



RESEARCH ARTICLE

Short-term resilience of Great Gray Owls to a megafire in California, USA

Rodney B. Siegel,^{1*} Stephanie A. Eyes,² Morgan W. Tingley,³ Joanna X. Wu,^{1,a} Sarah L. Stock,² Joseph R. Medley,⁴ Ryan S. Kalinowski,⁵ Angeles Casas,⁶ Marcie Lima-Baumbach,⁷ and Adam C. Rich⁸

¹ The Institute for Bird Populations, Point Reyes Station, California, USA

² Yosemite National Park, El Portal, California, USA

³ Ecology & Evolutionary Biology, University of Connecticut, Storrs, Connecticut, USA

⁴ Colibri Ecological Consulting, Fresno, California, USA

⁵ U.S. Forest Service, Stanislaus National Forest, Sonora, California, USA

⁶ Independent Researcher, San Francisco, California, USA

⁷ U.S. Forest Service, Stanislaus National Forest, Mi-Wuk Ranger District, Mi Wuk Village, California, USA

⁸ U.S. Forest Service, Stanislaus National Forest, Summit Ranger District, Pinecrest, California, USA

^a Current address: National Audubon Society, San Francisco, California, USA

* Corresponding author: rsiegel@birdpop.org

Submitted October 30, 2018; Accepted November 28, 2018; Published January 29, 2019

ABSTRACT

Throughout western North America, longer, hotter fire seasons and dense fuels are yielding more frequent, larger, and higher-severity wildfires, including uncharacteristically large “megafires.” Wildlife species associated with late-seral forest characteristics may be particularly vulnerable to habitat loss stemming from changing fire regimes. The Great Gray Owl (*Strix nebulosa*) is a state-listed endangered species in California that typically nests in large snags in well-shaded forests adjacent to montane meadows. The 2013 Rim Fire burned 104,000 ha in Yosemite National Park and Stanislaus National Forest, making it the largest recorded fire in California’s Sierra Nevada. The fire perimeter contained 23 meadows known to be occupied by Great Gray Owls during the decade prior to the fire, representing nearly a quarter of all known or suspected territories in California at the time. We analyzed 13 yr (2004–2016) of Great Gray Owl detection/non-detection data from 144 meadows in the central Sierra Nevada, including meadows inside and outside the Rim Fire perimeter in Yosemite National Park and on Stanislaus National Forest. During 3 yr of surveys after the fire, Great Gray Owls were detected at 21 of 22 meadows surveyed within the fire perimeter that were occupied during the decade prior to the fire. Bayesian hierarchical modeling revealed that, rather than decreasing after the fire, persistence of owls at meadows actually increased on both National Park Service (NPS) and non-NPS lands, while colonization rates exhibited no significant change. Within the burned area, these dynamics were unrelated to forest structure variables describing post-fire stands around individual meadows. Notably, post-fire increases in owl persistence occurred both inside and outside the fire perimeter, suggesting factors other than the fire were likely favorable to Great Gray Owls during the post-fire years. Great Gray Owls appear to have been largely resilient to effects of the Rim Fire during the 3 yr after it burned.

Keywords: Great Gray Owl, megafire, persistence, Sierra Nevada, *Strix nebulosa*

Resiliencia a corto plazo de *Strix nebulosa* a un mega-fuego en California, EEUU

RESUMEN

A través del oeste de América del Norte, las estaciones de fuego más calientes y largas y los combustibles más densos están produciendo fuegos silvestres cada vez más frecuentes, largos y severos, incluyendo inusualmente grandes ‘mega-fuegos’. Las especies de fauna silvestre asociadas con las características del bosque de las etapas sucesionales tardías pueden ser particularmente vulnerables a la pérdida de hábitat resultante del cambio en el régimen de fuego. *Strix nebulosa* es una especie en peligro listada a nivel de estado en California que típicamente anida en grandes troncos en bosques bien sombreados adyacentes a praderas de montaña. El Fuego Rim de 2013 quemó 104.000 ha en el Parque Nacional Yosemite y el Bosque Nacional Stanislaus, convirtiéndolo en el fuego registrado más grande en la Sierra Nevada de California. El perímetro del fuego incluyó 23 praderas ocupadas por *S. nebulosa* durante la década anterior al fuego, representando cerca de un cuarto de todos los territorios conocidos o sospechados en California en ese momento. Analizamos 13 años (2004–2016) de datos de detección/no detección de *S. nebulosa* provenientes de 144 praderas en el centro de Sierra Nevada, incluyendo praderas adentro y afuera del perímetro del Fuego Rim en el Parque Nacional Yosemite y el Bosque Nacional Stanislaus. Durante tres años de censos posteriores al fuego, *S. nebulosa* fue detectada en 21 de las 22 praderas muestreadas adentro del perímetro del fuego que estuvieron ocupadas durante la década previa al fuego. Los modelos jerárquicos bayesianos revelaron que, al contrario de disminuir luego del fuego, la persistencia de los búhos en las praderas de hecho aumentó tanto en el Servicio de Parques Nacionales como en tierras fuera de este

sistema, mientras que las tasas de colonización no mostraron un cambio significativo. Adentro del área quemada, estas dinámicas no estuvieron relacionadas a las variables de la estructura del bosque que describen los rodales post-fuego en los alrededores de las praderas individuales. Sorprendentemente, los aumentos en la persistencia de *S. nebulosa* luego del fuego se dieron tanto adentro como afuera del perímetro de fuego, sugiriendo que otros factores distintos al fuego fueron probablemente favorables para *S. nebulosa* durante los años posteriores al fuego. *S. nebulosa* parece haber sido en gran medida resistente a los efectos del Fuego Rim durante los tres años posteriores al fuego.

Palabras clave: mega-fuego, persistencia, Sierra Nevada, *Strix nebulosa*

INTRODUCTION

Fire regimes are changing rapidly across western North America (Dennison et al. 2014, Westerling 2016) and much of the world (Adams 2013, Williams et al. 2013, Stephens et al. 2014). In California's Sierra Nevada, longer, hotter fire seasons and dense vegetation are yielding more frequent, larger, and higher-severity forest fires (Collins and Stevens 2007, Miller et al. 2009, Miller and Safford 2012) including uncharacteristically large "megafires," generally defined as burning >10,000 ha (van Wagtenonk and Lutz 2007, Miller et al. 2009, Stephens et al. 2014). Spurred by climate change as well as historical fire suppression and silvicultural practices (Mallek et al. 2013, Dennison et al. 2014, Stephens et al. 2014), megafires in the region are often characterized by atypically large, continuous patches of high-severity fire in mature, live forest important for wildlife (Stephens et al. 2014). Species associated with late-seral forest characteristics are believed to be particularly vulnerable to habitat loss stemming from these changes (Roberts et al. 2015, Tempel et al. 2015, Jones et al. 2016, Stephens et al. 2016), although recent empirical efforts to assess consequences of megafires on one bird species associated with late-seral forest in the Sierra Nevada, the California Spotted Owl (*Strix occidentalis*), have yielded conflicting results and interpretations (Lee and Bond 2015, Jones et al. 2016, Ganey et al. 2017, Rockweit et al. 2017, Lee 2018).

Another bird species in the Sierra Nevada that could be vulnerable to the region's changing fire regime, particularly the increasing frequency of megafires, is the Great Gray Owl (*Strix nebulosa*). The Great Gray Owl is a state-listed endangered species in California (Winter 1980, California Department of Fish and Wildlife 2018) with a population recently estimated at fewer than 100 pairs in the state (Wu et al. 2016), most of which occur in the Sierra Nevada and belong to the California endemic subspecies *yosemitensis* (Hull et al. 2014). Although Great Gray Owl nest substrates and nesting habitats in California recently have been shown to be somewhat more diverse than previously understood (Wu et al. 2015, Polasik et al. 2016), most Great Gray Owls in the Sierra Nevada nest in large, broken-top conifer snags in forest stands with dense overstory that are adjacent to montane meadows (Winter 1986, Greene 1995, Whitfield and Gaffney 1997, van Riper and van Wagtenonk 2006, Keane et al. 2011). In a survey of nearly all known Great Gray Owl nest sites in California, Wu et al. (2015) summarized nest and forest stand

characteristics. The great majority of nests occurred in snags or live trees with dbh >60 cm (mean = 100.5 cm), presumably because the boles of smaller trees are unlikely to provide enough space for such large-bodied owls. Most nests were within stands with >60% canopy cover (mean = 81.5%), likely important for providing thermal cover for brooding females and nestlings (Beck and Smith 1987) and branches where young can climb and perch before they can fly (Nero 1980, Bull and Henjum 1990). Finally, most nests were within 300 m of the edge of a montane meadow, where the owls typically forage for small mammal prey (Winter 1986, Reid 1989).

