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Can the Hermit Warbler (*Setophaga occidentalis*) serve as an old-forest indicator species in the Sierra Nevada?

¿Puede el Chipe Cabeza Amarilla (*Setophaga occidentalis*) servir como especie indicadora de bosques antiguos de la Sierra Nevada?

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ABSTRACT. Changing fire regimes in western North America have raised the possibility of widespread loss of forest cover, making forest restoration a major priority. In one such ecosystem, the Sierra Nevada in California, the implications of forest management policy have been evaluated primarily via their potential effects on the California Spotted Owl (*Strix occidentalis occidentalis*). Yet the owl's cryptic life history, large home range, and declining population all make it difficult to study. The Hermit Warbler (*Setophaga occidentalis*) may be a valuable proxy species for the Spotted Owl because the two have similar associations with older forest habitat, but the former could enable researchers to achieve higher statistical power when studying changes to key habitats. We conducted passive acoustic surveys across the entire west slope of the Sierra Nevada between May and July 2021, identified both Hermit Warbler and Spotted Owl vocalizations in the resulting audio using the BirdNET algorithm, and used single-season occupancy models to examine the relationship between Hermit Warbler occupancy and six remotely sensed variables representing key attributes of older forests as well as Spotted Owl presence. Hermit Warblers were observed at all sites at which Spotted Owls were present, but those sites represented just 30.5% of the Hermit Warbler's total occupied range. Hermit Warbler site occupancy was positively associated with mean tree diameter and the presence of Spotted Owls (model weight = 0.97). The Hermit Warbler is more appropriate as a proxy for habitat beneficial to the California Spotted Owl than as a proxy for the owl itself. As such, monitoring and studying the Hermit Warbler could be a means of understanding the effects of forest restoration on important old-forest habitat.

RESUMEN. Los cambios en los regímenes de incendios en el oeste de América del Norte han incrementado la posibilidad de pérdidas generalizadas de la cobertura forestal, haciendo de la restauración forestal una prioridad importante. En uno de tales ecosistemas, la Sierra Nevada en California, las implicancias de la política de manejo forestal se han evaluado principalmente a través de sus posibles efectos sobre el Búho Moteado (*Strix occidentalis occidentalis*). Sin embargo, la historia de vida críptica, el amplio rango de hogar y la disminución de la población del búho dificultan su estudio. El Chipe Cabeza Amarilla (*Setophaga occidentalis*) podría ser una especie indicadora valiosa para el Búho Moteado, ya que ambas poseen asociaciones similares con hábitats forestales antiguos, pero la primera podría permitir a los investigadores obtener una mayor potencia estadística en los estudios sobre cambios en hábitats clave. Realizamos censos acústicos pasivos en toda la pendiente oeste de la Sierra Nevada entre mayo y julio de 2021, identificamos las vocalizaciones tanto del Chipe Cabeza Amarilla como del Búho Moteado en el audio resultante utilizando el algoritmo BirdNET, y utilizamos modelos de ocupación de una sola temporada para examinar la relación entre la ocupación del Chipe Cabeza Amarilla y seis variables detectadas remotamente que representan atributos clave de bosques más antiguos, así como la presencia del Búho Moteado. Los Chipe Cabeza Amarilla fueron observados en todos los sitios donde estaban presentes los Búhos Moteados, pero esos sitios representaron solo el 30.5% del rango total ocupado por el Chipe Cabeza Amarilla. La ocupación del sitio por el Chipe Cabeza Amarilla estuvo positivamente asociada con el diámetro promedio de los árboles y la presencia de Búhos Moteados (peso del modelo = 0.97). El Chipe Cabeza Amarilla es más apropiado como un indicador para el hábitat beneficioso para el Búho Moteado que como un indicador para el Búho en sí mismo. Como tal, estudiar y monitorear al Chipe Cabeza Amarilla podría ser un medio para entender los efectos de la restauración forestal en un importante hábitat forestal antiguo.

