

Changing Fire Regimes and Faunal Responses: Post-burn Habitat Use by Flammulated Owls in Colorado

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ABSTRACT

Human activities since European settlement have resulted in fires that have burned at higher severity and have affected larger areas than occurred historically across pine (*Pinus* sp.) forests of western North America. Based on global climate models and current fuel loading across the West, larger and more severe fires are predicted to become more common in the future. Despite the potentially severe consequences of such fires on landscape structure and function, there has been little study of the effects of altered fire regimes on the behavior and ecology of birds in western forests. We sought to determine how the Hayman Fire, which burned the largest area (560 km²) in Colorado history in 2002, affected habitat selection at multiple spatial scales by Flammulated Owls (*Psiloscops flammeolus*) that recolonized the burn area from 2003 to 2012. We radio-tracked five breeding male owls from 2007–2012 and quantified their habitat use patterns at multiple spatial scales. Males established breeding home ranges in areas containing less high-severity burned area and more low-severity burned or unburned area than was available within the entire fire perimeter. Additionally, home-range size was positively correlated with the proportion of high-severity burn, indicating that high-severity burned areas represent low-quality habitat for the species. Burn severity did not appear to be an important factor in the selection of habitats for foraging or day-roosting, indicating that habitat selection patterns were altered by fire only at the scale of the home-range. Our findings suggest that species with life histories highly adapted to low- and/or mixed-severity fire-dependent ecosystems may not be resilient to human modified fire regimes containing greater proportions and larger patches of high-severity burned forest. As the extent of high-severity burned area increases in modern fire regimes, larger areas of western forests may become unsuitable for occupancy by species that have otherwise evolved with naturally occurring low-severity fire.

INTRODUCTION

Across western North America, patterns of fire frequency, severity, and size are generally correlated with latitude, elevation, and floristic composition (Veblen et al. 2000, Brown and Shepperd 2001, Romme et al. 2003). Pine-dominated (*Pinus* sp.) forests at lower elevations and latitudes historically experienced frequent (every 5–30 years), low-severity fires, which typically consumed small trees, shrubs, and herbaceous growth, and promoted the maintenance of open forests containing clumps of larger, older trees (Covington and Moore 1994, Veblen et al. 2000, Brown and Shepperd 2001). Conversely, forests at higher elevations and latitudes typically experienced less frequent fires (every 100–400 years), and the relatively mesic conditions and low decomposition rates in these forests promoted the build-up of fuels between fires (Brown and Shepperd 2001, Schoennagel et al. 2004). Because of increased fuel loads, coupled with higher stand densities, fires in these environments were generally stand replacing (Brown and Shepperd 2001, Schoennagel et al. 2004).

Between these extremes, mixed-conifer forests at intermediate elevations and latitudes historically experienced mixed-severity fires every 30–100 years that resulted in a mosaic of burn severities across the landscape (Brown et al. 1999, Kaufmann et al. 2003, Romme et al. 2003). These mixed-severity fires typically occurred in heterogeneous environments consisting of a range of elevations, aspects, and dominant cover types (Romme et al. 2003, Schoennagel et al. 2004). In Colorado's Front Range, for example, north-facing slopes typically support denser and more mesic forests, which burn at higher severities, whereas south-facing slopes typically support less dense and more xeric forests, which burn at lower severities.

While the effects of all fire regimes on ecosystem function are important to understand, low- and mixed-severity fires are particularly important because they have strongly influenced

the evolution and ecology of Ponderosa Pine (*P. ponderosa*) and mixed conifer forests that are widespread across western North America (Covington and Moore 1994, Allen et al. 2002, Abella et al. 2007). Ponderosa Pines exhibit adaptations common to many pine species that evolved with frequent, low-severity fire, including thick, “fire resistant” bark and self-pruning of lower limbs (Binkley et al. 2007). Several species of fauna that inhabit dry pine forests are also known to be adapted to low- and mixed-severity fire-maintained environments (e.g., Conway and Kirkpatrick 2007, Hutto 2008, and Davis et al. 2012). For example, Pygmy Nuthatches (*Sitta pygmaea*) prefer habitats that are mediated by frequent, low-severity fire (widely spaced stands of large, old Ponderosa Pine; Szaro and Balda 1982, Brawn and Balda 1988).

In recent decades, a greater proportional area of dry pine-dominated forests across western North America have burned at higher severity (greater crown mortality) than occurred historically (Huckaby et al. 2001, Kaufmann et al. 2001, Fulé et al. 2014). Primary factors that have contributed to this trend include logging, over-grazing, and fire suppression, all of which have led to a prevalence of young, even-aged stands, increased fuel loads and stand densities, and more continuous canopy cover in many western forests (Veblen et al. 2000, Miller et al. 2009, Fulé et al. 2014). These changes in forest structure have resulted in an increase in the extent and severity of fires in many coniferous forests formerly characterized by low- or mixed-severity fire regimes, including those in Colorado’s Front Range (Covington and Moore 1994, Kaufman et al. 2001, Sherriff et al. 2014).

In addition, climate change is further modifying fire regimes across western North America. Extent, total biomass burned, and frequency of wildfires are strongly correlated with regional climate patterns (Westerling et al. 2006, Marlon et al. 2012), and increasingly hot and dry conditions are driving wildfires to burn larger areas at higher severities (Westerling et al.

2006). Given current predictions for long-term climate (IPCC 2013), western forests are expected to experience modified fire regimes compared to historical norms well into the future (Running 2006, Hurteau 2014, Rocca et al. 2014, Sherriff et al. 2014).

Historically, low- and mixed-severity fire regimes acted as important drivers of landscape heterogeneity by leaving a structurally variable post-fire landscape where forest overstory was left intact in some areas and experienced 100% mortality in others (Kaufman et al. 2003, Williams and Baker 2012, Odion et al. 2014). The recent trend toward landscape-scale, stand-replacing fires has homogenized forest structure by promoting recruitment of young, even-aged cohorts over large areas (Covington and Moore 1992, 1994, Allen et al. 2002, Fulé et al. 2003), which support lower overall biodiversity than structurally diverse forests (Allen 1998). Additionally, homogenized forests may no longer support the same suite of faunal inhabitants as they did historically (U.S. GAO 1999, Westerling et al. 2011).

Despite the extent to which fire regimes of western forests are being modified, few studies have focused on faunal responses to such changes. Recent research has indicated that avian responses to fire may be influenced by foraging behavior, as evidenced by a positive correlation between the relative abundance of species within particular guilds and the availability of preferred foraging habitats following fire (Kotliar et al. 2007). Still, there is a lack of information on how breeding birds adapted to low- or mixed-severity fire regimes use post-fire landscapes when establishing home-ranges and selecting habitats for foraging and day-roosting, particularly where fire regimes have been anthropogenically modified. The manner in which animals use habitats may influence their demographic performance (e.g., Breininger et al. 1994, Linkhart and Reynolds 2006) and affect species interactions across trophic levels (e.g., Schmitz et al. 1997, Fagan et al. 1998). A better understanding of avian responses to fire is critical to

illuminating how population-, community-, and ecosystem-level processes may be affected by changing fire regimes.