Considering their strong association with large snags, dense canopy cover, and proximal meadow foraging habitat, nesting Great Gray Owls in the Sierra Nevada occupy a relatively narrow habitat niche, which is one reason for the species' recent classification as being among the bird species in the region that are most vulnerable to climate change (Siegel et al. 2014). Fire may pose threats to Great Gray Owl nesting habitat by consuming actual or potential nest trees, or by eliminating or reducing canopy cover around those trees. These factors, along with a very small and patchily distributed population (Wu et al. 2016), have led to concern that the changing fire regime, particularly the emergence of frequent megafires, could threaten Great Gray Owl persistence in the Sierra Nevada (Siegel et al. 2014, Wu et al. 2016).

Alternatively, fire may pose less of a risk to Great Gray Owls if fire effects tend to be lower in forest stands adjacent to where owls nest. This spatial limitation of fire could be driven by higher soil moisture around meadow edges (Wood 1975) or meadows acting as firebreaks that either reduce a fire's intensity, or slow or prevent its spread into adjacent forest (Skinner and Chang 1996). Fire in the Sierra Nevada may also play an important, long-term role in sustaining meadows where Great Gray Owls forage (Ratliff 1985). Further, fire can kill large trees, promoting snag recruitment necessary for nesting structures. In several instances in both Yosemite National Park and on the Stanislaus National Forest, Great Gray Owls have nested within medium- to high-severity burned forest shortly after fire (Wu et al. 2015; Figure 1). Thus, it is unclear how substantial a threat fires are to Great Gray Owls in the Sierra Nevada and whether negative effects can be mitigated.

The 2013 Rim Fire provided an opportunity to assess the short-term vulnerability of Great Gray Owls to a megafire. Between August 17 and October 24, 2013, the



FIGURE 1. A Great Gray Owl (*Strix nebulosa*) scans a meadow in Yosemite National Park from an adjacent forest stand burned by the 2013 Rim fire. Photo by Dustin Garrison.

Rim Fire burned more than 104,000 ha (Figure 2), making it the largest fire on record in the Sierra Nevada (Lydersen et al. 2014). The fire-affected area straddled the boundary between Yosemite National Park and Stanislaus National Forest, with about one-third of the burned area occurring in the northwest quadrant of the park, and the remaining two-thirds on Stanislaus National Forest and private lands within the national forest perimeter. Although burn severity varied greatly across the fire-affected landscape, broad-scale patterns differed notably between the Yosemite and Stanislaus portions of the burned area, with substantially larger high-severity patches on the Stanislaus portion (Lydersen et al. 2017). The entire burned area lies in the core of the Great Gray Owl's range in California, and the area within the fire perimeter contained 23 meadows where Great Gray Owls had been detected during the breeding season at least once in the 10 yr prior to the fire, including 17 meadows in Yosemite and 6 meadows on National Forest or private lands (R. Siegel, personal observation). Together these 23 meadows and the immediately adjacent forest stands accounted for nearly a quarter of all known or suspected Great Gray Owl territories in California at the time of the fire (Wu et al. 2016).

Many researchers and land managers believe that forest thinning to reduce fire risk is critical to ensure the persistence of wildlife species associated with late-seral forest characteristics in western forests (reviewed in North et al. 2017). We sought to contribute to this debate by assessing

short-term vulnerability of Great Gray Owls to forest fire. Evidence that fire reduces persistence or colonization rates in the early post-fire years might suggest that efforts across much of the Sierra Nevada to increase resilience of forests to fire through thinning, prescribed burns, or other treatments should specifically prioritize stands that are occupied by Great Gray Owls. Alternately, fire may not be an urgent threat to the species, at least in the early years after fire, if post-fire persistence and colonization rates remain stable. Dynamic rates that remain steady after fire might suggest that forest resilience treatments are not needed to protect Great Gray Owls, and conservation efforts might be better directed to other needs of the species.

We capitalized on the wealth of Great Gray Owl occurrence data gathered by the U.S. Forest Service and the National Park Service during the 10 yr prior to, and the 3 yr following, the Rim Fire, to assess the short-term effects of the fire on Great Gray Owl site persistence and colonization across 2 distinct land management regimes. We hypothesized that rates of persistence, and perhaps colonization, might have decreased within the burned area after the fire due to loss of nesting habitat, and that post-fire changes in dynamic rates might differ between Yosemite National Park and Stanislaus National Forest due to differences in burn severity across the 2 land ownerships. We compiled data from sites within the perimeter of the Rim Fire and from additional sites outside the fire to assess whether any evident post-fire changes in colonization or persistence within the fire perimeter were likely attributable to the fire, or instead might reflect processes occurring across the broader region.

METHODS

Study Area and Sample Design

We compiled all available 2004–2016 breeding-season data from systematic presence/absence surveys for Great Gray Owl that our crews conducted within Yosemite National Park (“NPS sites”), or on Stanislaus National Forest, Sierra National Forest (one site only), or private inholdings within the Stanislaus National Forest (collectively “non-NPS sites”; Figure 2). Data collection methods during individual survey visits adhered to standard methods (Beck and Winter 2000; see below), but overall project objectives, sample design, funding, and staffing varied over the study period and between agencies and land ownership categories, yielding substantial heterogeneity in the number and identity of sites (each generally comprising a montane meadow or a complex of small meadows proximal to one another, and the immediately surrounding forest; hereafter “meadows”) surveyed in any given year. In some years, we surveyed some meadows because they were already known to have been occupied by Great Gray Owls in one or more previous years, while other meadows were randomly selected based

