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Quail on fire: changing fire regimes may benefit mountain quail in fire-adapted forests

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Abstract

Background Fire-adapted forests in western North America are experiencing rapid changes to fire regimes that are outside the range of historic norms. Some habitat-specialist species have been negatively impacted by increases in large, high-severity fire, yet, the responses of many species to fire, especially at longer time scales, remain ambiguous. We studied the response of a widely distributed species, the mountain quail (*Oreortyx pictus*), to wildfire across the Sierra Nevada of California, because its habitat selection patterns provided an opportunity to evaluate potentially contrasting responses among habitat specialists.

Results We used passive acoustic monitoring across > 22,000 km^2 of the Sierra Nevada and Bayesian hierarchical occupancy modeling to conduct the first study of the effects of habitat, fire severity, and time since fire (1–35 years) on the occupancy of a little-understood management indicator species, the mountain quail. Mountain quail responded positively to high-severity fire and neutrally to low-moderate-severity fire. Occupancy of quail peaked 6–10 years after high-severity fire and remained high even 11–35 years after an area burned at high severity.

Conclusions Our work demonstrates that high-severity fire is strongly and positively related to mountain quail occupancy, which is a markedly different response than previously studied species that are also of management concern in the Sierra Nevada. Taken together, our results suggest that mountain quail may actually be "winners" in the face of altered fire regimes in the Sierra Nevada. Given the forecasted intensification of large, severe wildfires in many fire-adapted forests, understanding the ecology and nuanced fire responses of species beyond those that have been historically considered is an important and time-sensitive effort. The relationship between mountain quail and high-severity fire is a reminder that there will be both winners and losers as the dynamics of wildfire change in the era of climate change.

Keywords Fire ecology, Habitat association, Wildlife response to fire, Occupancy, Mountain quail, *Oreortyx pictus*, Passive acoustic monitoring

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Resumen

Antecedentes Los bosques adaptados a fuegos en el oeste de Norteamérica están experimentando rápidos cambios en sus regímenes de fuegos que están por fuera de su normalidad histórica. Algunas especies hábitat-especialistas, han sido negativamente impactadas por el incremento de fuegos más grandes y de alta severidad, aunque las respuestas de muchas especies al fuego, especialmente a escalas de tiempo amplias, se expresan de manera ambigua. Estudiamos la respuesta al fuego de una especie ampliamente distribuida, la codorniz de montaña (Oreortyx pictus), a lo largo de la Sierra Nevada de California, debido a que su patrón de selección del hábitat provee de una oportunidad para evaluar potenciales respuestas contrastantes entre especialistas del hábitat.

Resultados Usamos monitoreo acústico pasivo a través de > 22.000 km2 de la Sierra Nevada y un Modelo Bayesiano de Ocupación Jerárquica para conducir el primer estudio del efecto del hábitat, severidad del fuego, y tiempo desde el fuego (de 1 a 35 años), sobre la ocupación de un muy poco conocido indicador de manejo, la codorniz de montaña. La codorniz de montaña respondió positivamente a los incendios de alta severidad y de manera neutral a fuegos de moderada severidad. La ocupación de esta codorniz de montaña llegó a su pico máximo entre 6 y 10 años después de un fuego de alta severidad, y permaneció alta aún luego de 11 a 35 años posteriores a que un área se quemó con una alta severidad.

Conclusiones Nuestro trabajo demostró que fuegos de alta severidad están positiva- y fuertemente relacionados con la ocupación del área quemada por la codorniz de montaña, lo que fue una respuesta marcadamente diferente de otras especies estudiadas y que resultan de interés para el manejo en la Sierra Nevada. Tomados en conjunto, nuestros resultados sugieren que la codorniz de montaña puede ser una "ganadora" en vista de la alteración de los regímenes de fuego en la Sierra Nevada. Dados los pronósticos de intensificación de fuegos más grandes y severos en muchos bosques adaptados al fuego, el entender la ecología y la sutil respuesta al fuego de algunas especies, más allá de aquellas que han sido consideradas, es un esfuerzo importante y apremiante. La relación entre la codorniz de montaña y los fuegos de alta severidad es un recordatorio de que va a haber ganadores y perdedores en la dinámica de los cambios en los regímenes de fuegos en la era del cambio climático.

Background

Ecological disturbance is one of the main drivers of habitat structure and composition, which subsequently affect biodiversity (Mackey and Currie 2001; Turner 2010; Swanson et al. 2011; He et al. 2019; Viljur et al. 2022). In forest ecosystems, wildfire is a major agent of disturbance that shapes species' distributions across the landscape (Steel et al. 2015; Hale et al. 2016). Consequently, some wildlife species have evolved resilience to, or even dependence upon, wildfire disturbance ((Probst and Donnerwright 2003; Gentry and Vierling 2007; Jager et al. 2021). Variation in fire severity and time since fire, as well as in the spatial configuration of fire (i.e., pyrodiversity), have been hypothesized to increase the diversity of species, as well as shape the distributions of individual species (Shaffer and Laudenslayer, Jr 2006; Ponisio et al. 2016; He et al. 2019; Jones and Tingley 2022; Jorge et al. 2022). But the responses of individual species to fire are often nuanced and idiosyncratic, with some species responding negatively and other species responding positively to specific, and sometimes narrow, combinations of fire severity and time since fire (Hutto and Patterson 2016). Hence, there is substantial uncertainty about the effects of changing fire regimes on wildlife in western North America.