We sought to determine how the 2002 Hayman Fire, which burned the largest area in Colorado history (Graham 2003), affected habitat selection at multiple spatial scales in breeding Flammulated Owls (*Psiloscops flammeolus*) from 2003–2014. Flammulated Owls are small forest raptors that breed across the western United States and Canada (Linkhart and McCallum 2013), and tend to prefer older stands of Ponderosa Pine/Douglas-fir (*Pseudotsuga menziesii*; Linkhart et al. 1998; Linkhart and Reynolds 2006, 2007). The Flammulated Owl is considered a “Sensitive Species” by the U.S. Forest Service in Regions 1, 2, and 4 (USFS 2005), a national “Bird of Conservation Concern” by the U.S. Fish and Wildlife Service (USFWS 2008), and a “Species of Special Concern” in Canada (COSEWIC 2010). The owl was also identified as a priority species for assessing effects of habitat alteration in western forests (Donovan et al. 2002). Currently, data are lacking concerning the owl’s use of habitats in areas subjected to altered fire regimes.

Our objectives were to (1) describe the size, shape, and juxtaposition of owl home-ranges within the Hayman Fire burn area; (2) compare burn severity patterns within owl home ranges to those of the entire burn area and (3) compare habitat variables (including burn severity) of foraging and day-roosting sites to available habitat within home ranges. We predicted owls would show a preference for unburned or low-severity burned habitats at all spatial scales, based on those habitats’ resemblance to unburned forests, where Flammulated Owls preferentially establish territories and forage in areas containing older stands of ponderosa pine/Douglas-fir (Linkhart et al. 1998).

METHODS

STUDY AREA

We conducted our study in the Pike National Forest in central Colorado, within the eastern portion of the area burned by the Hayman Fire in 2002 (Figure 1). This fire burned approximately 560 km² (Graham 2003), of which nearly 50% burned at high-severity versus the historic norm for this area of ~20% (Romme et al. 2003). Pre-fire forests within this portion of the Hayman burn area were typically dominated by open stands of mature (100- to 200-year-old) and old growth (>200-year-old) Ponderosa Pines on south-facing slopes, ridgetops, and flat areas, and denser stands of younger (largely <100-year-old) Ponderosa Pines, with some mature stands of Douglas-fir/Ponderosa Pine on north facing slopes (Finney et al. 2003). Drainage bottoms were dominated by Quaking Aspen (*Populus tremuloides*) or Quaking Aspen/Blue Spruce (*Picea pungens*; Finney et al. 2003). Elevations within the study area ranged from 2300–2600 m. Mean temperatures during summer (Jun.—Aug.) and winter (Dec.—Feb.) were 18.7 °C and -1.4 °C , respectively (NOAA 2010), and mean calendar year annual precipitation was 40.28 cm., over 60% of which falls from May—Sept. (WRCC 2015).

BURN SEVERITY ANALYSIS

The Hayman Fire burn area exhibited a mosaic of burn severities, which we defined according to the proportion of dominant/canopy trees that were killed: high-severity, areas where >90% were killed; moderate-severity, areas where 5–90% were killed; and, low-severity, areas where <5% were killed (sensu Key and Benson 2006; Figure 2). The highest burn severities within the Hayman Fire generally occurred in areas containing greater amounts of fuels and more continuous canopies (typically north- and east-facing slopes), whereas lower severity fires were

commonly associated with south- and west-facing slopes (Romme et al. 2003). While burn severity in drainage bottoms was variable, most Quaking Aspens were killed by the fire's heat but were not combusted.

We generated burn severity maps by calculating Normalized Difference Vegetation Index (δ NDVI) using Landsat 7 imagery from the U.S. Geological Survey from 2000 (pre-fire) and 2005 (post-fire). We calibrated δ NDVI values to field calculated composite burn index scores (CBI) for focal trees using linear regression, and we used a CBI threshold of 1.0 for low to moderate burn severity and 2.0 for moderate to high burn severity (Key and Benson 2006). We then used δ NDVI values that corresponded to CBI burn severity thresholds as cutoffs within the δ NDVI raster data to assign all δ NDVI pixels within the study area to one of three burn severity classes, based on *a priori* definitions: low-severity or unburned, moderate-severity, or high-severity (Figures 1 and 2). The raster data was clipped to a pre-defined Hayman Fire burn area provided by the USFS (USFS unpubl. data) which was approximately 93,250 ha in size, including unburned areas and other features, such as open water.

LOCATION OF OWL TERRITORIES AND NESTS

We surveyed the eastern portion of the burn area for occupancy by Flammulated Owls in June and July of 2003, 2004, and 2005 by conducting 5-minute point counts (Bibby et al 1997) at 0.8 km intervals along passable roads. In areas where we detected territorial males, we used spot-mapping (Bibby et al. 1997) to delineate boundaries of home ranges, which are synonymous with territories since the owls defend Type I territories (where all breeding behaviors occur within a defended area; Hinde 1956, Linkhart et al. 1998). We mapped home ranges boundaries in ArcGIS 10.1 (ESRI 2012).

We conducted nest searches during the incubation (late May to late June) and nestling phases (late June to late July) from 2004–2014 by listening for female food solicitation calls at night in portions of territories containing tree cavities (Reynolds and Linkhart 1984). In addition, we systematically checked tree cavities for occupancy during the day by tapping trees to induce females to rise to cavity entrances, and we also examined cavity contents with cameras mounted on telescopic poles.

RADIO TELEMETRY

We used radio-transmitters from Advanced Telemetry Systems (model A1030, Isanti, MN), which had a battery life of 40 d, and we detected signals from ≤ 1 km away. We affixed transmitters to owls during the incubation and nestling phases using a backpack harness constructed from flexible lycra straps and quick-drying glue (Reynolds and Linkhart 1984). Radio-transmitters weighed 1.9 g each, and total weight with harness was ~ 2.5 g. We conducted radio tracking using a handheld receiver (model R-1000, Communication Specialists; Orange, CA) and a three-element yagi antenna.

During nocturnal tracking, we traveled on foot to track individual males to specific trees, which we identified by searching for the strongest transmitter signal from multiple locations surrounding a suspected tree. We recorded a tree as a “fix” when we acquired an equally strong signal from multiple angles around a tree. We then attempted to assign a male’s behavior (foraging, resting, or singing) based on observation aided by headlamp, silhouette against the sky, or, if the owl could not be seen, researchers listened at the tree for ~ 1 –15 minutes and attempted to assign behavior based on aural cues. No observations indicated that owl behavior was directly affected by the presence or activities of the observer. We categorized the male’s behavior as foraging if a foraging attempt was observed or if wing flaps against foliage were

heard. We also stationed additional observers at nests, and we used observations of a radio-tagged male making a prey delivery at his nest immediately following a report of a fix (via 2-way radios) as confirmation that foraging had occurred. We categorized behavior as singing if territorial song was heard in the immediate vicinity and as resting in the absence of the above cues. We also attempted to locate day-roosting trees of males, but this was typically done diurnally. If observers were able to get close to a male's location but could not identify the specific tree as a fix, then a "general area" fix was recorded, which was used only for calculating home range. We recorded each location using a handheld global positioning system (GPS) unit and, if applicable, marked trees with flagging.

Between 2007 and 2012, we radio-tracked five unique breeding males, including two males tracked in consecutive years (2007–2008), over a total of 49 hours during June and July (corresponding to the incubation and nestling phases). In 2007, we tracked two males for 10 hours; in 2008, the same two males for 14 hours; in 2009, one male for 5.5 hours; in 2010, one male for 7 hours; and in 2012, one male for 12.5 hours. Nocturnal tracking efforts typically began shortly after sunset (2020–2045 hrs) and continued up to 0030 hrs. We recorded a total of 162 fixes, 19% of which were recorded from 2000–2059 hrs, 28% from 2100–2159 hrs, 33% from 2200–2259 hrs, 16% from 2300–2359 hrs, and 4% from 0000–0030 hrs. Approximately 23% of fixes (37) were recorded during the incubation phase and 77% (125) during the nestling phase.