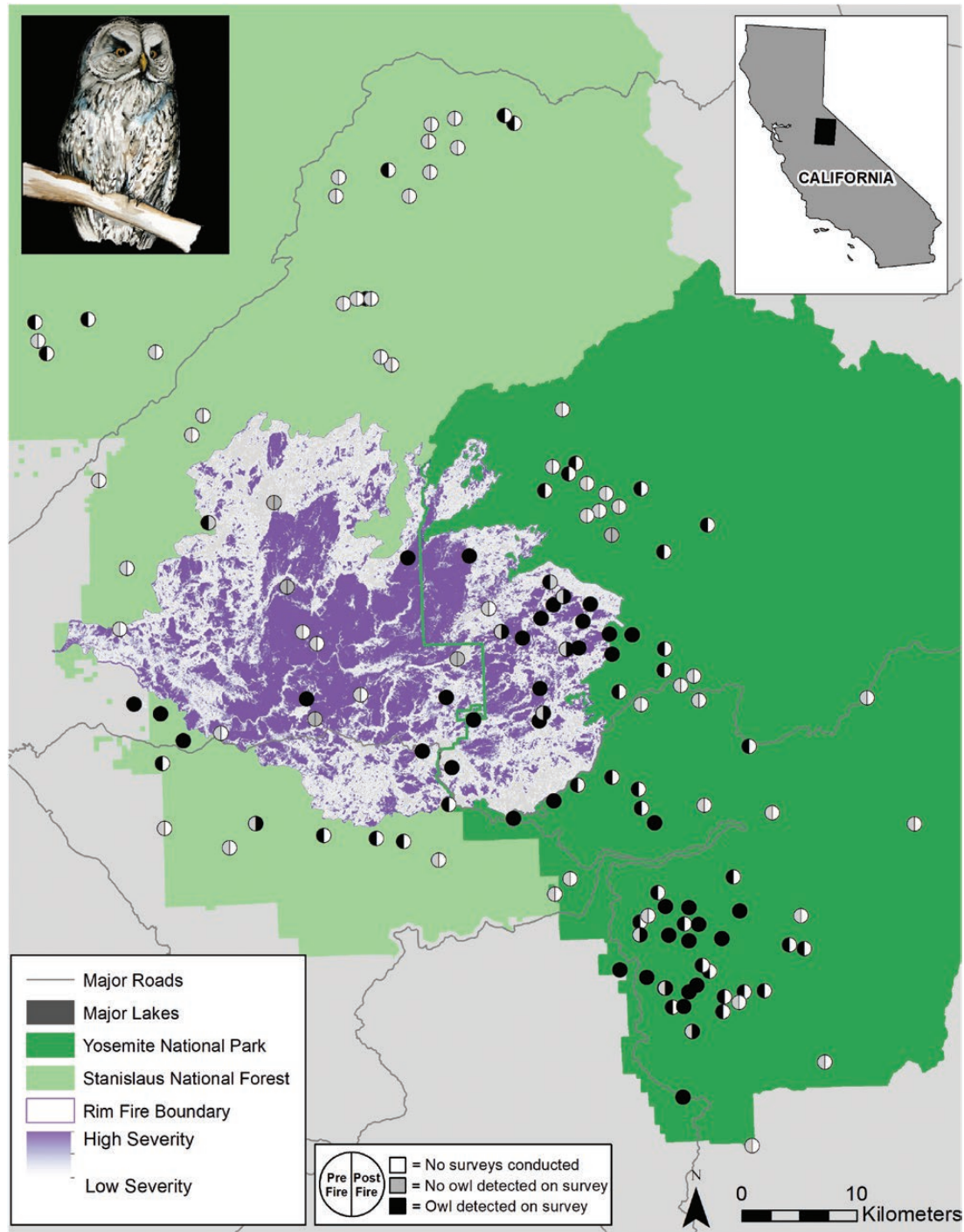


FIGURE 2. Great Gray Owl survey sites (bisected circles) in the central Sierra Nevada, California. For each site, the left semi-circle indicates survey results prior to the fall 2013 Rim Fire (2004–2013 breeding seasons pooled) and the right semi-circle indicates survey results after the fire (2014–2016 breeding seasons pooled). Black shading indicates at least one Great Gray Owl detection; gray shading indicates only non-detections; white indicates no surveys occurred. Inset artwork by Lynn Schofield.

on habitat models or other information indicating they might be appropriate nesting areas for Great Gray Owls. During 2014–2016, Yosemite National Park supplemented the existing dataset with annual surveys of all known or

potential breeding sites within the Yosemite portion of the Rim Fire, yielding proportionately greater sampling effort across those meadows in the post-fire years, compared to unburned sites, non-NPS sites, and even burned NPS sites

prior to the fire. Despite the heterogeneity in annual survey probability, most sites with potential breeding habitat within the overall study area (both within and outside the Rim Fire perimeter) were surveyed during at least 1 yr between 2004 and 2016.

Meadows selected for sampling in the 3 yr following the Rim Fire did not comprise a random sample of all previously sampled meadows. On NPS land, we attempted to monitor all meadows affected by the fire; regardless, there was a positive relationship between post-fire meadow sampling and pre-fire detections of owls in meadows ($\chi^2 = 5.6$, $P = 0.02$). On non-NPS land, post-fire sampling was largely opportunistic, and post-fire sampling more strongly resembled random, while still showing a slight skew toward favoring sampling at meadows that had owl detections before the fire ($\chi^2 = 2.7$, $P = 0.10$). While nonrandom sampling could bias inference on naïve estimates of occupancy (as a percentage of available meadows), our focus here on colonization and persistence dynamics explicitly accounts for potential sampling bias by treating meadows as discrete entities where the true occurrence status of a meadow is modeled in every year regardless of sampling. Estimates of post-fire persistence, for example, are not biased by a failure to survey sites where owls have never occurred. Nevertheless, to reduce sampling bias, we omitted data from meadows ($n = 6$) within our study area that were surveyed after the fire but had never been surveyed prior to the fire.

Consistent with known habitat associations of Great Gray Owls in California (Wu et al. 2016), we surveyed meadows that were adjacent to conifer forest or mixed oak-conifer forest, dominated by tree species including black oak (*Quercus kelloggii*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*Pinus lambertina*), Jeffrey pine (*Pinus jeffreyi*), red fir (*Abies magnifica*), and lodgepole pine (*Pinus contorta*). Meadow elevation averaged $1,904 \pm 513$ m above sea level (range: 779–2,593 m) and meadow size averaged 14 ± 16.5 ha (range: 1–128 ha). Management history varied both within and between ownership classes. Commercial livestock grazing has not occurred at meadows in Yosemite National Park in many decades (Blaney and Moore 2001), although some sites have been used for small-scale packstock grazing (Ballenger et al. 2010), and surrounding forests have generally been free of timber harvest or other active silviculture practices. The non-NPS sites include sites entirely on National Forest lands, sites on private lands within the National Forest perimeter, and sites that straddle boundaries between private and National Forest lands. Many of these sites were historically or are currently grazed by livestock at various intensities (Menke et al. 1996, Ryan Kalinowski, personal observation). Forests surrounding many of the non-NPS sites have been actively managed, including historical

timber harvest treatments that have generally resulted in fewer large trees than are present at many of the NPS sites (McKelvey and Johnston 1992, Collins et al. 2017, North et al. 2017).

Data Collection

We surveyed for Great Gray Owls in accordance with the protocol developed by Beck and Winter (2000), specifically for assessing Great Gray Owl presence within potential nesting habitat in the Sierra Nevada. The protocol prescribes 5 nocturnal visits distributed throughout the courtship, nesting, and post-fledging periods and 1 diurnal visit at the end of the summer. Precise date ranges are defined in the protocol, but vary with elevation and latitude, and are somewhat flexible when deep snowpack or other conditions prevent early-season access. For the nocturnal visits, we established call points ~200 m apart, generally along meadow edges. We surveyed each call point with 2 min of passive listening, followed by 10 min of mixed call broadcasting and listening. We typically surveyed the points at a given meadow in a different sequence during each survey visit. When a Great Gray Owl was detected, the survey was suspended and the remaining points at the meadow were not surveyed that night. Depending on the seasonal timing of the visit, broadcast calls included a variety of male and female territorial hoots, contact calls, and juvenile begging vocalizations. Call point surveys began no earlier than 30 min before sunset and often continued until well after midnight, depending on the size of the meadow. At some sites, rather than immediately playing aggressive vocalizations, we first conducted daytime visits to avoid disturbing potentially breeding owls. We also conducted daytime visits in late summer at the end of the breeding season, in accordance with Beck and Winter (2000). During the daytime visits, rather than conducting broadcast surveys, we searched along meadow edges for adult and fledgling Great Gray Owls or molted Great Gray Owl feathers. Feathers were collected and species identification was confirmed using photographs and reference feathers, generally with independent evaluations by more than one evaluator. We considered a meadow occupied when we established owl presence during at least one visit through vocalizations, visual observations, or positive identification of freshly molted feathers.

Beck and Winter (2000) suggest 6 visits as a minimum criterion for considering a survey in a given year to be “complete,” but their recommendation is intended primarily for legally required “compliance surveys” intended to ensure the species’ absence before implementation of activities that might disturb nesting or deleteriously alter habitat. In our dataset, numbers of visits within a year varied widely across land ownerships, years, and individual sites. We used data from any meadow with at least one formal survey visit (nocturnal or diurnal)

in any given year during the 10 yr prior to the fire. The final dataset for analysis was organized into two 3-dimensional arrays: a dataset of diurnal surveys, $d_{j,k,t}$ where $j = 1, \dots, 144$ meadows, $k = 1, \dots, 11$ visits per year, and $t = 1, \dots, 13$ yr; and a dataset of nocturnal broadcast surveys $n_{j,l,t}$ where $j = 1, \dots, 144$ meadows, $l = 1, \dots, 7$ visits per year, and $t = 1, \dots, 13$ yr. The 144 meadows included in the study were surveyed an average of 3.9 ± 3.7 yr (mean \pm SD), with the subset that was surveyed in any given year varying widely.

Modeling Framework

We used a single-species dynamic occupancy model (MacKenzie et al. 2003) to explore the effects of the Rim Fire on Great Gray Owl colonization and extinction dynamics at meadows within and outside the fire and with different land ownerships and environmental conditions. The Bayesian hierarchical model built for this analysis used a latent variable representing occupancy (Royle and Kéry 2007), which was simultaneously informed by both diurnal and nocturnal surveys. This model structure—increasingly used in ecological work—allows the inclusion of multiple sources of information to inform the detection of a true ecological state (Nichols et al. 2008).

