et al. 2010, Jenkins et al. 2019). However, elevations of ARU stations in this study area only varied from ~300 to 1300 m, which may obscure some patterns that occur over a larger range of elevations. Additionally, other work has found decreased landscape use by barred owls in areas with steeper slopes; however, elevation does not measure terrain ruggedness or slope and cannot be compared directly to these other metrics.

A cursory examination of counts (number of detections at each ARU station) suggests that using this information could further inform observations beyond just detection/non-detection data. For example, before excluding the lowest 1% of the range of detections for barred owls, this species was detected at some stations in all three fire severity classes (low/unburned: 84%; moderate: 64%; and high-severity: 45%). Without this lower threshold, using all detections in an occupancy framework may have revealed a pattern of landscape use related to post-fire forest conditions suggesting that barred owls will readily use severely burned areas, as ARUs detected them at nearly half of severely burned stations. However, comparing the average number of detections over the full survey season (including stations with few detections) revealed a striking pattern of increased vocal behavior at low-severity/unburned stations, with an average of 225 calls per station vs. 18 over the full season at high severity stations. Weekly, at low-severity and unburned stations ARUs detected an average of 18 barred owl vocalizations, compared to fewer than two vocalizations per week at moderately and severely burned stations. These patterns suggest that while barred owls do use severely burned areas on occasion, the intensity of use appears far lower than in low-severity or unburned areas. Alternatively, the infrequent detections observed in severely burned areas could indicate movement of non-territorial barred owls across the landscape. In either case, patterns observed here suggest that barred owls may not be an ecologically significant predator in severely burned forests. Incorporating count data into future analyses could reveal more subtle relationships or strengthen patterns observed using occupancy analyses (e.g., Wood et al. 2020).

In addition to changes in prey or other resources post-fire, interspecific dynamics may contribute to the patterns of landscape use observed in this study. Western screech-owls were more than three times as likely to use the most severely burned stations as were barred owls (Fig. 4), and the opposite was true as well—where barred owls had highest use in low-severity/unburned areas, western screech-owls had the lowest (Fig. 4). Considering the negative impact that barred owls can have on western

screech-owl populations (Elliott 2006, Acker 2012, COSEWIC 2012), any indication of space use or behavioral changes by the smaller owls to avoid depredation by this novel predator warrants further investigation. Results from this study suggest that in addition to taking advantage of resources, western screech-owls may use recently burned forests as refugia to avoid depredation by barred owls, which appear to use those areas much less frequently. Focused study of co-occurrence dynamics and other disturbance scenarios could clarify this relationship further.

CONCLUSION

In this study, we report previously unobserved relationships between Pacific Northwest owl species and burned landscapes, with each species showing a unique pattern of use in a post-fire landscape. Two years after a ~10,700-ha mixed-severity fire, we observed very little use by northern spotted owls in an area known to have had occupancy in the past (Dugger et al. 2016). In previous studies, reduced use of severely burned areas by spotted owls appears to be largely driven by the altered complex structure of forests suitable for nesting and roosting (Lesmeister et al. 2019, Kramer et al. 2020), but may be increasingly confounded by competition and displacement by high densities of barred owls. Western screech-owls and northern pygmy-owls showed patterns of higher use in more severely burned areas, while barred and great horned owls were more likely to use areas that burned at lower severity. Northern saw-whet owls appeared to avoid burned areas entirely. These results suggest that some forest owls, which are not typically considered fire-associated species, may take advantage of resources such as newly created tree cavities and increased prey availability that result from wildfires.

These novel findings support other recent work highlighting the complex and varied responses of wildlife to mixed-severity wildfire and the importance of wildfire on western landscapes. This is of particular importance as the spatial distribution of fire regimes will likely shift with climate change (Davis et al. 2017). In addition to revealing novel patterns of use post-fire by forest owls, our study also demonstrates the strength of passive acoustic methods for

community-level monitoring, particularly for nocturnal and otherwise cryptic species. We were able to identify subtle patterns of landscape use in a relatively small study; at larger spatial and temporal scales, this method could provide consistent, highly relevant information to researchers and managers about forest community dynamics. As it is, the results of this study can help policymakers and managers make post-disturbance restoration plans, evaluate post-fire habitat quality for various species, and continue to improve understanding of wildlife-wildfire relationships.

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DATA AVAILABILITY

Data for occupancy modeling are available from Dryad: <https://doi.org/10.5061/dryad.12jm63xzf>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3770/full>