HOME-RANGE ANALYSIS

We quantified owl home ranges using the minimum convex polygon (MCP) method and kernel density estimates (KDE). We delineated MCP boundaries in ArcGIS 10.1 (ESRI 2012) and calculated KDE rasters and isopleths in Geospatial Modelling Environment 0.7.2.1 (Beyer 2012),

which requires the integrated platform of ArcGIS 10.1 and Program R (R Core Team 2014). We produced 90% and 50% kernel isopleths, which estimated owl home ranges and core areas, respectively. We used likelihood cross-validation to determine the kernel smoothing parameters (*sensu* Horne and Garton 2006), and we set the grid cells at 30 m² to match the resolution of the Landsat Imagery used for burn severity analysis. Fixes recorded during extra-territorial movements were not used in delineation of home ranges but were included in modelling of foraging tree selection. We also excluded fixes recorded following fledging, given home-range boundaries break down after this time (Linkhart et al. 1998). Home ranges for the two males tracked in consecutive years were calculated using fixes combined from both years because of (1) high site fidelity shown by males in unburned forest (Linkhart and Reynolds 2007) and (2) the spatial distribution of recorded fixes for those two males was similar in both years, including reuse of the same nest site.

We calculated the proportion of MCP and kernel home-range estimates, and kernel core-area estimates that burned at the various severities in ArcGIS, and compared these to the same proportions available within the entire Hayman Fire burn area. We excluded δ NDVI raster cells (30 x 30 m) from this analysis that overlapped home-range and/or kernel core-area boundaries when centers of cells were outside home-range or core-area polygons.

MICRO- AND MESO-SITE HABITAT QUANTIFICATION

Within home ranges, we quantified habitat used by owls for breeding behaviors at two finer scales. We defined micro-site as a particular tree used by the owl for foraging or day-roosting, and meso-site as the forest stand within a ~10 m radius of a particular tree used for these behaviors.

Foraging and Roosting Habitat. We quantified habitat associated with foraging fixes and day-roosting fixes in July 2012. To assess whether foraging micro-sites were important factors in habitat selection, we determined condition (live vs dead), tree species, tree dbh, tree height (assessed with clinometer), and crown volume (program HTVOL; Mawson et al. 1976) for foraging trees (focal trees), and compared these variables to available but unused trees. We used the same habitat quantification regime for day-roosting micro-sites. We quantified meso-site variables immediately surrounding foraging and day-roosting trees using the point-quarter method (Cottam and Curtis 1956), where we recorded slope position, aspect, grade, canopy closure, ground cover, and CBI, as well as the same suite of characteristics as the focal tree for the nearest neighbors in each quadrant according to two size classes (≥ 20 cm dbh and < 20 cm dbh), and compared these characteristics to randomly selected but unused sites.

DATA ANALYSIS

We analyzed selection patterns in foraging and day-roosting at both micro- and meso-site scales. Initial models were subjected to bi-directional stepwise multivariate logistic regression (*sensu* Weber 2006). Akaike's Information Criterion (AIC) was used to distinguish among models, with the final model identified as having the lowest AIC value (Burnham and Anderson 2002). We conducted overall model evaluation using the likelihood ratio test and model goodness-of-fit was assessed using Pearson's chi-squared test (Hosmer and Lemshow 1989). The binary logistic regression coefficients were used to calculate odds ratios, which indicate the increase in the odds of the response variable (use by owls) for every unit increase in the given predictor variable. Wald tests were used to determine if categorical predictors were significant overall (Hosmer and Lemshow 1989). We attempted to minimize model over-fitting for both foraging and day-roosting meso-sites (given small sample sizes and a large number of potential model variables)

by reducing the number of variables initially considered in the models (*sensu* Weber 2006). Models run with the full suite of potential predictor variables indicated perfect separation as well as model non-convergence. The suites of predictor variables subjected to the stepwise selection process for both foraging meso-sites and day-roosting meso-sites were initially reduced by eliminating variables that showed a high degree of correlation with other variables (>0.75), measured biologically similar attributes, and/or were considered to be inapplicable to the specific selection behaviors being modelled (e.g., percent ground cover in day-roost sites).

Models and individual predictor variables were considered significant when $P \leq 0.05$, and a trend was inferred when $0.05 < P \leq 0.10$. We performed logistic regression and associated statistics in Program R (R Core Team 2014) and calculated descriptive statistics using Microsoft Excel (2013). We present all values hereafter as mean \pm 1 SE, unless otherwise stated.

RESULTS

HOME-RANGE

We collected a mean 23 ± 4 fixes per male per year (range = 13–40) for five breeding males from 2007–2012, including two males (CN7 and CN8) tracked in consecutive years. Seventy percent (114 of 162) of fixes were attributed to specific behaviors, and of these, foraging was the most frequently observed behavior ($n = 59$; 61%), followed by day-roosting ($n = 22$; 19%), territorial singing ($n = 18$; 16%), resting ($n = 12$; 11%), and other ($n = 3$; 3%). Mean home-range size estimated by the 90% kernel (19.4 ± 3.7 ha; range = 8.7–29.0 ha) was 50% larger than the mean home-range size estimate by MCP (12.9 ± 3.2 ha; range = 4.9–23.4 ha; Figure 1). All home-ranges encompassed at least one drainage bottom, where nests were typically located, and one or more ridge slopes and ridge-tops, the latter of which frequently served as common boundaries between adjacent home-ranges (Figure 1). Qualitatively, we recorded most territory

songposts along home-range boundaries shared among multiple males, and few where conspecific neighbors were absent. Four of five home ranges had a single kernel core area (mean = 4.3 ha, range = 0.4–7.5 ha), whereas one had two core areas (CN5; Figure 1), and core areas represented 27% of kernel home ranges (range = 24–32%).

δ NDVI were reliably calibrated to field-calculated CBI scores, which reflected moderately high correlation between the two metrics ($r^2 = 0.31$, $P < 0.001$), and CBI burn scores of 1.0 and 2.0 (thresholds for low-moderate and moderate-high burn severities) corresponded to δ NDVI values of -0.07 and -0.12, respectively. The MCP and kernel-estimated home ranges contained substantially less high-severity burned forest (24.4% and 22.8%, respectively) and more low-severity burned/unburned forest (51.9% and 56.6%) compared to the Hayman Fire burn area as a whole, which contained 48.7% high-severity burned forest and 33.6% low-severity burned/unburned forest (Figure 1). Owl MCP and kernel-estimated home ranges contained similar proportional amounts of moderate burn severity (23.7% and 20.6%, respectively) compared to the Hayman Fire burn area as a whole (17.7%). One territory (CN13) contained 44.7% high-severity burned forest, but this area likely was overestimated by the δ NDVI score, as evidenced by the low- or moderate-severity CBI scores for most use sites (mean = 1.1 ± 0.2) despite the majority of these sites occurring in areas mapped as high-severity by the δ NDVI raster (Figure 1). Similar to the pattern shown by most home ranges, kernel core areas contained 26.3% high-severity burned forest and 56.8% low-severity burned forest (Figure 1). Both the MCP and kernel estimates of home-range size trended toward a positive correlation with the proportion of area burned at high severity ($r^2 = 0.69$, $P = 0.08$ and $r^2 = 0.74$, $P = 0.06$, respectively).