We developed a temporally dynamic Bayesian hierarchical model, where $d_{j,k,t}$ is a binomial random variable that indicates if at least one Great Gray Owl was detected ($d_{j,k,t} = 1$) or not detected ($d_{j,k,t} = 0$) at meadow j during diurnal survey k in year t , and where $n_{j,l,t}$ is a binomial random variable that indicates if at least one Great Gray Owl was detected in nocturnal surveys. We used a mixture model specification to describe the data-generating process in terms of probability distributions, such that $d_{j,k,t} \sim \text{Bernoulli}(\alpha_{j,k,t} \cdot z_{j,t})$ and $n_{j,l,t} \sim \text{Bernoulli}(\beta_{j,l,t} \cdot z_{j,t})$, where $z_{j,t}$ is a latent variable used to indicate true occurrence of Great Gray Owls at meadow j in year t , modeled as $z_{j,t} \sim \text{Bernoulli}(\psi_{j,t})$. The probability of detecting a Great Gray Owl differs by survey methodology, and is defined by $\psi_{j,k,t}$ and $\psi_{j,l,t}$ for diurnal and nocturnal surveys, respectively. As both diurnal and nocturnal surveys involved trained field personnel who were experts in Great Gray Owl identification, we assumed that there were no false positives in the dataset (e.g., $(z_{j,t} | d_{j,k,t} = 1) = 1$) and that imperfect detection only created false negatives.

We modeled detectability differently for each survey method, using a suite of covariates defined a priori for inclusion as the measured factors most important for affecting each detection method. We thus modeled diurnal survey detection as:

$$\text{logit}(\alpha_{j,k,t}) = a_0 + a \cdot \text{year}_t + a_1 \cdot \text{temp}_{j,k,t} + a_2 \cdot \text{time}_{j,k,t} + a_3 \cdot \text{time}_{j,k,t}^2 + a_4 \cdot \text{date}_{j,k,t} + a_5 \cdot \text{effort}_{j,k,t}$$

where a_0 is the global intercept, a_1 – 5 are covariate coefficients, $\text{temp}_{j,k,t}$ is the temperature ($^{\circ}\text{C}$) when a survey began, $\text{time}_{j,k,t}$ is the time of day at which the survey started, $\text{date}_{j,k,t}$ is the Julian day of the year, $\text{effort}_{j,k,t}$ is the total time (min) spent in a meadow sit, and $a \cdot \text{year}_t$ is an annual random effect, where $a \cdot \text{year}_t \sim \text{Normal}(0, \tau_{\text{day}})$, to allow for unmodeled annual heterogeneity in diurnal detection probabilities. Time of day was modeled with both linear and quadratic terms, as diurnal meadow surveys occurred throughout daylight hours, and it was expected that detectability would be highest at both dawn and dusk.

We similarly modeled nocturnal survey detection as:

$$\text{logit}(\beta_{j,l,t}) = b_0 + b \cdot \text{year}_t + b_1 \cdot \text{temp}_{j,l,t} + b_2 \cdot \text{wind}_{j,l,t} + b_3 \cdot \text{time}_{j,l,t} + b_4 \cdot \text{date}_{j,l,t} + b_5 \cdot \text{effort}_{j,l,t}$$

where b_0 is the global intercept, b_1 – 5 are covariate coefficients, $\text{temp}_{j,l,t}$ is the minimum temperature ($^{\circ}\text{C}$) recorded during a night of surveys, $\text{wind}_{j,l,t}$ is a binary variable representing whether it was a windy night (Beaufort scale value >1), $\text{time}_{j,l,t}$ is the temporal midpoint in decimal hours of the time of day when surveys began and ended (with times after midnight represented as >24 hr), $\text{date}_{j,l,t}$ is the Julian day of the year, $\text{effort}_{j,l,t}$ is the number of broadcast points sampled in a given night of surveys, and $b \cdot \text{year}_t$ is an annual random effect, where $b \cdot \text{year}_t \sim \text{Normal}(0, \tau_{\text{night}})$. Time was modeled only as a linear effect on nocturnal detectability, as surveys typically began at dusk and finished long before dawn (99% of nocturnal point surveys were conducted between dusk and 0200 hr). By modeling diurnal and nocturnal detection processes separately, we accounted for the unique observation process that gives rise to detections in each methodology, while also accounting for the fact that common covariates (e.g., effort or time of day) likely have different relationships to the probability of detection across the 2 methods.

We modeled the initial occurrence probability during the first year of our study (2004) at each meadow, $\psi_{j,1}$, as a logit-linear function of 2 environmental covariates:

$$\text{logit}(\psi_{j,t=1}) = c_0 + c_1 \cdot \text{elev}_j + c_2 \cdot \text{size}_j$$

where elev_j is the mean elevation (m) of a meadow where surveys occurred, and size_j is the area (ha) of a meadow, using meadow delineations from Fryjoff-Hung and Viers (2012).

For subsequent survey years, $t = 2, \dots, 13$, we modeled occupancy as temporally dependent on the true occurrence status and modified by the relative probabilities that an unoccupied meadow would become colonized ($\gamma_{j,t}$) or that an occupied meadow would persist ($\phi_{j,t}$), such that:

$$\text{logit}(\psi_{j,t>1}) = \phi_{j,t} \cdot z_{j,t-1} + \gamma_{j,t} (1 - z_{j,t-1})$$

Inference on changes in occupancy was made through covariates modifying colonization and extinction probabilities:

$$\text{logit}(\gamma_{jt}) = g_0 + g \cdot \text{year}_t + g_1 \cdot Y_j + g_2 \cdot R_j + g_3 \cdot A_t \\ + g_4 \cdot A_t R_j + g_5 \cdot A_t R_j cc_j + g_6 \cdot A_t R_j hab_j$$

and

$$\text{logit}(\phi_{jt}) = p_0 + p \cdot \text{year}_t + p_1 \cdot Y_j + p_2 \cdot R_j + p_3 \cdot A_t \\ + p_4 \cdot A_t R_j + p_5 \cdot A_t R_j cc_j + p_6 \cdot A_t R_j hab_j$$

where Y_j is an indicator of whether meadow j is within the boundary of Yosemite National Park, R_j is an indicator of whether meadow j was within the perimeter of the Rim Fire, and A_t is an indicator of whether surveys in year t were before or after the Rim Fire. Additionally, cc_j is the mean burn severity (% change in canopy cover) due to the Rim Fire within a 300-m buffer around (but not including) the meadow (USFS 2017), and hab_j is a LiDAR-derived index of potential nesting habitat availability following the fire, as measured by the absolute number of 30 m² pixels within a 300-m buffer around each meadow that had at least one snag with dbh >60 cm and live canopy cover ≥60%. The buffer distance around meadows, minimum potential nest snag size, and minimum canopy cover for nesting habitat are all based on empirical findings in Wu et al. (2015). Most snags, even those with suitably large dbh and adequate nearby canopy cover for Great Gray Owl nesting are unlikely to actually provide suitable nesting opportunities, so our index assumes that a greater number of pixels around a meadow that meet our minimum criteria for potential nesting habitat corresponds with a greater likelihood of occurrence of at least one snag that actually is suitable for nesting. Individual snags were detected and characterized based on Airborne Laser Scanning (ALS) data that were collected in November 2013 by the National Center for Airborne Laser Mapping (NCALM) using an Optech Gemini Airborne Laser Terrain Mapper (ALTM) instrument that recorded up to 4 returns per pulse (with a scan angle of ±14 and a nominal 50% overlap between flight lines, yielding an average pulse density of 19 per m²), and analyzed according to methods detailed in Casas et al. (2016). The colonization and persistence effects of burn severity and nesting habitat availability were evaluated only on meadows within the Rim Fire and pertained only to years after the fire. Both colonization and persistence were modeled as having a global intercept (g_0 and p_0) offset by an annual normally distributed random effect ($g \cdot \text{year}_t$ and $p \cdot \text{year}_t$), which allows for year-to-year unmodeled heterogeneity in dynamic parameters.

We fit the model to the data with JAGS (Plummer 2003) using the statistical programming language R 3.2.1 (R Core

Team 2017). All first-order continuous covariates were standardized to a mean of 0 and a standard deviation of 1 before analysis. In all cases, we used vague priors (i.e. normal with $\mu = 0$, $\tau = 0.1$; gamma with $r = 0.1$, $\lambda = 0.1$). We ran 3 chains of 20,000 iterations with an adaptation period of 100, a burn-in of 2,000 followed by a posterior draw of 18,000 thinned by 20, yielding a posterior sample of 2,700 across all chains. Convergence was assumed when the Gelman–Rubin statistic of all monitored parameters calculated across both chains was less than 1.1 (Gelman et al. 2004). Inference was made via examination of 95% credible intervals of model parameters and by plotting model-derived empirical estimates of occupancy, colonization, and persistence.