In California's Sierra Nevada, the genocide of indigenous peoples who used fire as a management tool (Taylor et al. 2016; Madley 2017), a century of fire suppression to support the timber industry (Steel et al. 2015; North et al. 2015), and a warming climate (Westerling 2016; Abatzoglou and Williams 2016) have led to an increase in large and homogenously severe fires that can threaten biodiversity (Adams 2013; Wood and Jones 2019; Coop et al. 2020; Cova et al. 2023). Additionally, both the annual amount of area burned and the instances of extreme wildfire have been projected to increase in the future (Stevens et al. 2017; Westerling 2018; Anderegg et al. 2022). Two iconic Sierra Nevada species, the spotted owl (*Strix occidentalis*) and the black-backed woodpecker (*Picoides arcticus*), are both considered to be well-adapted to fire because of their evolution in fire-adapted forests. The former is considered adapted to frequent, low-to-moderate-severity fire (e.g., (Bond et al. 2002; Kramer et al. 2021), whereas the latter is dependent on high-severity, stand-replacing fires (Hutto 2008; Hutto and Patterson 2016; Tingley et al. 2020). Yet, both of these species have demonstrated negative responses to very large, high-severity fires (Jones et al. 2016; Jones et al. 2020; Stillman et al. 2019a). Further, both of these species have been shown to use small patches and edges of severely burned forest for foraging or nesting but to largely avoid the interiors of large, high-severity fire patches (Stillman et al. 2019a; Jones et al. 2020). Forest management and conservation planning typically revolve around these well-studied, threatened species. Consequently, the responses of other more common species, such as the mountain quail (*Oreortyx pictus*), are overlooked when assessing wildfire impacts at bioregional scales. The responses of overlooked species to changing climate and disturbance regimes are likely to be equally nuanced and, yet, many of them have not been explicitly investigated.

Mountain quail are an enigmatic species endemic to western North America. Although they have a large geographic range, which extends from southwestern British Columbia to the Baja Peninsula, and occur in many habitats, very little is known about them relative to other upland gamebirds (Gutiérrez and Delehanty 1999). Despite their name, mountain quail are more closely associated with early successional forest and shrub habitats than mountains per se (Brennan et al. 1987; Pope et al. 2004). Consequently, in the Sierra Nevada, the USDA Forest Service (USFS) has designated mountain quail as a management indicator species for early and mid-seral conifer forests, and information about quail populations is used to assess the effects of forest plan implementation (USDA Forest Service. 2007; Sierra Nevada Forests Management Indicator Species Amendment.Pacific Southwest Region 2007). Additionally, mountain quail are avidly pursued by both birders and hunters throughout their range (Mastrup et al. 2002). Thus, mountain quail serve not only as an indicator species but also as a species that generates conservation funding and public interest. Mountain quail are hypothesized to be fire-adapted because of their use of early successional forest and shrub habitat (Gutiérrez and Delehanty 1999). However, they also occur in riparian areas, conifer forest, and evergreen broad-leafed forest over a large altitudinal gradient. So, unlike spotted owls and black-backed woodpeckers that are narrowly associated with conifer forests, they are an ideal species to examine the effects of wildfire because they span such large gradients of habitat, latitude, and altitude. The primary reason for the lack of information about mountain quail is the logistical difficulty of collecting such data due to their elusive habits and affinity for impenetrable shrub vegetation and steep slopes (Gutiérrez and Delehanty 1999). However, mountain quail are quite vocal; thus, the combination of passive acoustic surveys and machine learning-based identification of animal sounds (Kahl et al. 2021; Wood et al. 2022) provide a unique opportunity to address the relationships between fire and mountain quail.

We used a very large-scale passive acoustic monitoring program to assess the relationships between mountain quail site occupancy and forest cover and structure, fire severity, and time since fire. This study represents the largest modeling effort ever undertaken to understand mountain quail fire associations. As a necessary first step in our wildfire assessment, we conducted a habitat assessment for mountain quail throughout the Sierra Nevada. We hypothesized that mountain quail occupancy would be related to both habitat cover type (e.g., shrub) and forest structure covariates (e.g., canopy cover). We predicted that mountain quail occupancy would be positively related to shrub cover and negatively related to grassland cover, and we predicted a negative relationship between mountain quail occupancy and canopy cover and between occupancy and canopy base height. After evaluating habitat associations, we proceeded with our fire analysis. We hypothesized that mountain quail occupancy would be related to both fire severity and time since fire (see Gutiérrez 1980; Gutiérrez and Delehanty 1999). We predicted that (1) in the short-term (1 year post-fire), mountain quail would have lower occupancy in areas that burned at any severity due to the lack of dense cover that they prefer (Gutiérrez and Delehanty1999); (2) at medium time scales (2–5 years and 6–10 years post-fire), mountain quail occupancy would be positively related to high-severity fire due to shrubby re-growth and not related to low-moderate-severity fire, which would likely maintain higher canopy cover; and (3) at the longest time interval, we examined (11–35 years post-fire) the positive effects of high-severity fire would fade, so mountain quail occupancy would be unrelated to fire of any severity. Characterizing the effects of fire on species beyond those that have been historically considered is an important first step in predicting how biodiversity may fare in potentially novel future fire regimes, and the forecasted intensification of severe wildfire in western North America generates even greater urgency for these efforts.

Methods

Study area and surveys

In June 2021, which coincides with the mountain quail breeding season (approximately May–July), we conducted passive acoustic surveys at 1636 sites on public lands across over 22,000 km^2 of the Sierra Nevada, California. We conducted our surveys during the breeding season when mountain quail are detectable via acoustic surveys due to their frequent territorial vocalizations (Gutiérrez and Delehanty 1999). Our study area encompassed seven national forests and three national parks (Fig. 1). Our surveys largely took place on the west slope of the Sierra Nevada, from mixed-forest foothills up through the upper conifer zone (~370–2880 m). This