FORAGING HABITAT

Foraging fixes were most commonly recorded in unburned or low-severity burned forest (mean CBI = 0.78 ± 0.14), and no foraging fixes were recorded in high-severity burned areas (CBI > 2.0). We recorded a mean 11.8 ± 1.4 (range = 1–16) foraging fixes per male ($n = 59$). Most foraging fixes were recorded during the nestling period (78%; 46 of 59), with the remainder recorded during the incubation period (22%; 13 of 59). Foraging fixes (including general area foraging fixes) were located a mean 137 ± 12 m (range = 15–399 m) from nests. While our sample sizes did not allow for robust quantitative analysis of the distance of foraging events from the nest based on time, qualitatively, we most frequently recorded foraging fixes in the immediate vicinity of nests (<25 m) in the early evening and at greater distances from nests as the night progressed. Gleaning prey from within live tree crowns was the most commonly observed foraging tactic by males, but we also saw owls gleaning from tree trunks, hawking between tree crowns, and ground foraging from low (1–3m high) perches.

For foraging fixes identified to specific trees ($n = 23$), models indicated that micro-site selection by owls was primarily based on tree dbh, species, condition, and crown volume ($\chi^2 = 39.64$, $df = 5$, $P < 0.0001$; AIC = 47.22; Table 1). Trees used for foraging had mean dbh that was more than twice as large, and mean crown volume that was more than four times as great, as available trees (Table 1). Compared to available trees, those used for foraging were also disproportionately Ponderosa Pines (61%; 14 of 23; $\chi^2 = 7.9$, $df = 3$, $P < 0.05$) and live (vs. dead; 91%; 21 of 23; $\chi^2 = 8.6$, $df = 2$, $P < 0.05$; Table 1).

Models did not indicate any selection based on burn severity; CBI scores for used and unused foraging locations were 0.78 ± 0.14 and 0.99 ± 0.14 , respectively (both low-severity CBI scores). Instead, models indicated that meso-site selection was primarily based on crown volume,

mean dbh of trees in the <20 cm size class, and dbh of trees in the >20 cm size class ($\chi^2 = 11.38$, $df = 3$, $P < 0.01$; AIC = 71.48; Table 1). Meso-sites used for foraging had roughly twice the overall mean crown volume of trees in the <20 cm dbh size class compared to available trees. Trees in the <20 cm dbh size class has roughly one third the mean dbh of available trees while trees in the >20 cm dbh size class had slightly larger mean dbh compared to available (Table 1).

DAY-ROOSTING HABITAT

Day-roosting fixes were most commonly recorded in low-severity burned stands (mean CBI = 0.93 ± 0.11); only one such fix was recorded in a high-severity burned stand (CBI > 2.0). We recorded a mean 4.4 ± 1.0 day roosts per male ($n = 22$; range = 0–7). Most day-roosting fixes were recorded during the nestling period (77%; 17 of 22) compared to the incubation period (23%; 5 of 22). Day-roosts were frequently located within 100 m of nest trees (mean = 81 ± 16 m from the nest; range = 3–256 m). Males typically perched within 1 m of trunks in areas surrounded by foliage within live crowns.

Models indicated that micro-site selection was primarily based on tree condition, height, and crown volume ($\chi^2 = 22.98$, $df = 4$, $P < 0.001$; AIC = 48.79; Table 2). Micro-sites used by owls for day-roosting were disproportionately live trees (96%; 22 of 23), and were approximately 50% taller, and had more than twice the mean crown volume compared to available trees (Table 2).

Models did not indicate any selection based on burn severity; CBI scores for used and unused day-roost sites were 0.93 ± 0.11 and 0.99 ± 0.17 , respectively (both low-severity CBI scores). Instead, at the meso-site scale, models indicated that selection was primarily based on canopy closure and crown volume of trees in the <20 cm dbh size class ($\chi^2 = 11.31$, $df = 2$, $P < 0.001$; AIC = 57.05; Table 2). Meso-sites used by owls had somewhat greater canopy closure

and slightly smaller overall crown volume of trees in the <20cm dbh size class compared to available trees (Table 2).

DISCUSSION

Flammulated Owls in this study appeared to avoid high-severity burned forests when establishing breeding territories, as home ranges of males contained less high-severity burned area and more low-severity burned/unburned area compared to the Hayman Fire burn as a whole. MCP estimates of home-range sizes (12.9 ± 3.2 ha) in this study were consistent with those reported for unburned habitats (14.2 ± 5.0 (SD) ha; Linkhart et al. 1998), suggesting that the unburned/low-severity burned habitats used by owls in this study were of similar quality to those in unburned forest. In addition, the proportion of high-severity burned area in home ranges was positively correlated with home-range size, suggesting that these high-severity burned areas represented low-quality habitat. Other studies suggested that intra-specific differences in avian home-range sizes were inversely correlated with habitat quality (e.g., Tufto et al. 1996, Clark 2007).

In contrast to the patterns observed at the home-range scale, our findings suggest that habitat selection by Flammulated Owls at finer spatial scales (foraging and day-roosting) did not reflect any apparent preference for or avoidance of habitat based on burn severity. Instead, the owls exhibited selection patterns that largely mimicked those observed in unburned habitat (e.g., Linkhart et al. 1998). Home ranges selected by breeding birds necessarily must contain all the resources required for breeding, including requisite habitats at finer spatial scales (Johnson 1980). By avoiding high-severity burned forests and selecting low-severity/unburned forests at larger spatial scales, selection by Flammulated Owls may ensure that home ranges contain sufficient resources for all breeding behaviors (nesting, roosting, foraging etc.). This type of

spatially dynamic habitat selection, where habitat selection patterns at finer spatial scales are contingent upon habitat selection decisions at broader spatial scales, has been reported across a structurally diverse spectrum of ecosystems, from grasslands (Chalfoun and Martin 2007, McNew et al. 2013) to forests (McClure et al. 2012). Overall, this strategy may reflect the owls' evolution with historic low-severity and/or mixed-severity fire regimes, since animals adapted to high-severity fires would be expected to exhibit responses that reflect a tolerance or preference for post-fire landscapes associated with high-severity fire (Hutto 2008).

The specific micro- and meso-site characteristics preferred by owls in this study for foraging and day-roosting, as well as in unburned forests (Linkhart et al. 1998, Linkhart and Reynolds 2006, 2007), indicated that owls selected habitats that contained large, old Ponderosa Pines with voluminous crowns. This habitat structure is specifically created and maintained by regular, low-severity fire (or the low-severity component of mixed-severity fires; Covington and Moore 1994, Veblen et al. 2000). The large, live trees preferred by the owls for foraging may be important because they offer greater prey availability, or because these trees may be structurally more conducive to the owls' preferred sit-and-wait/gleaning foraging tactics. Similarly, the owls' preferred day-roosting locations may provide greater concealment which, in other owl species, has been associated with lower risks of predation and mobbing (Young et al. 1998, Sunde et al. 2003, Willey and Van Riper III 2014).