Key Words: *bioacoustics; fire regime; forest restoration; megafire; passive acoustic monitoring; resilience; Spotted Owl (Strix occidentalis); statistical power*

INTRODUCTION

Wildfires are becoming larger and more severe across the western United States (Westerling et al. 2006, Westerling 2016, Stevens et al. 2017, Cova et al. 2023, Williams et al. 2023), raising the possibility of large-scale forest loss (Coop et al. 2020, Steel et al. 2022). In the Sierra Nevada, the loss of pre-colonial fire regimes, extensive fire suppression in the twentieth century, and climate change have combined to make these forests particularly vulnerable to severe fire and less likely to recover after fire (Taylor et al. 2016, Stephens et al. 2018, Hagmann et al. 2021). Restoring the resilience of Sierra Nevada forests to novel disturbance regimes is broadly considered a desirable outcome of forest management, but achieving this goal entails navigating many complex and potentially asymmetrical trade-offs (Wood and Jones 2019, Stephens et al. 2020). Balancing presumed long-term benefits of forest restoration for sensitive species against potential

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short-term costs is possible (Jones et al. 2021). However, characterizing the effects of forest management practices is complicated by the large sample sizes required to achieve high statistical power to observe a species' potential response to forest change (Popescu et al. 2012, Wood et al. 2019, Wood 2022).

The effects of forest management on wildlife in the Sierra Nevada have been primarily evaluated in the context of their observed or perceived impacts on the California Spotted Owl (*Strix occidentalis occidentalis*; e.g., Dow et al. 2016), and concerns about the Spotted Owl have motivated substantial research and shaped forest management (Stephens et al. 2019). Yet their population is slowly declining in many parts of the Sierra Nevada at least in part because of historical logging of large trees, contemporary megafires, and some forest management practices (Conner et al. 2013, Tempel et al. 2014, 2016, Jones et al. 2016, 2018, Hobart et al. 2019). The invasive Barred Owl (*Strix varia*) poses an existential threat to Spotted Owls, but a recent landscape-scale removal experiment suggests that Barred Owls do not presently threaten Spotted Owls in the Sierra Nevada (Hofstadter et al. 2022, Kelly et al. 2023). Ongoing Spotted Owl declines across much of the Sierra Nevada informed the recent proposal to list this population segment as Threatened under the Endangered Species Act (ESA; U.S. Fish and Wildlife Service 2023). Population declines may exacerbate the already difficult tasks of monitoring the status of Spotted Owls in the Sierra Nevada and assessing their responses to environmental change by reducing statistical power to identify further changes and responses to forest management (Popescu et al. 2012).

Historically, researchers used labor-intensive field methods to track individuals and populations, such as mark-recapture and vocal-lure surveys (Forsman 1983), which require skilled crews and cannot be applied at broad spatial scales because of their time and labor limitations. Recently, bioacoustics has emerged as a viable alternative method of owl monitoring, with passive acoustic surveys and semi-automated animal sound identification tools facilitating the implementation of ecosystem-scale monitoring in the Sierra Nevada (Wood et al. 2019, Kelly et al. 2023). However, adult Spotted Owls typically maintain approximately 400-ha territories in the Sierra Nevada (Tempel et al. 2016) which, along with their declining population, may challenge owl research because environmental changes must be individually extensive or collectively prevalent in order to affect enough individuals to achieve high statistical power (Popescu et al. 2012, Wood et al. 2019, Wood 2022). In contrast, the same changes will affect many more sampling units in monitoring programs focusing on smaller bodied species because of their smaller territory requirements, thus increasing statistical power to detect a population response (Wood 2022). In light of likely ESA protections for the California Spotted Owl in the Sierra Nevada (U.S. Fish and Wildlife Service 2023) and the collective urgency to implement forest restoration (Stephens et al. 2020, Knight et al. 2022), it may be valuable to identify small-bodied species to serve as proxies for Spotted Owls based on habitat associations in efforts to understand how forest management influences critical habitat.