RESULTS

Empirical Results

We surveyed 144 meadows during at least 1 yr prior to the 2013 Rim fire (2004–2013); 54 of these were also surveyed during at least 1 yr after the fire (Figure 2). We detected Great Gray Owls at least once at 89 meadows, with detections at 68 of 92 NPS meadows, and at 21 of 52 non-NPS meadows. Of meadows within the fire perimeter that had at least one Great Gray Owl detection prior to the fire, and were surveyed in at least 1 yr after the fire, 21 of 22 yielded at least one Great Gray Owl detection after the fire, including 16 of 17 NPS meadows, and 5 of 5 non-NPS meadows.

We detected owls at meadows with nearly the full range of post-fire forest conditions that occurred across all sites we surveyed. Mean burn severity at sites with post-fire owl detections averaged 21.1% (range: 0–99%; all sites mean = 11.8%, range: 0–99%). Total area within 300-m sampling area around all meadows ranged from 68 to 500 ha (mean = 182 ha) because meadows varied in size (range: 68–500 ha) and estimated amount of potentially suitable nesting habitat (i.e. area of pixels with at least one large snag and canopy cover >60%) within the 300-m sampling area of meadows that were occupied post-fire averaged 1.9 ha (range: 0.1–5.9 ha; all meadows, mean = 1.4 ha, range: 0–5.9 ha).

Model Results

Given that daytime surveys occurred a median of 1 time per breeding season, and nighttime surveys were repeated a median of 3 times per breeding season, the cumulative probability of detecting at least one Great Gray Owl at an occupied meadow across the breeding season (p^* ; MacKenzie et al. 2006) was 0.938 (95% CI: 0.875–0.982). Daytime surveys yielded, on average, higher detection probability than nighttime broadcast surveys (95% credible interval for daytime surveys = 0.568–0.777; for nighttime surveys = 0.287–0.610). Several covariates strongly affected

TABLE 1. Posterior means and 95% credible intervals for estimated parameters in the hierarchical model of Great Gray Owl dynamic occupancy at Sierra Nevada meadows. Slope parameters for which the 95% credible interval did not cross 0 (an index of certainty or “significance”) are bolded.

Parameter name	Parameter interpretation	Mean	Credible intervals	
			2.5%	97.5%
Detection: Diurnal surveys				
a_0	Intercept	0.736	0.273	1.246
τ_{dat}	Precision of random year effect	2.477	0.683	6.391
a_1	Effect of temperature	−0.144	−0.487	0.207
a_2	Effect of time of day (linear)	0.107	−0.116	0.325
a_3	Effect of time of day (quadratic)	0.146	−0.021	0.319
a_4	Effect of day of year	0.481	0.283	0.683
a_5	Effect of survey effort	0.345	0.102	0.612
Detection: Nocturnal broadcast surveys				
b_0	Intercept	−0.258	−0.910	0.446
τ_{night}	Precision of random year effect	0.984	0.283	2.403
b_1	Effect of temperature	0.128	−0.090	0.344
b_2	Effect of wind	−0.364	−0.595	−0.147
b_3	Effect of time of day	−0.387	−0.560	−0.213
b_4	Effect of day of year	0.041	−0.163	0.237
b_5	Effect of survey effort	−1.388	−1.620	−1.148
Initial occupancy				
c_0	Intercept	0.346	−0.610	1.422
c_1	Effect of elevation	1.962	0.773	3.430
c_2	Effect of meadow size	1.341	0.410	2.433
Colonization				
g_0	Intercept	−2.467	−4.535	−0.933
τ_{col}	Precision of random year effect	1.399	0.060	7.995
g_1	Effect of being inside the NPS perimeter	0.006	−1.072	1.107
g_2	Effect of being inside the Rim perimeter	−0.021	−1.319	1.246
g_3	Effect of being post-fire	0.910	−2.319	3.996
g_4	Effect of being post-fire and inside Rim (interaction)	−0.019	−3.769	3.823
g_5	Effect of burn severity inside Rim	0.578	−0.926	2.329
g_6	Effect of available nesting habitat inside Rim	0.837	−0.356	2.682
Persistence				
p_0	Intercept	1.300	0.368	2.546
τ_{per}	Precision of random year effect	5.433	0.281	23.478
p_1	Effect of being inside the NPS perimeter	2.007	1.021	3.033
p_2	Effect of being inside the Rim perimeter	0.437	−0.761	1.676
p_3	Effect of being post-fire	3.503	0.173	8.168
p_4	Interactive effect of being post-fire and inside Rim	1.020	−4.173	6.746
p_5	Effect of burn severity inside Rim	−0.248	−4.066	5.627
p_6	Effect of available nesting habitat inside Rim	0.870	−1.103	3.955

detection probability during surveys (Table 1). During daytime surveys, detection probability increased with day of year, and increased with the amount of time spent surveying a meadow. In contrast, during nighttime surveys, detection probability decreased with the number of broadcast points visited per night at a meadow and with time since sunset (both likely artifacts reflecting that a survey visit was suspended as soon as an owl was detected at any point) and also decreased on windy nights.

Initial occupancy (i.e. estimated probability of occupancy of a meadow in 2004, the first year of surveys) was 0.586 (95% CI: 0.352–0.806), with probability of occupancy increasing for higher-elevation meadows and larger meadows (Table 1). Occupancy in subsequent years, as defined by our model, was determined strictly as a derived

function of colonization and persistence dynamics at sites. Because of these processes, the estimated proportion of occupied meadows varied from year to year, but generally was between 0.4 and 0.8 before the Rim Fire, and then increased following the fire (Figure 3). Meadows inside and outside the fire perimeter differed negligibly in the proportion occupied before the fire, and showed no difference in occupancy after the fire (Figure 3B). Differences in occupancy estimates were greater when comparing meadows based on land ownership, with an additional 35.2% of sampled meadows (95% CI: 16.7–53.8%) likely to be occupied within Yosemite NP before the Rim Fire compared to meadows on non-NPS land (Figure 3C). Two and 3 years after the Rim Fire, this difference was reduced to 26.3%, but with broadly overlapping CIs (95% CI: 3.7–51.0%).

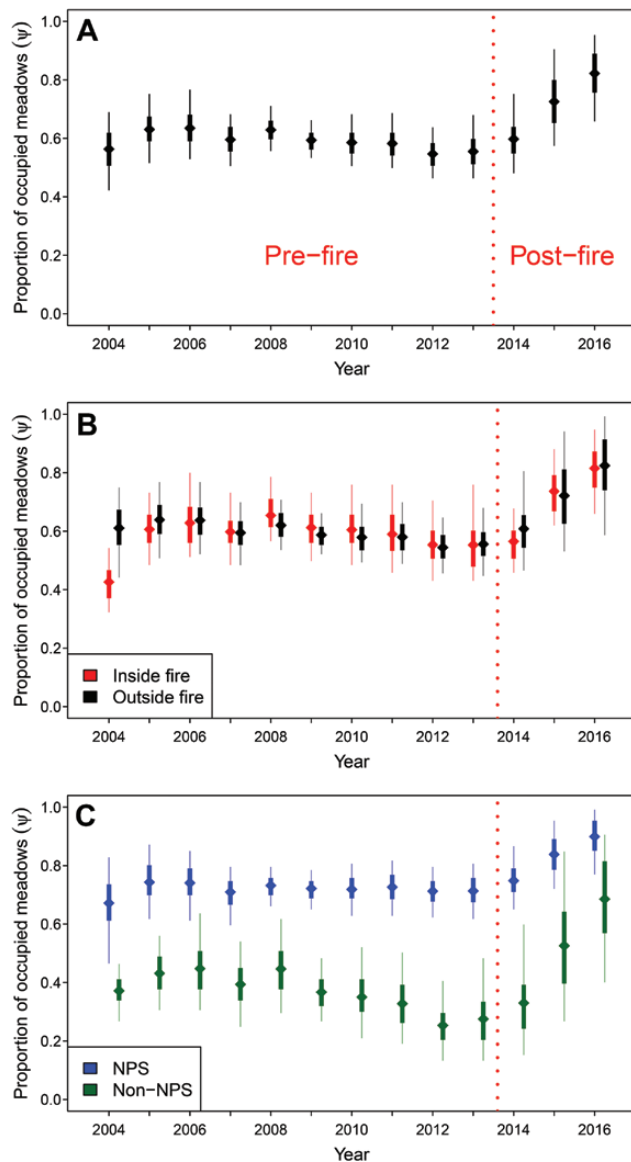


FIGURE 3. Derived model estimates of the mean proportion of surveyed meadows (lines show 50% and 95% credible intervals) occupied by Great Gray Owls over the study duration (A) at all meadows, (B) depending on whether within the Rim Fire, and (C) by land ownership. The Rim Fire (dotted red line), which burned 26% of monitored meadows, occurred after the conclusion of surveys in 2013.