Our results, combined with the fact that during our initial census of the Hayman Fire burn area, no Flammulated Owls were detected in the largest expanses of high-severity burn, suggest that animals whose life-histories are adapted to low- and/or mixed-severity fire-maintained environments may be displaced by high-severity fire regimes. Our results are consistent with other studies showing that habitat specialists lack resilience to modification and/or fragmentation

of preferred habitats (Cahill and Matthysen 2006, Owino and Ryan 2006, Mathews et al. 2014). The ongoing pattern of low- and mixed-severity fire regimes across the western United States transitioning to fire regimes that include much greater components of high-severity fire (Huckaby et al. 2001, Miller and Safford 2012, Fulé et al. 2014) has significant conservation implications. Increasingly large and more severe wildfires are predicted to occur in the future (Westerling et al. 2006, Marlon et al. 2012, Sherriff and Veblen 2014), potentially causing localized faunal extinctions, and modifying plant community distribution and composition for decades.

Male Flammulated Owls established breeding home-ranges in areas containing more low-severity burned/unburned area than was available within the Hayman burn as a whole. However, it is unclear if these habitats were similar enough to preferred unburned habitats, where crown volume and tree age at the scale of the home range has been strongly linked to demographic success (Linkhart and Reynolds 1997, Linkhart and Reynolds 2006), to maintain viable populations. Indeed, a larger dataset than is presented here indicated that males may exhibit lower return rates to at least some home ranges in the Hayman Fire burn area (Linkhart, unpubl. data) which may reflect either higher mortality or lower territory fidelity. Disturbance induced demographic effects have been reported in many other studies (e.g., Robinson et al. 1995, Dugger et al. 2010), including demographic effects mediated through changes to animals' habitat use patterns (e.g., Vanderwerf 2004). For example, fire increased the likelihood of breeding dispersal and reduced survival of male Northern Spotted Owls (*Strix occidentalis caurina*) in California (Clark et al. 2011). Future study with larger sample sizes than are presented here is needed to better understand demographic responses of Flammulated Owl populations that inhabit

post-fire landscapes and to determine whether burn severity plays a mediating role in these responses.

Given that our findings are based on a limited number of radio-tracked Flammulated Owls from one local population, further study is needed with larger sample sizes and in disparate areas across the owl's range to clarify the generality of our results. Further study also is needed to develop a broader understanding of landscape-scale responses to modified fire regimes and climate change and to assess long-term responses of species across trophic levels, especially in other geographic areas containing forests dominated by pine. Finally, range-wide monitoring of Flammulated Owls would be valuable in determining population trends at landscape scales as well as how these trends correlate to broad scale changes in ecosystem processes such as wildfire.

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LITERATURE CITED

- Allen, C. D., Savage, M., Falk, D. A., Suckling, K. F., Swetnam, T. W., Schulke, T., Stacey, P., Morgan, P. B., Hoffman, M., and Klingel, J. T. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: A broad perspective. *Ecol. Appl.* 12:1418–1433.
- Abella, S. R., Covington, W. W., Fulé, P. Z., Lentile, L. B., Sánchez Meador, A. J., and Morgan, P. 2007. Past, present, and future old growth in frequent-fire conifer forests of the western United States. *Ecol. and Soc.* 12:16.
- Beyer, H. L. 2012. Geospatial Modelling Environment, version 0.7.2.1; www.spataleecology.com/gme.
- Bibby, C. J., Burgess, N. D., and Hill, D. A. 1997. Bird census techniques. Harcourt Brace, San Diego.
- Binkley, D., Sisk, T., Chambers, C., Springer, J., and Block, W. 2007. The role of old-growth forests in frequent-fire landscapes. *Ecol. Soc.* 12:18.
- Brawn, J. D., and Balda, R. P. 1988. The influence of silvicultural activity on ponderosa pine forest bird communities in the southwestern United States, in *Bird Conservation 3* (J. A. Jackson, ed.), pp. 3–21. Univ. Wisconsin Press, Madison.
- Breiner, D. R., Larson, V. L., Duncan, B. W., Smith, R. B., Oddy, D. M., and Goodchild, M. F. 1994. Landscape patterns of Florida Scrub Jay habitat use and demographic success. *Conserv. Biol.* 9:1442–1453.

- Brown, P. M., M. R. Kaufmann, and W. D. Shepperd. 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecol.* 14:513–532.
- Brown, P. M. and W. D. Shepperd. 2001. Fire history and fire climatology along a 5° gradient in latitude in Colorado and Wyoming, USA. *Paleobotanist* 50:133–140.
- Burnham, K. P. and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer Science and Business Media, New York, NY.
- Cahill, J. R. A., and Matthysen, E. 2006. Habitat use by two specialist birds in high-Andean *Polylepis* forests. *Biol. Conserv.* 140:62–69.
- Chalfoun A. D. and Martin, T. E. 2007. Assessments of habitat preferences and quality depend on spatial scale and metrics of fitness. *J. Appl. Ecol.* 44:983–992.
- Clark, D. A. 2007. Demography and habitat selection of Northern Spotted Owls in post-fire landscapes of southwestern Oregon. M. S. thesis, Oregon State University, Corvallis.
- Clark, D. A., Anthony, R. G., and Andrews L. S. 2011. Survival rates of Northern Spotted Owls in post-fire landscapes of southwest Oregon. *J. Raptor Res.* 45:38–47.
- Conway, C. J. and Kirkpatrick, C. 2010. Effect of forest fire suppression on buff-breasted flycatchers. *J. Wildl. Mgmt.* 71:445–457.
- COSEWIC. 2010. COSEWIC assessment and update status report on the Flammulated Owl *Otus flammeolus* in Canada. Committee on the Status of Endangered Wildlife in Canada, Ottawa; www.registrelep-sararegistry.gc.ca/document/default_e.cfm?documentID=2011
- Cottam, G. and Curtis, J. T. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451–460.

- Covington, W. W., and Moore, M. M. 1992. Post-settlement changes in natural disturbance regimes: Implications for restoration of old-growth ponderosa pine ecosystems, in Old-growth forests in the Southwest and Rocky Mountain Regions, Proceedings of a Workshop (M. R. Kaufmann, W. H. Moir and W. H. Bassett, tech. eds.), pp. 81–99. USDA Forest Serv. Gen. Tech. Rep. RM-213.
- Covington, W. W., and Moore, M. M. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *J. Forest.* 92:39–47.
- Davis, R. S., Hood, S., and Bentz, B. J. 2012. Fire-injured ponderosa pine provide a pulsed resource for bark beetles. *Can. J. Forest.* 42:2022–2036.
- Donovan, T. M., Beardmore, C. J., Bonter, D. N., Brawn, J. D., Cooper, R. J., Fitzgerald, J., Ford, R., Gauthreaux, S. A., George, T. L., Hunter, W. C., Martin, T. E., Prince, J., Rosenberg, K. V., Vickery, P. D., and Wigley, T. B. 2002. Priority research needs for the conservation of Neotropical migrant landbirds. *J. Field Ornithol.* 73:329–339.
- Dugger, K. M., Ainley, D. G., Lyver, P. O'B., Barton, K., and Ballard, G. 2010. Survival differences and the effect of environmental instability on breeding dispersal in an Adelie Penguin meta-population. *Proc. Natl. Acad. Sci. USA* 107:12375–12380.
- Fagan, W. F., Cantrell, R. S., and Cosner, C. 1998. How habitat edges change species interactions. *Am. Nat.* 153:165–182.
- Finney, M. A., McHugh, C. W., Bartlette, R., Close, K., and Langowski, P. 2003. Fire behavior, fuel treatments, and fire suppression on the Hayman Fire. Part 2: Description and interpretations of fire behavior, in Hayman fire case study (Graham, R. T., tech. ed.), pp. 59–95. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-114.