Decades of research have painted a relatively clear picture of the Spotted Owl as dependent upon older forest conditions, most notably wide (> 60 cm DBH; Jones et al. 2018, Stephens et al. 2019), tall trees (North et al. 2017), with high canopy cover (> 70%; Tempel et al. 2014). High basal area (Burnett and Roberts 2015) and canopy layer count (Mills et al. 1993) are also important. The Hermit Warbler (*Setophaga occidentalis*) is closely associated with Spotted Owl habitat, selecting for stands with older forest characteristics: large-diameter trees (Hershey et al. 1998), densely layered canopies, and high canopy cover (Tempel et al. 2016). Like Spotted Owls, Hermit Warblers are fire sensitive, though they have been reported to respond negatively to both lower and higher severity fire (Bagne and Purcell 2011, Raphael et al. 2018). More directly, Hermit Warblers ranked first of 81 northern Sierra Nevada birds in terms of their affinity to Spotted Owl Protected Activity Centers (121 ha areas that have been designed to preserve the Spotted Owl; Burnett and Roberts 2015). Critically, a Hermit Warbler weighs only about two percent of a Spotted Owl, meaning the former are likely to have much smaller territories than the latter (Haskell et al. 2002). Thus, the small territories maintained by Hermit Warblers mean that sample sizes within any given disturbance (e.g., fire or forest management) would be higher relative to those of Spotted Owls, yielding greater statistical power to observe a population response (Wood 2022).

We used passive acoustic monitoring data that spanned the entire Sierra Nevada to test the suitability of the Hermit Warbler as a proxy for the Spotted Owl. Specifically, we evaluated the Hermit Warbler's associations with old-forest characteristics and with Spotted Owls themselves. We predicted that Hermit Warbler site occupancy would increase with canopy height, canopy cover, canopy layer count, mean tree diameter, total basal area, and the presence of Spotted Owls, and that occupancy would be negatively associated with fire. If Hermit Warbler and Spotted Owl habitat associations align, or the two species are positively associated, Hermit Warblers could be used to evaluate the effects of forest management on critical habitat in the Sierra Nevada.