Colonization and persistence probabilities differed greatly and showed contrasting relationships to covariates and over time (Figure 4). Colonization probability was generally quite low, with a mean across all years of 0.078 (95% CI: 0.011–0.282; Figure 4C). There were no strongly supported covariates of colonization.

In contrast to colonization, annual persistence was high, with a mean probability across all years of 0.786 (95% CI: 0.591–0.927; Figure 4B, 4C). In addition, Great Gray Owls were more likely to persist at meadows during the 3 yr after

the Rim Fire (posterior mean of $p_3 = 3.50 \pm 2.07$) and at meadows within Yosemite National Park (Figure 4C; posterior mean of $p_1 = 2.00 \pm 0.53$). The estimated increase in owl persistence following the Rim Fire applied to all meadows, both those inside and outside the fire perimeter, although post-fire persistence at meadows inside the fire perimeter showed greater uncertainty than meadows outside (Figure 4). This increase in uncertainty was due to a poor model fit for parameter p_4 —the interaction of being post-fire and inside the fire—likely arising from all but one pre-fire occupied meadows inside the fire persisting in occupancy after the fire. Although precision was low for many parameters (Table 1), post hoc model runs with fewer covariates failed to achieve greater precision for remaining covariates.

DISCUSSION

We found no evidence that the 2013 Rim Fire negatively affected rates of colonization or persistence of Great Gray Owls during the 3 yr after the fire. At nearly every surveyed meadow (21 of 22 meadows) within the fire area where we detected Great Gray Owls in at least 1 yr during the decade before the fire, we also detected Great Gray Owls after the fire. Our model, based on data from 144 sites surveyed at least once before the fire, yielded colonization and persistence rates within the fire perimeter that did not decrease after the fire, with persistence actually increasing markedly after the fire, irrespective of land ownership. While spatial and temporal variability in survey effort and study design may bias absolute estimates of occurrence and may add uncertainty to colonization estimates, they should not affect annual estimates of site persistence at meadows with pre-fire survey histories.

In a demographic study of Northern Spotted Owls (*Strix occidentalis caurina*) involving 10 fires in northwestern California, Rockweit et al. (2017) reported that wildfires with different mixtures of burn severity represented a continuum of effects on owl vital rates. Like Great Gray Owls, Spotted Owls also rely on large trees and dense canopy cover, but are not tied to forest stands adjacent to meadows. Predominantly lower-severity fires were associated with minimal impacts on Spotted Owl survival and recruitment, moderate- to higher-severity fires were associated with a reduction in survival but increased recruitment, and predominantly higher-severity fires were associated with a large reduction in survival with little effect on recruitment. We expected that post-fire occupancy and persistence of Great Gray Owls at individual sites within the Rim Fire footprint might similarly depend on the severity of site-specific fire effects. However, Great Gray Owls persisted at sites with a broad range of fire effects, including one meadow with 99% loss of canopy cover in the surrounding forest—although fire severity was much

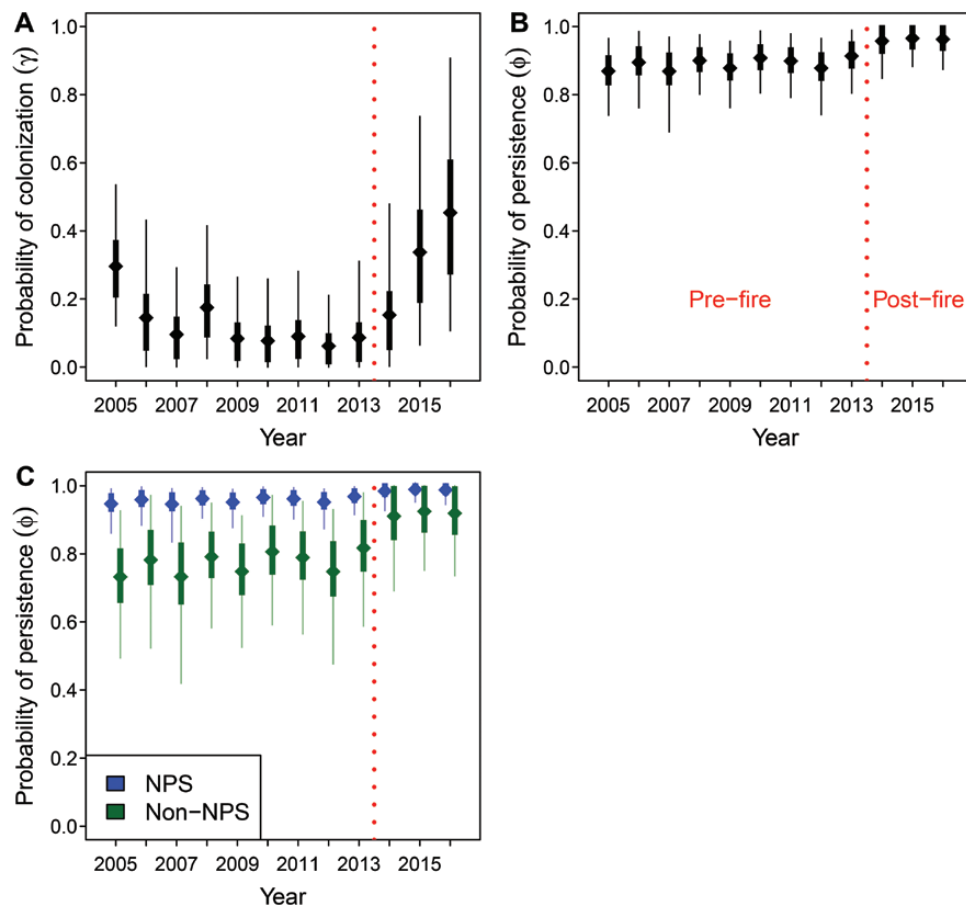


FIGURE 4. Derived model estimates of the mean probability of meadow colonization (**A**) and persistence (**B, C**) of Great Gray Owls over time (lines show 50% and 95% credible intervals). Plots differentiate between (**A, B**) all meadows and (**C**) meadows based on ownership. The Rim Fire (dotted red line) occurred after the conclusion of surveys in 2013.

lower around most meadows (mean change in canopy cover = 21%). Our index of potentially suitable nesting habitat (i.e. areas with at least one large snag and canopy cover >60%) within a 300-m buffer around the meadow similarly ranged widely at occupied meadows, including one meadow with <1 ha meeting these conditions (mean across occupied meadows = 14.1 ha).

We lack systematic data on whether owls attempted nesting or successfully fledged young at most sites, so even though post-fire habitat conditions appeared not to reduce occupancy or dynamic rates, we cannot say whether habitat conditions affected breeding status or nest success. Data from before the fire show Great Gray Owls to have strong site fidelity; this trait could have compelled them to return to (or remain in) altered habitat after the fire, even if their territories were no longer suitable for nesting or meeting other life-history needs. However, anecdotal data indicate successful nesting occurred at some of the burned sites after the fire. Finding Great Gray Owl nests can be extremely difficult and time-consuming because the species is secretive and does not respond well to mousing,

a technique that makes finding Spotted Owl nests fairly routine (Forsman 1983). We did not attempt to find nests or document reproduction in a systematic or intensive manner at most sites during most years in this study. Nevertheless, anecdotal observations during occupancy surveys at several sites within the fire footprint yielded definitive evidence of successful nesting after the fire.

Stable occupancy and increased site persistence after fire suggest an overall resilience to the effects of the fire during the 3 yr after it burned. Any negative effects stemming from loss in nesting habitat appear to have been counterbalanced by other factors. Fire could potentially enhance Great Gray Owl nesting habitat by killing large trees that may eventually become suitable nesting structures. However, Great Gray Owls most typically nest in the rotting boles of broken-top snags that are substantially deteriorated (Wu et al. 2015). It seems unlikely that such structures could have fully developed during our study period in trees that were killed by the Rim Fire. A more immediate positive effect of fire could be to enhance conditions for populations of meadow-inhabiting voles

(*Microtus* spp.) and pocket gophers (*Thomomys* spp.), the primary prey of Great Gray Owls (Winter 1986, Greene 1995, van Riper and van Wagten 2006, Kalinowski et al. 2014). However, we observed similar increases in persistence (and no change in colonization) during the same time period at meadows outside the Rim Fire, suggesting that factors other than the fire likely played a role in the observed increase in site persistence.