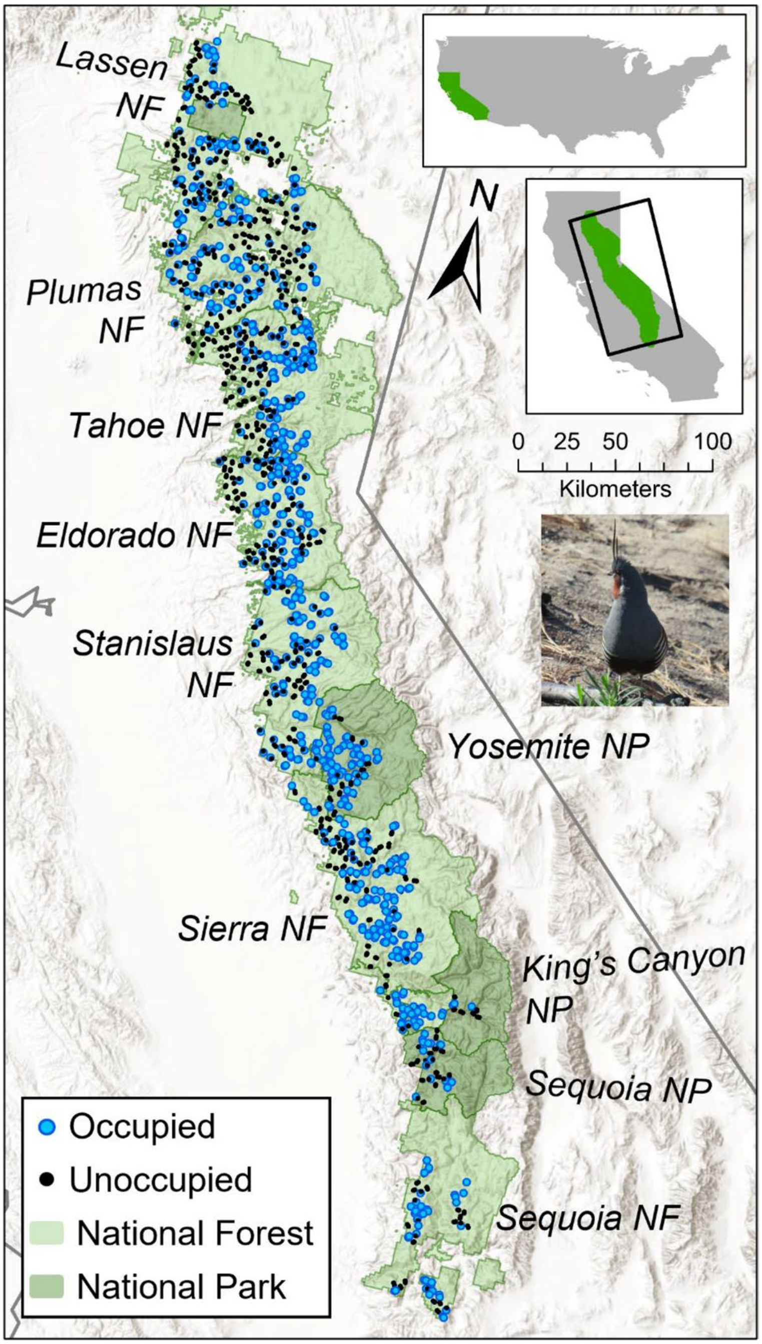

Fig. 1 Map of the study area showing naïve occupancy at each recording unit

broad elevational gradient was characterized by a variety of landcover types including conifer forest, mixed hardwood/conifer forest, and shrub/scrub habitats, which can all serve as mountain quail habitat.

To aid our interpretation of mountain quail response to wildfire, we first modeled their habitat relationships because they are known to occupy habitats ranging from shrub-dominated communities to forests. We overlaid our entire study area with 400-hectare hexagonal grid cells, each of which contained two autonomous recording units (SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology) spaced at least 500 m apart and at least 250 m from a cell border. We programmed each recording unit to record continuously between 0500–0900 and 1800–2000 for at least 5 weeks. Each unit had one omnidirectional microphone and recorded at a sampling rate of 32 kHz.

Survey data and processing

We identified putative mountain quail vocalizations using the machine learning algorithm BirdNET (Kahl et al. 2021), a deep convolutional neural network that is trained to recognize > 3000 species worldwide (Kahl et al. 2021). We used a customized version of BirdNET that was fine-tuned for 243 avian species in the Sierra Nevada, including the mountain quail, and overfit to our recording hardware and settings. BirdNET produced a prediction score (a relative measure of algorithm confidence) for mountain quail for every 3-s interval in our entire dataset. To eliminate false positives while still retaining true positives, we manually verified 200 randomly selected BirdNET predictions from across the range of BirdNET prediction scores and used these to conduct a logistic regression that related prediction scores to outcome (correct/incorrect) such that we could assign each putative quail detection a probability of accuracy (Fig. S1). Based on the logistic regression, we selected a detection threshold for mountain quail that corresponded with a 99% chance that a given mountain quail prediction was correct.

We designed the stringent probability-based threshold to eliminate misclassifications, but we also wanted to reduce "ecological false positives" in which a mountain quail vocalization was correctly identified but the detected individual did not meaningfully associate with that habitat (see Reid et al. 2021), thus violating the assumption of site closure. Therefore, we also applied a site-level temporal filter to detections. For a site to qualify as "occupied," we required detections (with a 0.99 probability of being correct) to have occurred on at least two different days; we considered sites at which mountain quail were detected on only 1 day as unoccupied. The strict definition of "occupancy" that we used here is tailored to the goals of our study—eliminating false positives and drawing inference from sites where mountain quail frequently associated with habitat. Finally, to ensure that our criteria effectively eliminated false-positive detections from the data, we validated detections at a subset of 10 sites that had the most tenuous detection histories (i.e., only 2 days with detections and the fewest total detections).

Habitat and fire covariates

We quantified habitat and fire histories within a 390-m radius (47.8 ha) buffer around each recording unit. Although no studies have examined home range sizes for mountain quail in the Sierra Nevada, one study of translocated mountain quail in Oregon found they had an average home range size of 141 ha (Pope et al. 2004). While the buffer size we selected is potentially small relative to an average home range, we accounted for the possibility of non-independence between sites in our modeling scheme (see below).