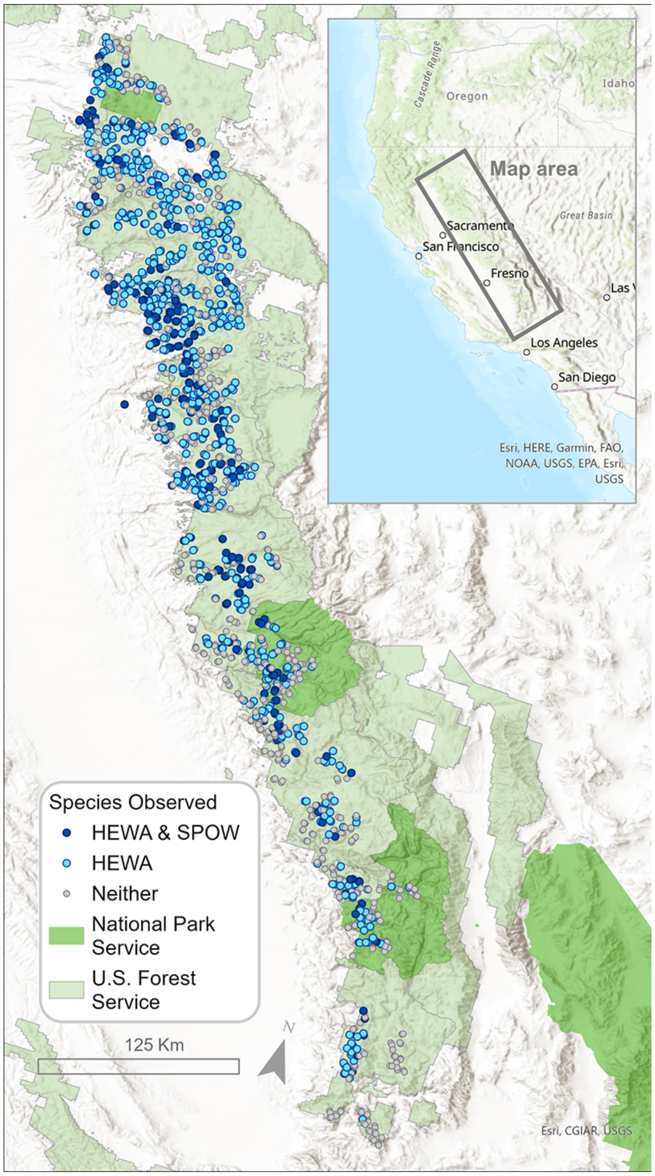
METHODS

Passive acoustic surveys and audio analysis

In the summer of 2021, we conducted passive acoustic surveys across the entire western slope of the Sierra Nevada (six National Forests and three National Parks; Fig. 1). During May 1–August 1 2021, 1652 autonomous recording units (ARUs; SwiftOne recorder, K. Lisa Yang Center for Conservation Bioacoustics) were deployed in 851 randomly selected, non-contiguous 400 ha hexagonal grid cells (most cells had two ARUs) for an average of 34.5 days each (Fig. 1). ARUs were deployed ≥ 500 m apart within each cell in areas that were acoustically advantageous (e.g., along ridges rather than in gullies) and had one omnidirectional microphone that recorded 18:00–09:00 (local time) at a sample rate of 32 kHz (see Wood et al. 2019, Kelly et al. 2023 for details). In situ testing indicated that the effective range of these recorders was 200–300 m for Spotted Owls; for Hermit Warblers that distance is likely to be much less (~ 50 m).

We analyzed the audio with the BirdNET algorithm, a deep artificial neural network capable of identifying the vocalizations of > 95% of Sierra Nevada birds, including the Hermit Warbler and Spotted Owl (Kahl et al. 2021). We used a customized version of BirdNET that incorporated training data from our study area, an important step because the Hermit Warbler is known to have diverse song dialects across California (Furnas et al. 2020). We

Fig. 1. Naïve occupancy of Hermit Warblers (*Setophaga occidentalis*; HEWA) and California Spotted Owls (*Strix occidentalis occidentalis*; SPOW) across 1519 autonomous recording units in the Sierra Nevada, USA, in May–July, 2021. Hermit Warblers were observed at all 300 sites at which Spotted Owls were observed as well as 684 others.



manually validated a random selection of Hermit Warbler predictions and used logistic regression to relate BirdNET's unitless confidence score to the probability that any given prediction was correct. We treated predictions occurring within 05:00–09:00 or 18:00–20:00 with a pr(true positive) ≥ 0.99 as correct and discarded all other observations and then excluded observations prior to June 1 to focus our analyses on the breeding season, which left 354,734 Hermit Warbler observations. For Spotted Owls, we focused on audio recorded May 1–August 1, during 20:00–06:00, local time and manually reviewed 22,828 high-scoring, BirdNET-based Spotted Owl predictions, classifying each as correct or incorrect. We then calculated the number of sites at which both, either, or neither species was observed (naïve occupancy).

Site covariates

We used three sources of data as site covariates in an occupancy analysis. First, we treated Spotted Owls as present or absent at each ARU. An occupancy analysis conducted by Kelly et al. (2023) indicated that seasonal detection probability of Spotted Owls was > 0.98 at the level of survey grid cells. We applied this near-perfect detection rate to individual ARUs such that the Spotted Owl data was a categorical present/absent site covariate. The spatial mismatch between the territory size of Spotted Owls and Hermit Warblers complicated a formal two-species occupancy analysis (MacKenzie et al. 2004).