- Fulé, P. Z., Crouse, J. E., Heinlein, T. A., Moore, M. M., Covington, W. W., and Verkamp, G. 2003. Mixed-severity fire regime in a high-elevation forest of Grand Canyon, Arizona, USA. *Landscape Ecol.* 18:465–486.
- Fule, P. Z., Swetnam, T. W., Brown, P. M., Falk, D. A., Peterson, D. L., Allen, C. D., Aplet, G. H., Battaglia, M. A., Binkley, D., Farris, C., Keane, R. E., Margolis, E. Q., Grissino-Mayer, H., Miller, C., Sieg, C. H., Skinner, C., Stephens, S. L., and Taylor, A. 2014. Unsupported inferences of high-severity fire in historical dry forests of the western United States: Response to Williams and Baker. *Global Ecol. Biogeogr.* 23:825–830.
- Graham, R. T., tech. ed. 2003. Hayman fire case study. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-114.
- Hinde, A. 1956. The biological significance of the territories of birds. *Ibis* 98:340–369.
- Horne, J. S., and Garton, E. O. 2006. Likelihood cross-validation versus least squares cross-validation for choosing the smoothing parameter in kernel home-range analysis. *J. Wildl. Mgmt.* 70:641–648.
- Hosmer, D. W., and Lemshow, S. 1989. *Applied logistic regression*. Wiley, New York, NY.
- Huckaby, L. S., Kaufmann, M. R., Stoker, J. M., Fornwalt, P. J. 2001. Landscape patterns of montane forest age structure relative to fire history at Cheedman Lake in the Colorado Front Range, in *Ponderosa pine ecosystem restoration and conservation: Steps toward stewardship* (Vance, R. K., Edminster, C. B., Carleton, B., Covington, W. W., and Blake, J. A., comps.), pp. 19–27. USDA Forest Serv. Proceedings RMRS-P-22.
- Hurteau, M. D., Bradford, J. B., Fulé, P. Z., Taylor, A. H., Martin, K. L. 2014. Climate change, fire management, and ecological services in the southwestern US. *Forest Ecol. and Mgmt.* 327:280–289.

- Hutto, R. L. 2008. The ecological importance of severe wildfires: Some like it hot. *Ecol. Appl.* 18:1827–1834.
- Intergovernmental Panel on Climate Change (IPCC). 2013. *Climate Change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change* (Stocker, T. F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S. K., Boschung, J., Nauels, A., Xia, Y., Bex, V., and Midgley, P. M., eds.). Cambridge Univ. Press, Cambridge, UK, and New York, NY; www.ipcc.ch/report/ar5/wg1/.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 6: 65–71.
- Kaufman, M. R., Fornwalt, P. J., Huckaby, L. S., and Stoker, J. M. 2001. Cheesman Lake – A historical ponderosa pine landscape guiding restoration in the South Platte watershed of the Colorado Front Range, in *Ponderosa pine ecosystem restoration and conservation: Steps toward stewardship* (Vance, R. K., Edminster, C. B., Carleton, B., Covington, W. W., and Blake, J. A., compls.), pp. 9–18. USDA Forest Serv. Proceedings RMRS-P-22.
- Kaufmann, M. R., Huckaby, L. S., Fornwalt, P. J., Stoker, J. M., and Romme, W. H. 2003. Using tree recruitment patterns and fire history to guide restoration of an unlogged ponderosa pine/Douglas-fir landscape in the southern Rocky Mountains after a century of fire suppression. *Forestry* 76:231–241.
- Key, C. H. and Benson, N. C. 2006. FIREMON - Landscape assessment (LA): Sampling and analysis methods, in *FIREMON: Fire effects monitoring and inventory system* (Lutes, D. C., tech. ed.), pp. LA 1–55. USDA Forest Serv. Gen. Tech. Rep. RMRS-GTR-164-CD.

- Kotliar, N. B., Kennedy, P. L., and Ferree, K. 2007. Avifaunal responses to fire in the southwestern montane forests along a burn severity gradient. *Ecol. Appl.* 17:491–507.
- Linkhart, B. D. and Mccallum, D. A. 2013. Flammulated Owl (*Psilosops flammeolus*), in *The Birds of North America Online* (Poole, A., ed.), no. 93. Cornell Lab of Ornithol., Ithaca, NY; <http://bna.birds.cornell.edu/bna/species/093>. (Accessed March 20, 2015)
- Linkhart, B. D. and Reynolds, R. T. 1997. Territories of Flammulated Owls (*Otus flammeolus*): Is occupancy a measure of habitat quality? in *Biology and Conservation of Owls of the Northern Hemisphere* (J. R. Duncan, Johnson, D. H., and Nicholls, T. H., eds.), pp. 226–230. USDA Forest Serv. Gen. Tech. Rep. NC-190.
- Linkhart, B. D. and Reynolds, R. T. 2006. Lifetime reproduction of Flammulated Owls in Colorado. *J. Raptor Res.* 40:29–37.
- Linkhart, B. D. and Reynolds, R. T. 2007. Return rate, fidelity, and dispersal in a breeding population of Flammulated Owls (*Otus flammeolus*). *Auk* 124:264–275.
- Linkhart, B. D., Reynolds, R. T. and Ryder, R. A. 1998. Home range and habitat use of breeding Flammulated Owls in Colorado. *Wilson Bull.* 110:342–351.
- Marlon, J. R., Bartlein, P. J., Gavin, D. G., Long, C. J., Anderson, R. S., Briles, C. E., Brown, K. J., Colombaroli, D., Hallett, D. J., Power, M. J., Scharf, E. A., and Walsh, M. K. 2012. Long-term perspective on wildfires in the western USA. *Proc. Natl. Acad. Sci. USA* 109:E535–E543.
- Mathews, T. J., Cottee-Jones, H. E., and Whittaker, R. J. 2014. Habitat fragmentation and the species-area relationship: A focus on total species richness obscures the impact of habitat loss on habitat specialists. *Divers. and Distrib.* 20:1136–1146.

- Mawson, J. C., Thomas, J. W., and DeGraaf, R. M. 1976. Program HTVOL: The determination of tree crown volume by layers. USDA For. Serv. Res. Pap. NE-354.
- McClure, C. J. W., Rolek, B. W., and Hill, G. E. 2012. Predicting occupancy of wintering migratory birds: Is microhabitat information necessary? *Condor* 144:482–490.
- McNew, L. B., Gregory, A. J., and Sandercock, B. K. 2013. Spatial heterogeneity in habitat selection: nest site selection by Greater Prairie-chickens. *J. Wildl. Mgmt.* 77:791–801.
- Miller, J. D., Safford, H. D., Crimmins, M., and Thode, A. E. 2009. Quantitative evidence of increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12:16–32.
- Miller, J. D. and Safford, H. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. *Fire Ecol.* 8:41–57.
- National Oceanographic and Atmospheric Administration (NOAA). 2010. Normals Annual/Seasonal for Cheesman, CO, Station ID: GHCND:USC00051528; www.ncdc.noaa.gov/cdo-web/datasets/normal_ann/stations/GHCND:USC00051528/detail. (Accessed March 16, 2015)
- Odion D. C., Hanson, C. T., Arsenault, A., Baker, W. L., DellaSala, D. A., Hutto, R. L., Klenner, W., Moritz, M. A., Sherriff, R. L., Veblen, T. T., and Williams, M. A.. 2014. Examining historical and current mixed-severity fire regimes in Ponderosa Pine and mixed-conifer forests of western North America. *PLoS One* 9:e87852.
- Owino, A. O., and Ryan, P. G. 2006. Habitat associations of papyrus specialist birds at three papyrus swamps in western Kenya. *Afr. J. Ecol.* 44:438–443.