To compute the proportion of land cover types within the buffers encompassing our recording units, we used data from the 2019 National Land Cover Database (Dewitz and US Geological Survey 2021). We calculated the proportion of four major cover types—Evergreen Forest (*evergr*), Mixed Forest (*mixed*), Shrub/Scrub (*shrub*), and Grassland/Herbaceous (*grass*)—using zonal statistics in ArcGIS Pro (Esri 2023). Within forested areas (i.e., $evergr \cup mixed$), we expected that mountain quail occupancy would be more closely related to forest structure than to the forest cover types per se (Gutiérrez 1980; Brennan et al. 1987). Therefore, we quantified forest structure using data from the California Forest Observatory (Salo Sciences, Inc., 2020). Within each buffer, we calculated the mean canopy cover (*cc*) and the mean canopy base height (*cbh*). The Sierra Nevada spans a wide range of both latitudes and elevations, which interact to influence bird distributions (Siegel et al., 2011). To assess the effects of latitude and elevation on occupancy independently, we included both the latitude (*lat*) of recording units and the residuals of a linear regression of elevation on latitude (*elev.resid*) as covariates in our models. In this context, the *elev.resid* covariate represented purely the effect of elevation on occupancy, while controlling for latitude (Saracco et al. 2011). Finally, we also used a quadratic form of *elev.resid* to allow for a nonlinear relationship between site occupancy and elevation because high and low elevations may not contain suitable habitat.

To assess the effects of time since fire and fire severity on mountain quail, we created two sets of fire covariates, one for *low- to moderate-severity fire* and one for *high-severity fire*. We quantified fire history at each site using a fire severity atlas that covers the entire Sierra Nevada ecoregion and includes all fires > 4 ha occurring since 1985, as mapped by the all-lands historical fire perimeter dataset maintained by the California Department of Forest and Fire Protection (CAL FIRE) and the Fire and Resource Assessment Program (FRAP) (Cova et al. 2023). The (Cova et al. 2023) burn severity atlas maps the Composite Burn Index (CBI; Key and Benson 2006) following the method developed by Parks et al. (2019) mean pre- and post-fire composites of multiple Landsat-derived spectral indices (including Normalized Difference Vegetation Index, Mid-Infrared Bi-Spectral Index, and Relativized Burn Ratio), along with climatic variables, and latitude, are used to predict CBI using a Random Forest model implemented in Google Earth Engine. We defined "low-moderate severity" as fire with a CBI score between 0.1 and 2.25 and "high severity" as fire with a CBI score of 2.25 or greater (Miller and Thode 2007). Then, to create our fire covariates at four different time intervals—within the last year, and within the last 2–5, 6–10, and 11–35 years—we calculated the proportion of each 47.8 ha buffer that burned at each severity class, *low- to moderate-severity* and *high-severity fire*. In areas where fires overlapped, the severity of the most recent fire was used to calculate fire covariates.

Modeling procedure

We used single-season occupancy models in a Bayesian framework to assess the associations between mountain quail occupancy and both habitat and fire. Occupancy models rely on repeated surveys to correct for imperfect detection of target species (Mackenzie et al. 2002), and the Bayesian framework allows for incorporation of random effects to account for spatial patterns. We used the month of June as our primary sampling period because it coincides with egg hatching and juvenile rearing and avoids any migratory movements by adults (Gutiérrez and Delehanty 1999); thus, this survey period mitigates potential violations of the closure assumption of occupancy models (Mackenzie et al. 2002). We split our primary sampling period into five 6-day secondary sampling periods.

Within our model, observations (y_{ij}) at each site (i) and secondary sampling period (j) are assumed to be imperfect representations of the latent true state of a site, z_i. In truth, sites are either occupied (1) or unoccupied (0), but our observations are dependent upon the detection probability at each site during each secondary sampling period, p_{ij}, such that

$$y_{ij} \sim \text{Bernoulli}(z_i * p_{ij})$$

Our model estimates the true state of a site (z_i), which is assumed to be constant across secondary sampling periods, using the probability of occupancy of a site (ψ_i), as

$$z_i \sim \text{Bernoulli}(\psi_i)$$

We modeled the probability of detection (p_{ij}) as a logit-linear function of covariates. We included detection covariates in our models to account for factors that could influence detection. First, we included survey effort (*eff*), a continuous covariate that indicated the number of hours of survey effort during a secondary sampling period (maximum = 36 h). We also included canopy cover (*cc*) and elevation (*elev*) in our detection models because both have been shown to affect detection probabilities (Furnas and Callas 2015; Rolek et al. 2021). We also included the proportion of evergreen forest (*evergr*) and the terrain ruggedness index (*tri*) because both could affect the propagation of mountain quail calls and subsequently alter detection probabilities. We allowed detection probability to vary among secondary sampling periods (*ssp*) because we expected that detection probabilities would decline as mountain quail vocalized less as the breeding season progressed (Gutiérrez and Delehanty 1999). Lastly, we included a random effect for the hexagonal grid cell in which any two recording units were deployed to account for more similar detection probabilities at sites located within the same cell. Thus, our detection model for all analyses was of the form:

$$\begin{aligned} logit(p_{ij}) = {} & \alpha_{ssp[ij]} + \alpha_1 * eff_{ij} + \alpha_2 * cc_{\text{i}} \\ & + \alpha_3 * elev_i + \alpha_4 * evergr_i \\ & + \alpha_5 * tri_i + cell_i \end{aligned}$$

For the occupancy component of the model, we first modeled habitat associations using a model that included both proportion of cover types and forest structure covariates. The model estimated occupancy as a function of nine covariates and included a random effect for cell to account for spatial autocorrelation resulting from multiple recording units being in the same cell (non-independence). The full model structure was

$$\begin{aligned} logit(\psi_i) = {} & \beta_0 + \beta_1 * lat_i + \beta_2 * elev.resid_i \\ & + \beta_3 * elev.resid_i^2 + \end{aligned}$$

$$\begin{aligned} & \mathrm{B}_4 * shrub_i + \beta_5 * grass_i + \beta_6 * evergr_i \\ & + \beta_7 * mixed_i + \beta_8 * cc_i + \beta_9 * cbh_i + cell_i \end{aligned}$$

All of the habitat covariates had correlation < 0.6. We assessed the importance of habitat components using 95% Bayesian credible intervals estimated by the model. Specifically, to test the hypothesis that quail responded to forest structure rather than to forest cover type per se, we assessed the importance of the forest cover covariates (*evergr* and *mixed*).