Next, we drew on two sets of remote sensed data, which we represented at a 120-m radius around each ARU (4.5 ha, a resolution that reflects the 30-m resolution of our data sources). We used fire data compiled by Cova et al. (2023). Briefly, a geospatial dataset of historical fire perimeters maintained by the California Department of Forest and Fire Protection (CAL FIRE), Fire and Resource Assessment Program (FRAP) was used to identify fires that burned between 1985 and 2020 within the study area; spectral indices (including Normalized Difference Vegetation Index, Mid-Infrared Bi-Spectral Index, and Relativized Burn Ratio), climatic variables, and latitude were used to model the Composite Burn Index (CBI; 0–3 scale; Key and Benson 2006) using Google Earth Engine code provided by Parks et al. (2019). We summarized fire data over a 35-year interval (CBI) and a five-year interval (proportion of the area burned at low or moderate severity). Using the most recent data (spring 2020) from the California Forest Observatory (2020; A Statewide Tree-Level Forest Monitoring System, Salo Sciences Inc., San Francisco, CA, USA https://forestobservatory.com), we compiled the following forest structure data: mean canopy cover (%), mean canopy layer count (number of distinct vertical canopy layers), mean stand height (ft), mean tree diameter (mm), and total basal area (ft²/acre). We excluded from our analysis 16 ARUs that lacked the full set of forest structure data and 129 that burned between when the forest structure and bird observation data were generated (spring 2020 and summer 2021, respectively); the fires that occurred in summer/fall 2020 would have resulted in changes to forest structure that were not reflected in our data. In total, we had 1507 survey sites, 672 of which were affected by fire in the previous 35 years (45% of all sites).

Occupancy modeling

We used single-season occupancy models (MacKenzie et al. 2002) to assess Hermit Warbler habitat associations. Because there were high correlations between all forest structure variables (r = 0.6–0.97) and we wanted to assess the strength of associations between the warbler and each covariate, we chose to evaluate the support for competing models (the seven forest structure variables and the presence of Spotted Owl), rather than fit a single global model. We considered sites occupied only if they had observations (with pr[true positive] ≥ 0.99) on two or more different days to provide further insurance against spurious detections (either correct classifications of non-resident individuals, or high-scoring misclassifications). We then consolidated our Hermit Warbler data from 1519 sites into eight six-day secondary sampling periods between June 1 and July 18.

We then used a three-step occupancy modeling approach in which we evaluated support for competing models using Akaike's Information Criterion (AIC) and considered models with ΔAIC ≤ 2 to be supported by the data (Burnham and Anderson 2010). The most-supported model structure from each step was carried forward to subsequent steps. First, we tested for variation in detection based on date (Julian start date of each secondary sampling period) and survey effort (recording hours per site in each secondary sampling period). We evaluated the support for two univariate models, an additive bivariate model, and a null model in which detection probability was uniform. Second, we tested for biogeographic variation in occupancy by comparing latitude, elevation, and the residuals of latitude and elevation. We evaluated support for those three univariate models, an additive latitude and elevation model, and a null model.

Then, building upon most-supported detection and biogeographic occupancy model structures, we tested the influence of our site covariates on Hermit Warbler occupancy via seven univariate forest structure models, a Spotted Owl presence/absence model, seven bivariate forest structure + Spotted Owl models, and a null model (i.e., the most-supported model from the previous steps). We used the package unmarked (Fiske and Chandler 2011) in Program R (R Core Development Team 2020) to fit and evaluate our models.

RESULTS

When limiting BirdNET predictions to pr(true positive) ≥ 0.99 and requiring such an observation on at least two different days during the study period, we observed Hermit Warblers at 984 of 1519 ARUs across the Sierra Nevada in 2021 (naïve occupancy = 0.65; Fig. 1). Hermit Warblers were observed at all 300 sites at which Spotted Owls were observed, but that represented just 30.5% of the sites at which the former was observed (n = 984; Table 1). The probability of detecting a Hermit Warbler decreased through the season, from 0.96 on June 1 to 0.063 by July 12. The biogeographic occupancy step indicated that site occupancy was positively related to elevation (Table A1). Models containing other detection structures and biogeographic covariates were not competitive.