- R Core Team. 2014. R: A language environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; <http://www.R-project.org/>.
- Reynolds, R. T. and Linkhart, B. D. 1984. Methods and materials for capturing and monitoring Flammulated Owls. *Great Basin Nat.* 44: 49–51.
- Robinson, S. K., Thompson III, F. R., Donovan, T. M., Whitehead, D. R., and Faaborg, J. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267: 1987–1990.
- Rocca, M. E., Brown, P. M., MacDonald, L. H., Carrico, C. M. 2014. Climate change impacts on fire regimes and key ecosystem services in Rocky Mountain forests. *Forest Ecol. and Mgmt.* 327:290–305.
- Romme, W. H., Veblen, T. T., Kaufmann, M. R., Sherriff, R., and Regan, C. M. 2003. Ecological effects of the Hayman fire; Part 1: Historical (pre-1860) and current (1860–2002) fire regimes, in Hayman fire case study (Graham, R. T., tech. ed.). USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-114.
- Rumble, M. A., Flake, L. D., Mills, T. D., and Dykstra, B. L. 2001. Do pine trees in aspen stands increase bird diversity? USDA For. Serv. Proc. RMRS-P-18.
- Running, S. W. 2006. Is global warming causing more, larger wildfires? *Science* 313:927–928.
- Schmitz, O. J., Beckerman, A. P., and O'Brien, K. M. 1997. Behaviorally mediated trophic cascades: Effects of predation risk on food web interactions. *Ecology* 78:1388–1399.
- Schoennagel, T., Veblen, T. T., and Romme, W. H. 2004. The interaction of fire, fuels, and climate across Rocky Mountain forests. *BioScience* 54: 661–676.
- Sedgwick, J. A. and Knopf, F. L. 1992. Describing Willow Flycatcher habitats: Scale perspectives and gender differences. *Condor* 94:720–733.

- Sherriff, R. L. and Veblen, T. T. 2006. Ecological effects of changes in fire regimes in *Pinus ponderosa* ecosystems in the Colorado Front Range. *J. Veg. Sci.* 17:705–718.
- Sherriff, R. L., Platt, R. V., Veblen, T. T., Schoennagel, T. L., and Gartner, M. H. 2014. Historical, observed, and modeled wildfire severity in montane forests of the Colorado Front Range. *PLoS One* 9: e106971.
- Sunde, P., Bølstad, M. S., and Desfor, K. B. 2003. Diurnal exposure as a risk sensitive behavior in tawny owls *Strix aluco*? *J. Avian Biol.* 34:409–418.
- Szaro, R. C. and Balda, R. P. 1982. Selection and monitoring of avian indicator species: An example from a ponderosa pine forest in the southwest. USDA For. Serv. Gen. Tech. Rep. RM-GTR-89.
- Tufto, J. R. Anderson, and Linnell, J. 1996. Habitat use and ecological correlates of home range size in a small cervid: The roe deer. *J. Animal Ecol.* 65:715–724.
- U.S. General Accounting Office (U.S. GAO). 1999. Western National Forests: A cohesive strategy is needed to address catastrophic wildfire threats. GAO/RCED-99-65; www.gao.gov/archive/1999/rc99065.pdf.
- U.S. Fish and Wildlife Service (USFWS). 2008. Birds of Conservation Concern 2008. United States Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Arlington, Virginia; www.fws.gov/migratorybirds/.
- U.S. Forest Service (USFS). 2005. Forest Service sensitive species that are not listed or proposed under the ESA; http://www.fs.fed.us/biology/resources/pubs/tes/fs_ss_310ct05.pdf
- Vanderwerf, E. A. 2004. Demography of Hawai'i 'Elepaio: Variation with habitat disturbance and population density. *Ecology* 85:770–783.

- Veblen, T. T., Kitzberger, T., and Donnegan, J.. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecol. Appl.* 40:1178–1195.
- Weber, T. T. 2006. Northern Goshawk (*Accipiter gentilis*) nesting habitat in northwestern California. An examination of three spatial scales: The nest area, the post-fledging area, and the home range. M.S. thesis, Humboldt State Univ., Arcata, CA; <http://humboldt-dspace.calstate.edu/handle/2148/145>.
- Westerling, A. L., Hidalgo, H. G., Cayan, D. R., and Swetnam, T. W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313: 940–943.
- Westerling, A. L., Turner, M. G., Smithwick, E. A. H., Romme, W. H., Ryan, M. G. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proc. Natl. Acad. Sci. USA* 108:13165–13170.
- Western Regional Climate Center (WRCC). 2015. Cheeseman, Colorado period of record general climate summary – precipitation. <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?co1528> (Accessed: November 20, 2015)
- Willey, D. and Van Riper III, C. 2014. Home range characteristics of Mexican Spotted Owls in the Rincon Mountains, Arizona. *Wilson J. Ornithol.* 126:53–59.
- Williams, M. A. and Baker, W. L. 2012. Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. *Global Ecol. Biogeogr.* 21:1042–1052.
- Young, K. E., Valdez, R., Zwank, P. J., and Gould, W. R. 1998. Density and roost site characteristics of spotted owls in the Sierra Madre Occidental, Chihuahua, Mexico. *Condor* 100:732–736.

Figure 1. Location of the 2002 Hayman Fire within Colorado, juxtaposition and location of male Flammulated Owl home-ranges studied using radio-telemetry from 2007–2012, and 90% kernel home range and 50% core area boundaries, raw telemetry fixes, and nest sites overlaid on δ NDVI-based burn severity maps.