Next, we assessed the effects of fire severity and time since fire on mountain quail occupancy. Because some of our habitat and fire covariates were correlated to one another and we wanted to examine the effects of fire explicitly on mountain quail occupancy, we assessed habitat and fire in separate models. The fire model included latitude, the linear and quadratic elevation residuals, and the eight fire covariates:

$$\begin{aligned} logit(\psi_i) = {} & \beta_0 + \beta_1 * lat_i + \beta_2 * elev.resid_i \\ & + \beta_3 * elev.resid_i^2 + \end{aligned}$$

$$\begin{aligned} & \mathrm{B}_4 * hsev\_1yr_i + \beta_5 * hsev\_2to5yr_i \\ & + \beta_6 * hsev\_6to10yr_i + \beta_7 * hsev\_11to35yr_i + \end{aligned}$$

$$
\begin{aligned}
&\mathrm{B}_8 * lmsev\_1yr_i + \beta_9 * lmsev\_2to5yr_i \\
&+ \beta_{10} * lmsev\_6to10yr_i \\
&+ \beta_{11} * lmsev\_11to35yr_i + cell_i
\end{aligned}
$$

The fire model also included the random effect to account for non-independence of sites within the same cell.

We implemented all models in the R Statistical Environment (R Core Team 2020) using the *spOccupancy* package (Doser et al. 2022). We centered and standardized all continuous covariates, and we specified weakly informative priors for all parameters (normal, mean = 0 and variance = 2.72 for all fixed effects; inverse gamma, shape = 0.1 and scale = 0.1 for random effects; (Northrup and Gerber 2018). For each model, we ran three chains of 40,000 iterations with a burn-in of 20,000 and a thinning rate of 2, for a posterior sample of 30,000 across all chains. We checked convergence visually using trace plots and by confirming that all Gelman-Rubin statistics were < 1.1, and we assessed model fit using posterior predictive checks and Bayesian *p*-values (Gelman et al. 1996). We drew inference from parameters using a 95% Bayesian credible interval (hereafter CI), and coefficient estimates are reported as mean (95% CI).

Results

Survey effort

We analyzed 227,922 h of audio data from June 2021 with an average of 33.16 h of effort per survey. Our BirdNET analysis yielded 678,104 mountain quail detections with a pr(correct) ≥ 0.99 across 735 sites throughout the season, for a naïve site occupancy of 0.45 (Fig. 1).

Habitat model

We estimated an overall mean site occupancy probability of 0.54 (0.48–0.61). Several covariates influenced mountain quail occupancy during the breeding season (Fig. 2). Mountain quail occupancy was negatively related to latitude and peaked at mid- to high-elevations (after adjusting for latitude) (Fig. 3A, B). The proportion of shrub cover had the largest effect on occupancy, where each 25% increase in the proportion of the sampling area with shrub cover (about 12 ha) resulted in the odds of occupancy increasing by a factor of 3.7 (Fig. 3C). The proportions of grassland, evergreen forest, and mixed forest all had 95% credible intervals that overlapped zero (Figs. 2 and 3D–F), but the effect size of evergreen forest cover was rather large, suggesting that evergreen forest cover may still play an ecological role in determining mountain quail occupancy. Additionally, mountain quail occupancy increased with decreasing canopy cover and with decreasing canopy base height (Fig. 3G, H), which indicated the importance of areas with open canopies and denser cover near the ground.

Detection probabilities declined through the season, increased with hours of survey effort, and decreased with canopy cover and evergreen forest. Credible intervals for the coefficients of elevation and terrain ruggedness both overlapped zero. Mean detection probability in the first secondary survey period (i.e., the first 6 days of June) was high, 0.94 (0.91–0.96), but detection probability declined

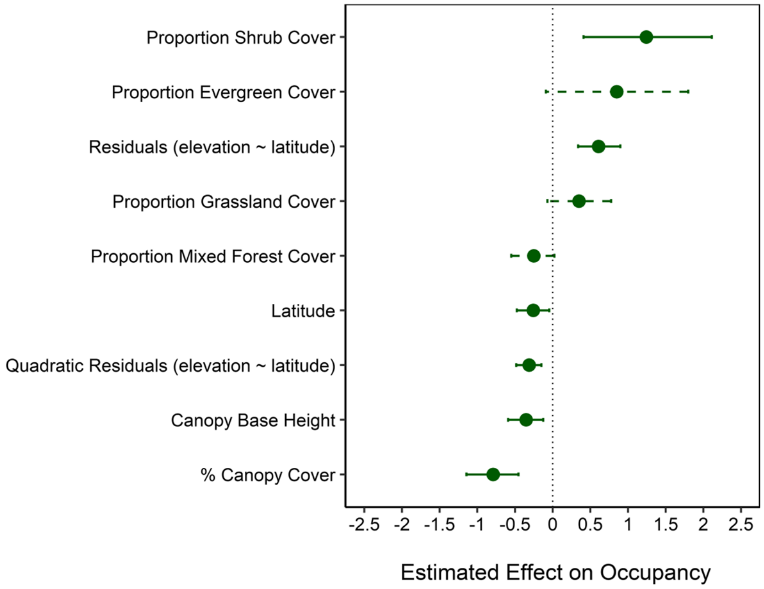

Fig. 2 Mean and 95% credible intervals for the posterior distribution of each coefficient in the habitat model. Solid lines represent coefficients with credible intervals that did not overlap zero; dashed lines represent coefficients with credible intervals that did overlap zero