Hermit Warbler site occupancy was best explained by positive associations with both mean tree diameter and Spotted Owl presence (w = 0.97; Table 2). Without considering Spotted Owl presence/absence, Hermit Warbler site occupancy was strongly positively related to mean tree diameter (1.30, SE = 0.0777; Fig. 2; Table 2). There was also support for a positive relationship between site occupancy and total basal area (1.311, SE = 0.0776; Table 2). Parameter estimates were similar, and the two variables were highly correlated (r = 0.97). Interestingly, Spotted Owl presence alone was not among the top models (ΔAIC = 375.9), but including Spotted Owl presence/absence with forest structure variables improved model fit.

Despite the overwhelming support for a positive response to tree diameter and total basal area, all but two other models—stand height and five-year low/moderate severity fire—had substantially more support than the null model (Table 2). The relationships between Hermit Warbler site occupancy and all occupancy covariates were in the predicted direction (occupancy was positively associated with diameter, total basal area, canopy cover, canopy layer count, Spotted Owl presence, and stand height) and negatively associated with 35-year average CBI (Table 2). Notably, Hermit Warbler site occupancy was not influenced by the proportion of a site that burned at low- to moderate-severity fire within the last five years (Table 2).

Table 1. Sites occupied by both, either, or neither species (naïve occupancy).

		Hermit Warbler (*Setophaga occidentalis*) Present	Absent	Total
Spotted Owl (*Strix occidentalis*)	Present	300	0	300
	Absent	684	535	1219
	Total	984	535	1519

DISCUSSION

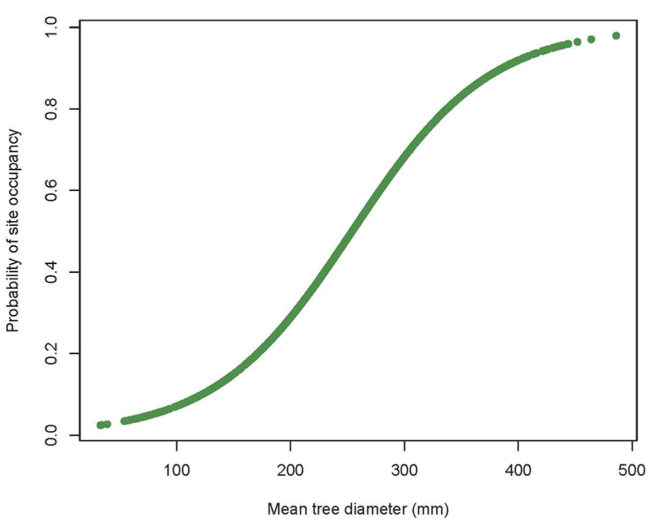
Can the Hermit Warbler serve as a small-bodied proxy species for the Spotted Owl in the Sierra Nevada? Not directly, given that the presence of Spotted Owls alone was only a moderate predictor of Hermit Warbler site occupancy (ΔAIC = 375.9 relative to the most-supported model but 43 AIC lower than the null model; Table 2), a finding that was likely driven by the fact that Spotted Owls were present at fewer than one-third of the sites occupied by Hermit Warblers (Table 1). Moreover, although both species are distributed throughout the study area, Spotted Owl occupancy peaks at mid-elevations and mid-latitudes (Kelly et al. 2023). Hermit Warblers, in addition to being much more prevalent, are positively associated with higher elevations (Table A1). Differing prevalence may be caused by their differing body sizes, with the Hermit Warbler better able to utilize relatively small stands of older forests as well as a broader range of conditions, whereas Spotted Owls may require larger such stands for nesting and roosting. Thus, the Hermit Warbler is not a one-to-one small-bodied proxy for the California Spotted Owl in the Sierra Nevada, though correcting for geographic factors like latitude and elevation, as well as landscape configuration (i.e., patch size) could facilitate comparisons.