The Rim Fire occurred shortly after the onset of a multi-year drought in California (Robeson 2015, Asner et al. 2016) that began during winter 2011–2012 and continued until winter 2016–2017. One possibility that might explain increases in Great Gray Owl persistence both within and outside the fire perimeter is that the anomalous weather was beneficial to nesting owls. Great Gray Owls in the region can begin laying eggs as early as March (Beck and Winter 2000), making nests vulnerable to late-winter storms that can cause nest abandonment (Beck and Winter 2000). A series of relatively dry years with few storms may have elevated nest success rates, although systematic data on nest success are not available. Additionally, the drought could have yielded less direct ecological benefits for the owls, such as increased abundance of pocket gophers, which thrive in drier meadow conditions (Kalinowski et al. 2014), or unusually easy access to prey during winters with less than normal snowpack.

Great Gray Owls may also have been resilient to the fire if increased soil moisture in stands adjacent to wet meadows reduced fire severity or if meadows slowed or reduced the spread of the fire. Nevertheless, large snags near meadow edges are not immune to being consumed by fire. Indeed, 25 of 35 known natural nests and artificial nest structures (not all of which were used) within the Rim Fire perimeter on Stanislaus National Forest were burned to a non-usable state (Ryan Kalinowski, personal observation). Sites with few large snags or large trees available to be recruited into the snag population may be vulnerable to fire because many or all of the potential nesting opportunities could be eliminated by a single fire. Even though we observed no deleterious effects of the Rim Fire on Great Gray Owl dynamic rates, we recommend that land managers continue to focus on recruiting and retaining large trees and snags near meadow edges, particularly given patterns of declining abundance of large trees globally and across California (Lindenmayer et al. 2012, McIntyre et al. 2015). We also urge land managers to retain large dead trees within areas surrounding meadows following fires to minimize loss of potential nesting structures.

The Great Gray Owls we studied appeared to be resilient to the Rim fire during the 3 yr after it burned, suggesting that fuel reduction treatments targeted in Great Gray Owl habitat may not be warranted for facilitating post-fire persistence at burned sites in the short-term. However,

longer-term dynamic rates after fire may be influenced by processes not evident during the short timeframe of our study, including recruitment and decay of snags suitable for nesting, recruitment of large trees through forest growth, and the loss or development of canopy cover suitable for nesting. Further study will be needed to determine whether Great Gray Owls continue to be resilient to fire over longer timeframes. Sites within the burned area clearly retained enough suitable habitat to support widespread persistence of owls during the 3 yr after the fire, as well as allowing some to nest, but the fire nevertheless consumed individual large trees and snags around many meadows and in some cases entire forest stands. Most of these dead trees remained standing during the 3 yr after the fire, but suitable nesting structures could become rare in the coming decades after the fire-killed trees deteriorate and fall. Development of new nesting structures and forest stands suitable for Great Gray Owl nesting may require decades or even centuries. As the current cohort of suitable nesting snags senesces, it is unclear whether there will be sufficient large snags to support continued nesting in the future.

ACKNOWLEDGMENTS

We are grateful to the many field technicians who conducted Great Gray Owl surveys over the 13-yr study period. We thank T. Beck, R. Bridgman, J. Keane, and W. Moriarty for many years of dedication to Great Gray Owl monitoring in the Sierra Nevada. This is Contribution No. 616 of The Institute for Bird Populations.

Funding statement: Data collection and analysis were funded by Yosemite Conservancy, Yosemite National Park, the U.S. Forest Service, and Sierra Foothills Audubon Society. None of the funders had any influence on the content of the submitted or published manuscript. None of the funders require approval of the final manuscript to be published.

Ethics statement: Fieldwork was conducted in compliance with the *Guidelines to the Use of Wild Birds in Research*.

Author contributions: S.L.S., S.A.E., J.R.M., R.S.K., J.J.K., M.B., and A.C.R. collected data and supervised research; R.B.S., S.A.E., J.W., and S.L.S. formulated the research questions; M.W.T. and A.C. analyzed the data; R.B.S. and M.W.T. wrote the paper, which all authors then reviewed and edited.

Data deposits: Data are available by formal request from the U.S. Forest Service and the National Park Service.

LITERATURE CITED

Adams, M. A. (2013). Mega-fires, tipping points and ecosystem services: Managing forests and woodlands in an uncertain future. *Forest Ecology and Management* 294:250–261.

- Asner, G. P., P. G. Brodrick, C. B. Anderson, N. Vaughn, D. E. Knapp, and R. E. Martin (2016). Progressive forest canopy water loss during the 2012–2015 California drought. *Proceedings of the National Academy of Sciences USA* 113:249–255.
- Ballenger, E., J. Baccei, and L. Acree (2010). 2008 pack stock use assessment in subalpine meadows of the Tuolumne River watershed. *Resources Management and Science*, Yosemite National Park, CA, USA.
- Beck, T. W., and R. A. Smith (1987). Nesting chronology of the great gray owl at an artificial nest site in the Sierra Nevada. *Journal of Raptor Research* 21:116–118.
- Beck, T. W., and J. Winter (2000). Survey protocol for the Great Gray Owl in the Sierra Nevada of California. *USDA Forest Service*, Vallejo, CA, USA.
- Blaney, C., and P. Moore. (2001). Grazing and Yosemite's meadows: Keeping the balance. *Sierra Nature Notes* No. 1. November 2001.
- Bull, E. L., and M. G. Henjum (1990). Ecology of the Great Gray Owl. *USDA Forest Service General Technical Report PNW-GTR-265*, Portland, OR, USA.
- California Department of Fish and Wildlife (2018). Natural Diversity Database. August 2018. Special animals list. Periodic publication.
- Casas, A., M. Garcia, R. B. Siegel, C. Ramirez, A. Koltunov, and S. L. Ustin (2016). Burned forest characterization at single-tree level with airborne laser scanning for wildlife habitat assessment. *Remote Sensing of Environment* 175:231–241.
- Collins, B. M., and S. L. Stephens (2007). Managing natural wildfires in Sierra Nevada wilderness areas. *Frontiers in Ecology and the Environment* 5:523–527.
- Collins, B. M., D. L. Fry, J. M. Lydersen, R. Everett, and S. L. Stephens (2017). Impacts of different land management histories on forest change. *Ecological Applications* 27:2475–2486.
- Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz (2014). Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters* 41:2014GL059576.
- Forsman, E. D. (1983). Methods and materials for locating and studying spotted Owls. *USDA Forest Service General Technical Report PNW-162*, Pacific Northwest Research Station, Portland, OR, USA.
- Fryjoff-Hung, A., and J. Viers. (2012). *Sierra Nevada Multi-Source Meadow Polygons Compilation* (version 1.0). University of California Center for Watershed Sciences, Davis, CA, USA.
- Ganey, J. L., H. Yi Wan, S. Cushman, and C. Vojta (2017). Conflicting perspectives on Spotted Owls, wildfire, and forest restoration. *Fire Ecology* 13:146–165.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin (2004). *Bayesian Data Analysis*. 2nd ed. Chapman and Hall/CRC, Boca Raton, FL, USA.
- Greene, C. (1995). Habitat requirements of Great Gray Owls in the Central Sierra Nevada. Ph.D. dissertation, University of Michigan, Ann Arbor, MI, USA.
- Hull, J. M., A. Engilis Jr., J. R. Medley, E. P. Jepsen, J. R. Duncan, H. B. Ernest, and J. J. Keane (2014). A new subspecies of Great Gray Owl (*Strix nebulosa*) in the Sierra Nevada of California, U.S.A. *Journal of Raptor Research* 48:68–77.
- Jones, G. M., R. J. Gutiérrez, D. J. Tempel, S. A. Whitmore, W. J. Berigan, and M. Z. Peery (2016). Megafires: An emerging threat to old-forest species. *Frontiers in Ecology and the Environment* 14:300–306.
- Kalinowski, R. S., M. D. Johnson, and A. C. Rich (2014). Habitat relationships of Great Gray Owl prey in meadows of the Sierra Nevada Mountains. *Wildlife Society Bulletin* 38:547–556.
- Keane, J. J., H. B. Ernest, and J. M. Hull (2011). Conservation and management of the Great Gray Owl 2007–2009: Assessment of multiple stressors and ecological limiting factors. *National Park Service, Yosemite National Park and U.S. Forest Service, Pacific Southwest Research Station Interagency Report*, Davis, CA, USA.
- Lee, D. E. (2018). Spotted Owls and forest fire: A systematic review and meta-analysis of the evidence. *Ecosphere* 9:e02354.
- Lee, D. E., and M. L. Bond (2015). Occupancy of California Spotted Owl sites following a large fire in the Sierra Nevada, California. *The Condor: Ornithological Applications* 117:228–236.
- Lindenmayer, D. B., W. F. Laurence, and J. F. Franklin (2012). Global decline in large old trees. *Science* 338:1305–1306.
- Lydersen, J. M., B. M. Collins, M. L. Brooks, J. R. Matchett, K. L. Shive, N. A. Povak, V. R. Kane, and D. F. Smith (2017). Evidence of fuels management and fire weather influencing fire severity in an extreme fire event. *Ecological Applications* 27:2013–2030.
- Lydersen, J. M., M. P. North, and B. M. Collins (2014). Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. *Forest Ecology and Management* 328:326–334.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200–2207.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines (2006). *Occupancy Estimation and Modeling*. Academic Press, Burlington, VT, USA.
- Mallek, C., H. Safford, J. Viers, and J. Miller (2013). Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere* 4:153.
- McIntyre, P. J., J. H. Thorne, C. R. Dolanc, A. L. Flint, L. E. Flint, M. Kelly, and D. D. Ackerly (2015). Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. *Proceedings of the National Academy of Sciences USA* 112:1458–1463.
- McKelvey, K. S., and J. D. Johnston (1992). Historical perspectives on forest of the Sierra Nevada and the Transverse Range of southern California: Forest conditions at the turn of the century. In *The California Spotted Owl: A Technical Assessment of Its Current Status* (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutierrez, G. I. Gould Jr., and T. W. Beck, Editors). General Technical Report PSW-GTR-133, Pacific Southwest Research Station, USDA Forest Service, Albany, CA, USA.
- Menke, J., C. Davis, and P. Beesley (1996). Rangeland assessment. In *Status of the Sierra Nevada: Sierra Nevada Ecosystem Project: Final Report to Congress*, vol. 3. Centers for Water and Wildland Resources, University of California, Davis, CA, USA. pp. 901–972.
- Miller, J. D., and H. Safford (2012). Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. *Fire Ecology* 8:41–57.
- Miller, J. D., H. Safford, M. Crimmins, and A. Thode (2009). Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12:16–32.
- Nero, R. W. (1980). *The Great Gray Owl: Phantom of the Northern Forest*. Smithsonian Institution Press, Washington, DC, USA.