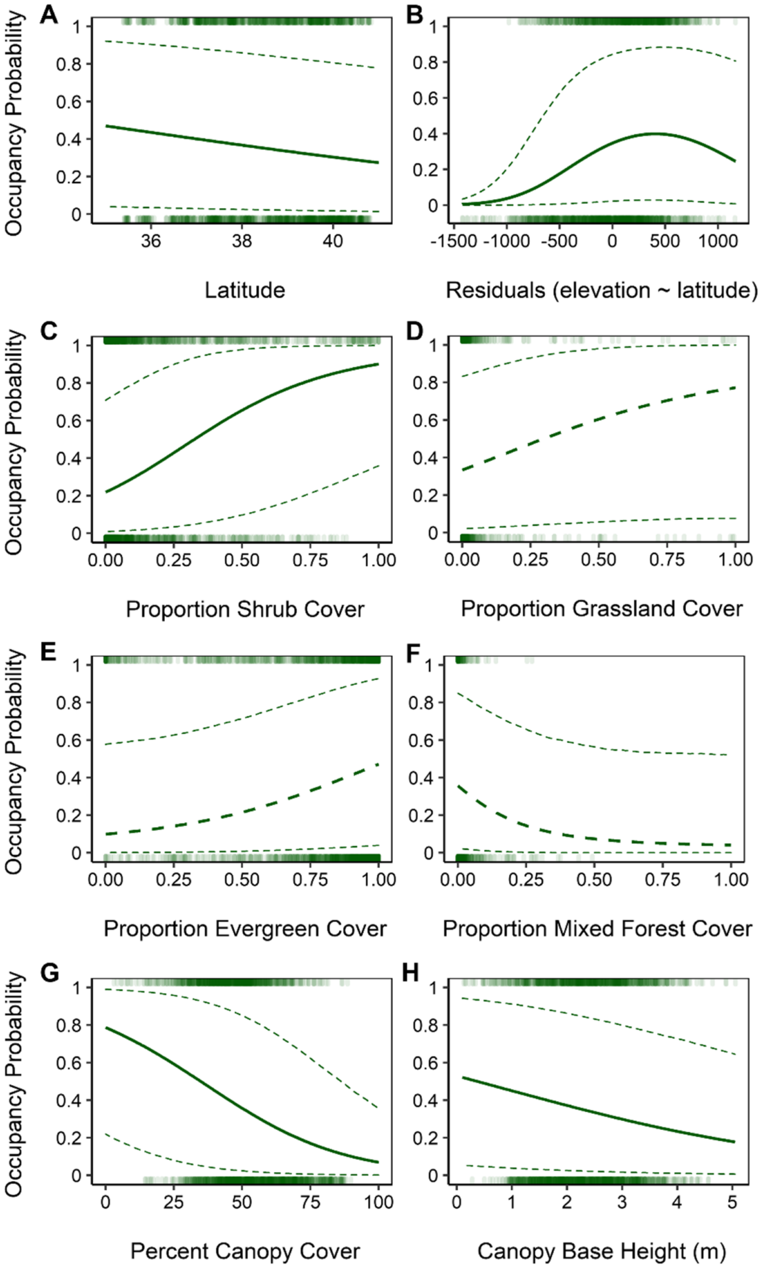

Fig. 3 Relationships between the probability of occupancy (heavy lines, with fine dashed lines representing 95% credible intervals) and each covariate in the habitat model. Predictions for each covariate were made with all other covariates held at their mean value. Heavy dashed lines (**D**–**F**) represent coefficients with 95% credible intervals that overlapped zero. Data rugs along the top and bottom of each panel indicate the distribution of the covariate at occupied (top) and unoccupied (bottom) sites (occupied and unoccupied according to naïve occupancy)

such that by the last secondary survey period (i.e., the last 6 days of June), the mean detection probability was 0.25 (0.18–0.33), which followed our prediction that vocalizations decline toward the end of the breeding season.

Fire model

The fire model revealed that mountain quail occupancy was strongly related to high-severity fire but not to low-moderate-severity fire (Fig. 4). For high-severity fire, we found positive relationships between mountain quail occupancy and the proportion of area burned 1 year ago, 6–10 years ago, and 11–35 years ago, but we found no relationship between occupancy and the proportion of area burned 2–5 years ago (Fig. 5). We found no significant relationships between low-moderate-severity fire and occupancy in any of the time steps we considered.

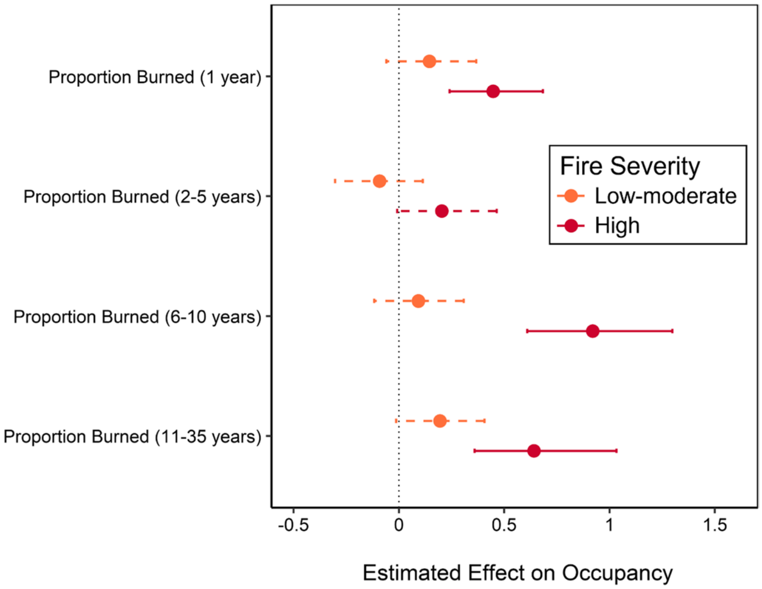

Fig. 4 Mean and 95% credible intervals for the posterior distribution of each coefficient in the fire model. Solid lines represent coefficients with credible intervals that did not overlap zero; dashed lines represent coefficients with credible intervals that overlapped zero