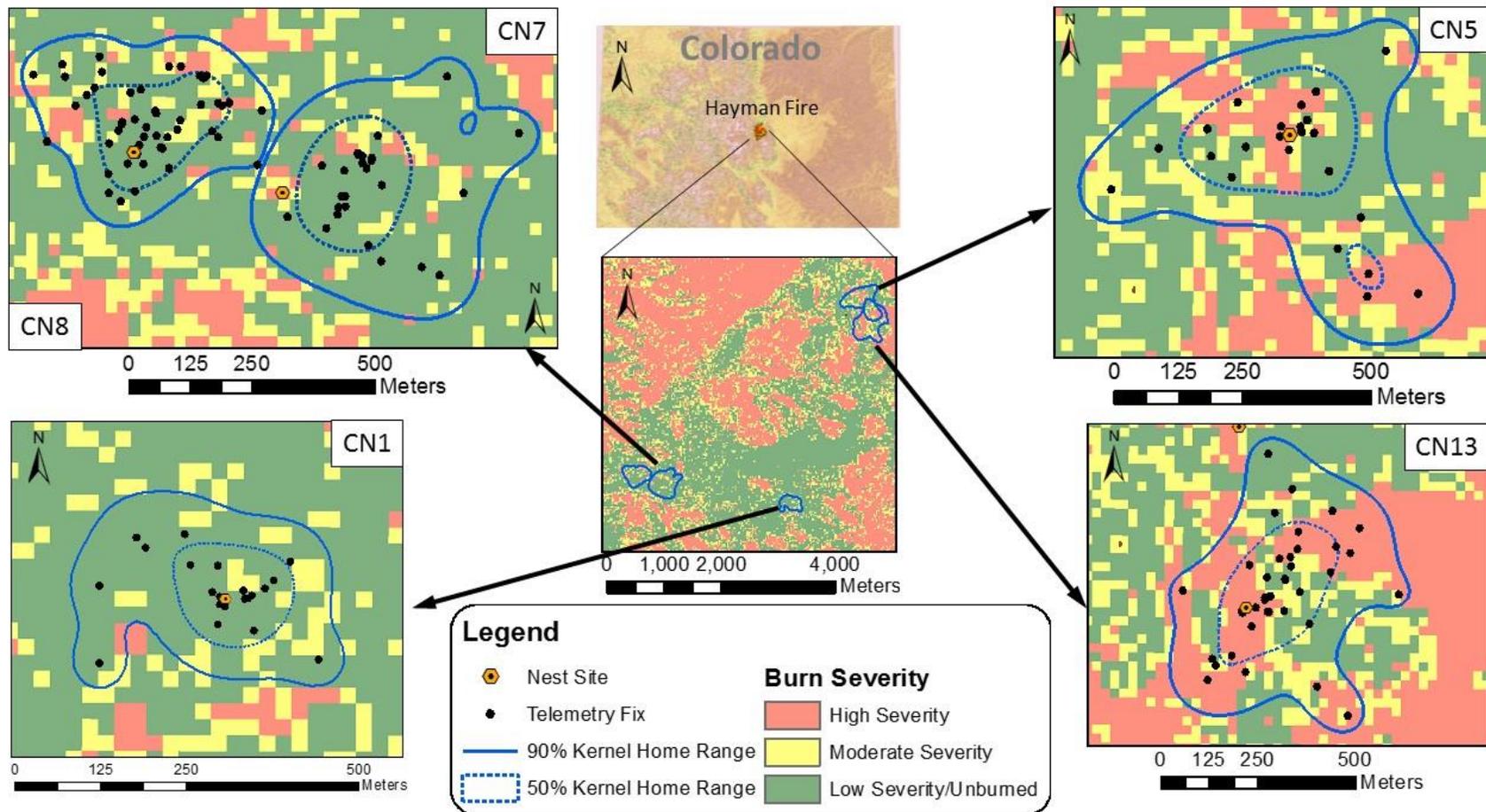
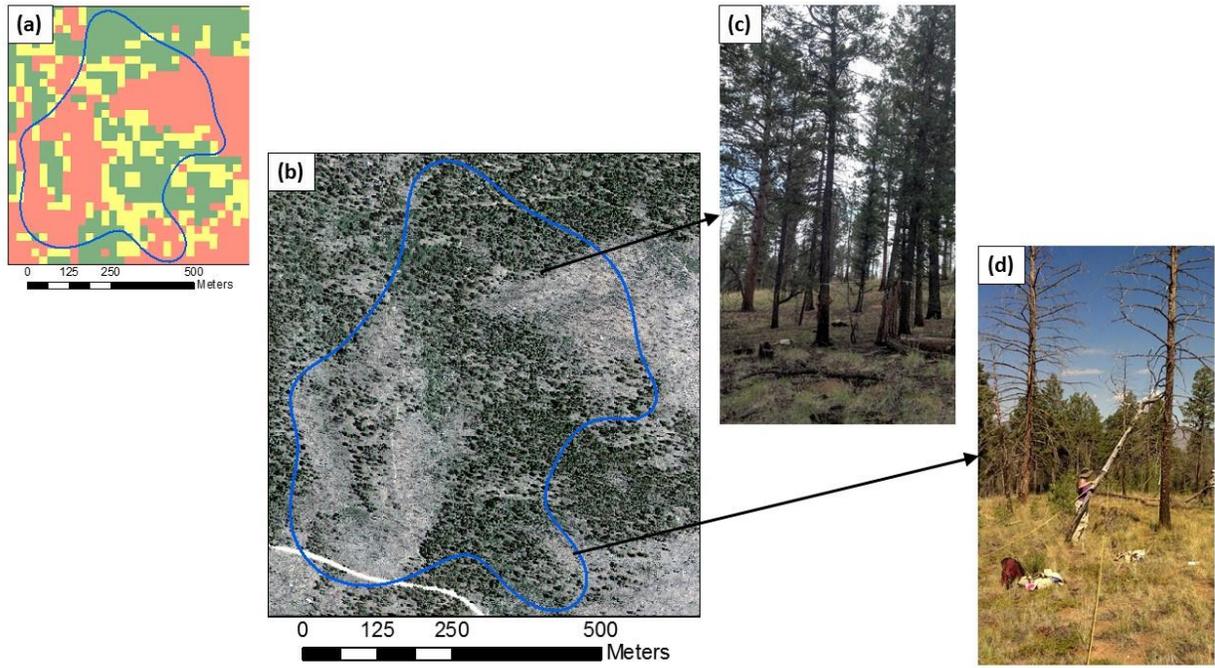


Figure 2. (a) δ NDVI-based burn severity map for CN13 with 90% kernel home range boundary in blue; (b) Aerial imagery of CN13 with 90% kernel home range boundary in blue; and, examples of (c) a low-severity burned site (CBI = 0.1) and (d) a high-severity burned site (CBI = 2.63). Arrows from (b) to (c) and (d) indicate approximate photo location.



Habitat variable	Used		Unused		Odds ratio	<i>P</i>
	Mean	SE	Mean	SE		
Micro-site						
DBH (cm)	43.8 ± 2.0		18.5 ± 3.1		1.281	0.004
Tree Species	n/a		n/a		7.064 ^a	0.049 ^b
Tree condition	n/a		n/a		0.104 ^c	0.014 ^b
Crown volume (m³)	1,195.0 ± 162.4		315.7 ± 122.7		0.998	0.053
Meso-site						
Overall crown volume (m³) of <20 cm size class	66.1 ± 11.5		32.3 ± 7.1		1.026	0.008
Dbh (cm) of trees in <20 cm size class	3.2 ± 0.6		9.7 ± 0.6		0.781	0.048
Dbh (cm) of trees in >20 cm size class	31.2 ± 0.6		31.4 ± 1.2		0.943	0.305

^aOdds ratio refers to change in odds of selection for Ponderosa Pine compared to Douglas-fir.

^bP-values derived from Wald test.

^cOdds ratio refers to change in odds of selection for dead compared to live trees.

Table 2. Final binary logistic regression models for foraging micro- and meso-site selection by male Flammulated Owls breeding within the post-burn area of the Hayman Fire in Colorado.

Habitat variable	Used		Unused		Odds ratio	<i>P</i>
	Mean	SE	Mean	SE		
Micro-site						
Tree condition	n/a		n/a		0.011 ^a	0.02 ^b
Tree height (m)	15.7 ± 0.9		10.5 ± 1.4		1.356	0.02
Crown volume (m³)	603.3 ± 110.3		285.8 ± 117.2		0.998	0.083
Meso-site						
Canopy closure (%)	71.7 ± 2.4		56.8 ± 5.0		1.069	0.007
Overall crown volume (m³) of <20 cm size class	49.9 ± 9.1		60.9 ± 11.2		0.983	0.056

^aOdds ratio refers to change in odds of selection for dead trees compared to live trees.

^bP-values derived from Wald test.

Table 2. Final binary logistic regression models for day-roost micro- and meso-site selection by male Flammulated Owls breeding within the post-burn area of the Hayman Fire in Colorado.