- Nichols, J. D., L. L. Bailey, A. F. O'Connell Jr., N. W. Talancy, E. H. Campbell Grant, A. T. Gilbert, E. M. Annand, T. P. Husband, and J. E. Hines (2008). Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology* 45:1321–1329.
- North, M. P., M. W. Schwartz, B. M. Collins, and J. J. Keane (2017). Current and projected condition of mid-elevation Sierra Nevada forests. In *The California Spotted Owl: A Technical Assessment of Its Current Status* (J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutierrez, G. I. Gould Jr., and T. W. Beck, Editors). General Technical Report PSW-GTR-254, Pacific Southwest Research Station, USDA Forest Service, Albany, CA, USA. pp. 109–157.
- Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DCS2003)*, March 20–22 (K. Hornik, F. Leisch, and A. Zeileis, Editors). Technische Universität, Vienna, Austria. pp. 1–10.
- Polasik, J. S., J. X. Wu, K. Roberts, and R. B. Siegel (2016). Great Gray Owls nesting in atypical, low-elevation habitat in the Sierra Nevada, California. *Journal of Raptor Research* 50:194–206.
- R Core Team. 2017. R: A Language and Environment for Statistical Computing. Vienna, Austria.
- Ratliff, R. D. (1985). Meadows in the Sierra Nevada of California: State of knowledge. USDA Forest Service General Technical Report PSW-84. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, USA.
- Reid, M. E. (1989). The predator–prey relationships of the Great Gray Owl in Yosemite National Park. U.S. Department of the Interior, Cooperative National Park Resources Studies Unit Report 35, Davis, CA, USA.
- Roberts, S. L., D. A. Kelt, J. W. van Wagtendonk, A. K. Miles, and M. D. Meyer (2015). Effects of fire on small mammal communities in frequent-fire forests in California. *Journal of Mammalogy* 96:107–119.
- Robeson, S. M. (2015). Revisiting the recent California drought as an extreme value. *Geophysical Research Letters* 42:6771–6779.
- Rockweit, J. T., A. B. Franklin, and P. C. Carlson (2017). Differential impacts of wildfire on the population dynamics of an old-forest species. *Ecology* 98:1574–1582.
- Royle, J. A., and M. Kéry (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology* 88:1813–1823.
- Siegel, R. B., P. Pyle, J. H. Thorne, A. J. Holguin, C. A. Howell, S. Stock, and M. Tingley (2014). Vulnerability of birds to climate change in California's Sierra Nevada. *Avian Conservation and Ecology* 9:7.
- Skinner, C. N., and C. Chang. (1996). Fire regimes, past and present. In *Sierra Nevada Ecosystem Project: Final Report to Congress, Volume II. Assessments and Scientific Basis for Management Options*. Wildland Resources Center Report No. 37. Centers for Water and Wildland Resources, University of California, Davis, CA, USA.
- Stephens, S. L., N. Burrows, A. Buyantuyev, R. W. Gray, R. E. Keane, R. Kubian, S. Liu, F. Seijo, L. Shu, K. G. Tolhurst and J. W. van Wagtendonk (2014). Temperate and boreal forest mega-fires: Characteristics and challenges. *Frontiers in Ecology and the Environment* 12:115–122.
- Stephens, S. L., J. D. Miller, B. M. Collins, M. P. North, J. J. Keane, and S. L. Roberts (2016). Wildfire impacts on California Spotted Owl nesting habitat in the Sierra Nevada. *Ecosphere* 7:01478.
- Tempel, D. J., R. J. Gutiérrez, J. J. Battles, D. L. Fry, Y. Su, Q. Guo, M. J. Reetz, S. A. Whitmore, G. M. Jones, B. M. Collins, et al. (2015). Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species. *Ecosphere* 6:261.
- [USFS] U.S. Forest Service (2017). Pacific Southwest Region 5: Regional Level Datasets. <https://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=stelprdb5327833>
- van Riper, C., III, and J. van Wagtendonk (2006). Home range characteristics of Great Gray Owls in Yosemite National Park, California. *Journal of Raptor Research* 40:130–141.
- van Wagtendonk, J. W., and J. A. Lutz (2007). Fire regime attributes of wildland fires in Yosemite National Park, USA. *Fire Ecology* 3:34–52.
- Westerling, A. L. R. (2016). Increasing western US forest wildfire activity: Sensitivity to changes in the timing of spring. *Philosophical Transactions of the Royal Society, Series B* 371:20150178.
- Whitfield, N. B., and M. Gaffney (1997). Great Gray Owl habitat use within altered forest landscapes. In *Biology and Conservation of Owls of the Northern Hemisphere* (J. R. Duncan, D. H. Johnson, and T. H. Nicholls, Editors.). USDA Forest Service, General Technical Report NC-190, St. Paul, MN, USA. pp. 498–505.
- Williams, J. (2013). Exploring the onset of high-impact mega-fires through a forest land management prism. *Forest Ecology and Management* 294:4–10.
- Winter, J. (1980). Status and distribution of the Great Gray Owl in California. State of California Department of Fish and Game Project W-54-R-12, Sacramento, CA, USA.
- Winter, J. (1986). Status, distribution, and ecology of the Great Gray Owl (*Strix nebulosa*) in California. Ph.D. dissertation, San Francisco State University, San Francisco, CA, USA.
- Wood, S. H. (1975). Holocene stratigraphy and chronology of mountain meadows, Sierra Nevada, California. California Institute of Technology, Pasadena, CA, USA.
- Wu, J. X., H. L. Loffland, R. B. Siegel, C. Stermer (2016). A Conservation Strategy for Great Gray Owls (*Strix nebulosa*) in California. Interim version 1.0. The Institute for Bird Populations and California Partners in Flight, Point Reyes Station, CA, USA.
- Wu, J. X., R. B. Siegel, H. L. Loffland, M. W. Tingley, S. L. Stock, K. N. Roberts, J. J. Keane, J. R. Medley, R. Bridgman, and C. Stermer (2015). Diversity of nest sites and nesting habitats used by Great Gray Owls in California. *Journal of Wildlife Management* 79:937–947.