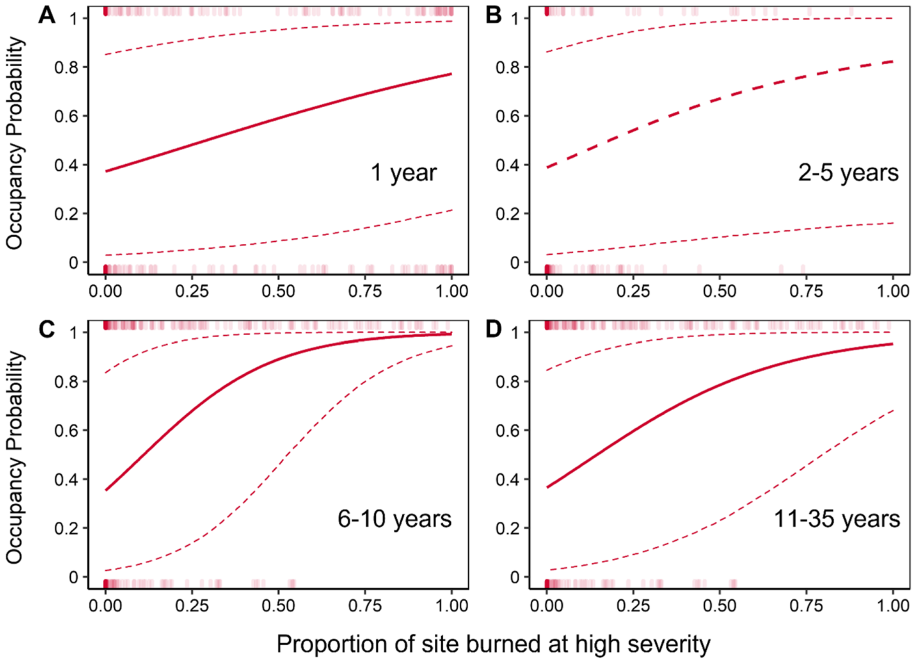

Fig. 5 Relationships between the probability of occupancy (heavy lines, with fine dashed lines representing 95% credible intervals) and the proportion of a site burned at high severity in four temporal scales. Predictions for each covariate were made with all other covariates held at their mean value. Heavy dashed lines represent coefficients with 95% credible intervals that overlapped zero. Data rugs along the top and bottom of each panel indicate the distribution of the covariate at occupied (top) and unoccupied (bottom) sites (occupied and unoccupied according to naïve occupancy)

The strongest positive effects of fire occurred in areas that burned 6–10 years ago, where a 25% increase in the proportion burned at high severity resulted in the odds of occupancy increasing by a factor of 6.1. Even 11–35 years after high-severity fire, a 25% increase in the area burned at high severity resulted in the odds of occupancy increasing by a factor of 5.7. Even just 1 year after fire, a 25% increase in the proportion burned with high severity increased the odds of mountain quail occupancy by a factor of 1.8.

Discussion

Mountain quail occupancy and habitat selection

The mountain quail is an enigmatic bird. Although it has a large geographic range, it is often perceived as uncommon because it is secretive and prefers dense vegetation that defies inquiry (Gutiérrez and Delehanty 1999). We demonstrated that in the core of its distribution, the mountain quail is far more common than perceived, with mean site occupancy of 54% across 1636 survey sites spanning over 22,000 km^2 of the Sierra Nevada (Fig. 1). However, its relatively high occupancy over a very large area demonstrates it is a good model species for examining the effect of both large and small wildfires of various intensities. Thus, the perception of the mountain quail's rarity is apparently an illusion influenced by its behavior and habitat selection. Our habitat modeling efforts largely reflected what is known about mountain quail breeding season habitat associations from other studies—they are forest and dense understory species that do not rely on ruggedness of terrain as implied by their name (Gutiérrez 1980; Brennan et al. 1987; Brennan 1991). However, the absence of strong associations with forest cover types and, instead, associations with forest structure (i.e., canopy cover and canopy base height) supported our hypothesis that forest structure is more important than forest cover per se in determining mountain quail occupancy. Nevertheless, we note that evergreen forest can have a potentially large, positive effect on mountain quail occupancy, particularly when canopy cover and canopy base height are low. While mountain quail habitat selection is strongly associated with microhabitat features such as distance to water and distance to escape cover (Brennan 1991; Brennan et al. 1987; Gutierrez, 1977), our habitat analysis necessarily focused on macrohabitat features, which may have contributed to imprecision in occupancy estimates. Nevertheless, our work indicates that even coarse resolution habitat information is useful for understanding mountain quail ecology at a landscape-scale.

Response to wildfire

High-severity fire was positively correlated with mountain quail occupancy, while low-moderate-severity fire was neutral. Our fire models suggested that mountain quail occupancy peaked within 10 years after a high-severity fire, which is likely a function of shrub regeneration. One study exploring the impacts of fire on avian populations in the northern Sierra Nevada and southern Cascades found that mountain quail density peaked 10 years after 100% canopy cover reduction (Taillie et al. 2018), which was consistent with our findings. It is likely that mountain quail respond less positively to low- and moderate-severity fires because these fires tend to reduce the understory while retaining canopy cover, promoting conifer regeneration in the long term (Crotteau et al. 2013). High-severity fire, on the other hand, tends to promote shrubby re-growth in the Sierra Nevada and can limit regeneration of forest by depleting the seedbank (Crotteau et al. 2013; Collins and Roller 2013). Thus, high-severity fire is more likely to create habitat conditions associated with mountain quail occupancy. We note, however, that mountain quail occupancy is also partly a function of regional population dynamics, which are strongly influenced by weather (i.e., winter precipitation) (Gutiérrez and Delehanty 1999). Thus, it is also possible that site occupancy, in general, was relatively low in the Sierra Nevada at the time of our surveys given California was enduring drought during the years prior to our study. If this was the case, it could obscure any positive associations with low-moderate-severity fire owing to the predictions of ideal free distribution (i.e., the highest quality habitat is colonized first (Fretwell and Lucas 1969). Consequently, either a multi-year study or one that happens to capture high quail populations would help clarify whether low-moderate-severity fire can also create viable habitat for mountain quail.