However, our results do suggest that it could be appropriate to treat the Hermit Warbler as a proxy for habitat suitable to Spotted Owls. The probability of Hermit Warbler site occupancy increased with tree diameter (Fig. 2), a key indicator of older forest conditions and Spotted Owl presence (Table 2), suggesting that both species are selecting for similar habitat features that are not represented by our forest structure variables. Tree diameter and total basal area are highly correlated (r = 0.97), and, unsurprisingly, the diameter-only occupancy model was highly competitive with the basal area-only model (ΔAIC 1.20 between models; Table 2), suggesting that Hermit Warblers are responding more strongly to large trees per se than to dense forest. Yet when Spotted Owl presence/absence was included with both variables, the difference in support increased (ΔAIC 7.10 between the models), providing further evidence that some unmeasured forest conditions selected by Spotted Owls are also important to Hermit Warblers. Overall, all habitat relationships were as predicted: we observed positive associations between Hermit Warblers and canopy cover, canopy layer count, stand height, mean diameter, and basal area and a negative association with 35-year CBI. Ultimately, small patches of Hermit Warbler habitat could serve

Table 2. Model selection for Hermit Warbler (*Setophaga occidentalis*) site occupancy. All models included Julian date as a detection covariate and elevation as an additional occupancy covariate (see Table S1). w is model weight; β and SE are parameter estimates and associated standard error, respectively (listed in the same order as in the model structure). CSO represents a categorical variable for California Spotted Owl (*Strix occidentalis occidentalis*) presence/absence at a site; CBI represents the Composite Burn Index.

Model	AIC	ΔAIC	w	Intercept	β	SE
Tree Diameter + CSO	5382.2	0.00	0.97	–0.111	1.274 + 0.624	0.079 + 0.162
Total Basal Area + CSO	5389.3	7.10	0.03	0.542	1.194 + 0.570	0.0757 + 0.161
Tree Diameter	5396.2	14.00	0.00	–0.024	1.300	0.0777
Total Basal Area	5397.4	15.20	0.00	0.925	1.311	0.0776
Canopy Cover + CSO	5480.5	98.30	0.00	–2.282	1.369 + 0.615	0.0782 + 0.162
Canopy Cover	5481.4	99.20	0.00	–1.504	1.286	0.0745
Canopy Layer Count + CSO	5562.5	180.30	0.00	–0.0431	0.833 + 0.744	0.069 + 0.154
Canopy Layer Count	5583.0	200.80	0.00	0.160	0.923	0.0700
Fire (35-yr CBI) + CSO	5651.4	269.20	0.00	–0.251	–0.684 + 1.011	0.073 + 0.151
Fire (35-yr CBI)	5683.7	301.50	0.00	0.306	–0.695	0.0710
Stand Height + CSO	5746.5	364.30	0.00	–0.00155	0.151 + 1.05	0.056 + 0.147
CSO	5758.1	375.90	0.00	–0.320	1.115	0.1479
Fire (5-yr Low/Mod) + CSO	5760.5	378.30	0.00	–0.347	–0.063 + 1.10	0.065 + 0.148
Null	5801.1	418.90	0.00	0.522	N/A	N/A
Stand Height	5804.1	421.90	0.00	0.129	0.120	0.0545
Fire (5-yr Low/Mod)	5825.2	443.00	0.00	–0.241	–0.054	0.0517

Fig. 2. Hermit Warbler (*Setophaga occidentalis*) site occupancy increased with the mean tree diameter as estimated for the 120 m radius around each recording site (4.5 ha stand).



as anchor points for activities meant to increase the presence of Spotted Owl habitat. This could include actively excluding wildfire fire from Hermit Warbler habitat during peak fire season (e.g., maintaining fire refugia; Meddens et al. 2018) or engaging in silviculture treatments meant to accelerate complex forest stand structure development (e.g., Palik et al. 2020).