The positive association between mountain quail occupancy and high-severity fire in the previous year was surprising. One explanation for higher occupancy in the first year than in 2 to 5 years after fire is selection for areas that burned the previous year as foraging sites. We expected low mountain quail occupancy in sites 1 year after a high-severity fire because of the lack of dense cover to which mountain quail appear to be inextricably linked (Gutiérrez 1977; Gutiérrez 1980). However, the first plants to return after high-severity fire in mixed conifer forests are typically ephemeral wildflowers and forbs (Burcham 1970), which could provide good food sources for mountain quail (Gutiérrez and Delehanty 1999). Two to 5 years after a high-severity fire, grasses typically compose a higher proportion of the vegetation (Burcham 1970), which mountain quail are expected to avoid (Gutiérrez and Delehanty 1999). Indeed, other species, such as spotted owls (Jones et al. 2020) and golden eagles (Kochert et al. 1999), are known to utilize recently burned areas as foraging sites. More detailed studies of mountain quail use of recently burned habitat would reveal more information about when and how—or if—recently burned areas factor into the life history of this enigmatic species. Additionally, a contributing factor to the lack of association we observed between occupancy and 2–5-year-old fire could be our small sample size of sites that burned at high severity in that time period (Fig. S2). Because of the scarcity of burned sites, our power to detect associations between occupancy and fire during that time interval may have been limited. Therefore, it is possible that mountain quail are associated positively with fire even 2–5 years after a high severity burn, but occupancy was higher after habitat regenerated for a longer time interval (i.e., 6–10 years).

Perhaps the most striking result was that unlike other iconic Sierra Nevada species (i.e., spotted owl and black-backed woodpecker), mountain quail site occupancy was highest in areas that burned with high severity 6–10 years earlier. A before-after, control-impact study of California spotted owls showed that after high-severity fire, territory occupancy was eliminated entirely within 2 years and indicated no signs of recovery even after 6 years (Jones et al. 2021), while black-backed woodpecker site occupancy was highest between 1 and 5 years after fire (Tingley et al. 2020). Thus, it appears that as habitat suitability declines for black-backed woodpeckers, it begins to peak for mountain quail. Notably, black-backed woodpeckers (Stillman et al. 2019b; Stillman et al. 2019a and spotted owls (Jones et al. 2020) generally avoid the interiors of large, high-severity fires. Importantly, we designed our study so that we could detect mountain quail in the interiors of large fire patches (see Fig. S3 as an example of comprehensive sampling). The interspecific variation in response to fire severity and time since fire emphasizes the importance of a diversity of fire severities and fire return intervals across the landscape to maintain appropriate habitats for the diverse Sierra Nevada bird community (Taillie et al. 2018). Additionally, both the spotted owl and the black-backed woodpecker have been shown to benefit to some extent, in nuanced ways, from pyrodiversity (Jones and Tingley 2022). A more detailed understanding of how the size and spatial configuration of fire may affect mountain quail occupancy, abundance, and demography would be a worthwhile next step in understanding the potentially complex relationship between fire and this recreationally valued indicator species.

Conclusions

Our results highlight the importance of fire return intervals of at least 6–10 years, but possibly even longer, to maintain high mountain quail occupancy. Some post-fire successional pathways can generate positive feedback loops that increase the chances of reburning at high severity over a shorter time interval (Coppoletta et al. 2015), which can negatively impact species. However, even these shorter fire return intervals may not be detrimental to mountain quail, because occupancy was positively related to proportion of a site burned even 1 year after a high severity fire. Indeed, our work demonstrates that high-severity fire is positively correlated with mountain quail occupancy, which suggests that mountain quail may actually be “winners” under the current and future altered fire regimes in the Sierra Nevada.

More broadly, our passive acoustic monitoring infrastructure can be used to detect birds and other acoustically active taxa throughout the biologically diverse western Sierra Nevada. The Sierra Nevada is experiencing rapid change: the number of large fires and the amount of area burned have increased across western North America (Dennison et al. 2014) and are projected to continue to increase over the next 30 years (Abatzoglou et al. 2021). Additionally, mega-droughts have caused extensive tree mortality in the last decade (Fettig et al. 2019), further exacerbating fire trends (Goodwin et al. 2021; Stephens et al. 2022). In the context of all these changes, understanding the ecology and nuanced fire responses of species beyond those that have been historically considered is an important and time-sensitive step in predicting how they will respond to future fire regimes. The relationship between mountain quail and high-severity fire is a reminder that there will be both winners and losers as the dynamics of wildfire change in the era of climate change.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-023-00180-9.

Additional file 1: Figure S1. Logistic regression used to choose the BirdNET prediction score threshold. **Figure S2.** Histograms showing the frequency distribution of each fire covariate. **Figure S3**. A map showing an example of the intersections between our survey sites and fire footprints.

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Authors' contributions
KMB conceived the idea; KMB, RJG, MZP, and CMW designed the methodology; MZP and CMW coordinated field data collection and curation; SK facilitated acoustic data processing; CAC and KMB extracted habitat and fire data; KMB performed the analysis; KMB and RJG wrote the manuscript; and all authors contributed to editing and revising the manuscript.

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Availability of data and materials
Data and code to reproduce our results are publicly available at: https://github.com/KBrunk01/Brunketal2023_QuailOnFire.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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