The positive relationship between Hermit Warbler occupancy and elevation (Table A1) suggests that this species may be responding to cooler temperatures. Large trees themselves can also moderate temperatures by creating cool microclimates (Moen and Gutiérrez 1997, McGinn et al. 2023). Indeed, Spotted Owls' selection for stands with large trees and their elevated extinction rates in the absence of such trees (Jones et al. 2018) may be influenced by the cool microclimates they create and the owl's comparatively low upper critical temperature (Weathers et al. 2001). As temperatures continue to rise and heat waves become more frequent, it may be valuable to identify and conserve thermal refugia for Spotted Owls, Hermit Warblers, and other thermally limited species (Balantic et al. 2021).

Although negative effects of fire of all severities on Hermit Warblers have been observed (Raphael et al. 2018), we found no evidence that low-to-moderate severity fire in the past five years influenced site occupancy (Table 2). Such fires were common and widespread in the pre-colonial Sierra Nevada, and our findings contribute to the mounting evidence that many species, including Spotted Owls (Jones et al. 2020, Kramer et al. 2021), are adapted to precisely those conditions. Low-to-moderate severity fire is considered a target outcome of prescribed fire (Van Mantgem et al. 2011), which is considered a valuable forest management tool in the Sierra Nevada, albeit one that is challenging to implement (North et al. 2010). The negative association between Hermit Warbler occupancy and the 35-year CBI was expected and substantially outperformed the null model (ΔAIC 117.4 between models; Table 2), but likely performed poorly overall (ΔAIC = 301.5) because fire history is reflected in the most supported variable (tree diameter).

Our study has several important limitations. First, we did not explicitly test for an association between the two focal species, instead using Spotted Owl presence/absence as a categorical variable in a single-species occupancy model focused on the Hermit Warbler. An explicit multi-species approach (Rota et al. 2016) could provide a more direct test of their association. Second, we used only one year of data; particularly in dynamic, frequent-fire landscapes, drawing on multiple years of data may be necessary to discern salient ecological processes. Second, sampling was constrained to mid-elevation mixed conifer forests such that lower-elevation forests (i.e., private land west of our study area) was excluded as were high-elevation subalpine forests.

It is likely that important variation in the habitat associations of both species exists beyond our study area such that the interpretation of our findings should be limited to the area sampled (Fig. 1). Finally, the bioacoustic approach (passive acoustic surveys and machine learning-based species observations) is not without error, even with our highly conservative threshold (pr[true positive] ≥ 0.99 required for inclusion). In particular, detection accuracy could vary by dialect type, which itself varies systematically with the phenomena in question—large, severe fires (Furnas et al. 2020). Our customization of BirdNET to this ecosystem and the large quantity of data collected could mitigate these issues.

In the context of potential tension between likely ESA protections for the Sierra Nevada population segment of the California Spotted Owl (U.S. Fish and Wildlife Service 2023) and the urgent need for broadscale forest restoration in the Sierra Nevada (Stephens et al. 2020, Knight et al. 2022), the Hermit Warbler could be an unexpected asset. It is challenging to assess the effects of forest change on Spotted Owls with high statistical power (Popescu et al. 2012, Wood et al. 2019); it is comparatively easy to do so for Hermit Warblers (Wood 2022). The judicious use of Hermit Warbler monitoring could provide insights into the potential effects of forest restoration projects on Spotted Owls via their similar habitats. Fortunately, as we and others (Brunk et al. 2023) have shown, passive acoustic surveys for Spotted Owls can be leveraged for the study of many other species: Hermit Warbler monitoring need not entail substantial additional costs. Using the Hermit Warbler in conjunction with the Spotted Owl for more comprehensive ecosystem monitoring could be a key asset, particularly in the face of continued Spotted Owl declines and an increasingly urgent need for forest restoration.

Author Contributions:

CMW conceived the idea; CMW and MZP developed the underlying monitoring program; CAC, KM, CMW, and LB developed the datasets; LB conducted the analyses and wrote the first draft of the paper with support from CMW; MZP secured funding and managed the monitoring program.

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Data Availability:

The data used for this analysis are available on Zenodo (https://doi.org/10.5281/zenodo.10436571). Contact the authors for permissions.

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Appendix 1. Model selection for Hermit Warbler site occupancy.

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