




ORIGINAL RESEARCH

Open Access



Camera traps link population-level activity patterns with wildfire smoke events for mammals in Eastern Washington State

Jessalyn Ayars^{1*} , Robert L. Emmet², Sarah B. Bassing³, Olivia V. Sanderfoot⁴, Sierra Raby⁵, Alexandra Karambelas⁶, Eric P. James^{7,8}, Ravan Ahmadov^{7,8} and Beth Gardner³

Abstract

Background Due to anthropogenic climate change and historic fire suppression, wildfire frequency and severity are increasing across the western United States. Whereas the indirect effects of fire on wildlife via habitat change are well studied, less is known about the impacts of wildfire smoke on animal health and behavior. In this study, we explore the effects of wildfire smoke on the behavior of eight medium- to large-bodied mammalian species in a heterogeneous study area in Washington, USA. We linked population-level activity metrics derived from camera trap data to concentrations of fire-specific fine particulate matter (PM_{2.5}). We hypothesized that mammalian activity would decline during smoke events, as animals attempt to reduce potential health impacts of smoke inhalation. We used occupancy models and Poisson regression models to test the effect of fire-specific PM_{2.5} levels on daily detection probability and the number of detections per day, respectively, for each study species.

Results While we did not observe any significant responses to daily mean concentrations of PM_{2.5} in the occupancy models, we found three species with significant responses in their rates of detections per day in the Poisson regression. Specifically, for each standard deviation increase in the daily mean concentration of PM_{2.5}, there was a 12.9% decrease in the number of bobcat detections per day, an 11.2% decrease in the number of moose detections per day, and a 5.8% increase in the number of mule deer detections per day. In general, the effects of PM_{2.5} were small compared to other relevant covariates.

Conclusions We generally found little evidence to support our hypothesis that animals would reduce their activity in response to wildfire smoke. However, our study demonstrated that mammals exhibited species-specific behavioral responses to smoke, which are possibly adaptive responses to reduce health impacts from smoke inhalation. Though we found only a few immediate behavioral responses to smoke exposure, we note that longer-term health consequences of smoke exposure for wildlife are also likely and generally unknown. Our study shows how camera traps, which are already widely used to study wildlife, can also be used to investigate the impacts of wildfire smoke on animal behavior and provides a step towards developing methods to better understand this increasing source of environmental stress on wildlife.

Keywords Air pollution, Air quality, Climate change, Detection probability, Occupancy modeling, PM_{2.5}, Wildfire smoke, Wildlife behavior

*Correspondence:

Jessalyn Ayars

jessalyn.ayars@gmail.com

Full list of author information is available at the end of the article

Resumen

Antecedentes Debido al cambio climático de origen antrópico y la histórica supresión de fuegos, la frecuencia e intensidad de los incendios se están incrementando a lo largo y ancho del oeste de los EEUU. Mientras que los efectos indirectos del fuego sobre la fauna, a través de los cambios en el hábitat, han sido bien estudiados, es menos conocido el impacto del humo causado por los incendios sobre la salud y el comportamiento animal. En este trabajo, exploramos los efectos del humo causado por incendios en el comportamiento de ocho mamíferos, de tamaños medianos a grandes, en un área de estudios heterogénea en Washington, EEUU. Relacionamos las medidas de actividad a nivel de poblaciones, derivadas de datos de cámaras trampa, con concentraciones de partículas finas ($PM_{2.5}$) generadas específicamente por fuegos. Hipotetizamos que la actividad de los mamíferos podría declinar durante eventos que producen humos, dado que los animales tienden a reducir el riesgo potencial sobre su salud al inhalar esos humos. Usamos modelos de ocupación y regresiones de Poisson para probar los efectos específicos de niveles de $PM_{2.5}$ en la probabilidad de detección diaria y en el número de detecciones diarias para cada especie en estudio, respectivamente.

Resultados Aunque no observamos ninguna respuesta significativa a las concentraciones diarias de $PM_{2.5}$ en los modelos de ocupación, encontramos tres especies con respuestas significativas en su tasa de detección diaria mediante el modelo de regresión de Poisson.

Específicamente, para cada incremento en la desviación estándar en la concentración media de $PM_{2.5}$, hubo un 12.9% de decrecimiento en la detección de lince por día, un 11.2% de decremento en el número de alces americanos detectados, y un 5.8% de incremento en la detección de ciervos mulos por día. En general, los efectos del $PM_{2.5}$ fueron muy pequeños en relación a otras covariables relevantes.

Conclusiones Encontramos en general poca evidencia para avalar nuestra hipótesis de que los animales podrían reducir su actividad en respuesta al humo de incendios de vegetación. Sin embargo, nuestro estudio demostró que los mamíferos exhibieron respuestas de comportamiento especie-específicas al efecto del humo, las cuales podrían revelar respuestas adaptativas para reducir impactos en su salud por inhalación de humo. Aunque encontramos solamente muy pocas indicaciones de comportamiento inmediatas a la exposición al humo, notamos que las consecuencias a largo plazo en la salud para la fauna son posibles, aunque desconocidas. Nuestro estudio mostró como las cámaras trampa, que son ampliamente usadas para estudiar la fauna silvestre, pueden ser usadas para investigar los impactos del humo de los incendios sobre la conducta animal, y que proveen de un paso más para el desarrollo de métodos para entender mejor esta fuente incremental de estrés ambiental sobre la fauna.

Background

Wildfire activity is increasing globally, including in the western United States, exacerbated by anthropogenic climate change and the build-up of fuels from decades of fire suppression (Abatzoglou and Williams 2016). Many studies of the effects of wildfires on wildlife focus on indirect impacts, such as habitat loss in post-fire landscapes. However, an increasing and understudied threat to wildlife is large-scale smoke exposure (Sanderfoot et al. 2022). Wildfire smoke is a known threat to human health—exposure to smoke has been linked to increases in short-term mortality rates and hospital admissions for respiratory illness (Kollanus et al. 2016; Chen et al. 2021). Fine particulate matter ($PM_{2.5}$; solid and liquid particles less than 2.5 μm in diameter), a major component of wildfire smoke, as well as of other sources of pollution (Chen et al. 2021), is the leading cause of outdoor air pollution-related mortality globally (Lelieveld et al. 2015). Just as communities worldwide are increasingly exposed to wildfire

smoke, wildlife is also experiencing more frequent and severe wildfire smoke events. However, research on the impacts of smoke on the health and behavior of wild animals is extremely limited, and the impacts of wildfire smoke on wildlife populations are largely unknown (Sanderfoot et al. 2022). As a result, understanding the consequences of wildfire smoke for wildlife populations is becoming increasingly relevant for conservation.

Smoke inhalation affects animal physiology and behavior. Smoke inhalation can lead to carbon monoxide poisoning, immunosuppression, and respiratory, cardiovascular, and neurological pathologies and may result in mortality (Drobatz et al. 1999a, b; Sanderfoot and Holloway 2017). Behavioral responses to smoke could be indicative of such underlying, adverse health effects. For example, mounting an immune response to smoke would consume energy that could otherwise be used for behaviors such as defending territories or attracting mates, resulting in decreased activity (Erb et al. 2018; Sanderfoot et al. 2022). Several studies of

the impacts of air pollution on domestic and captive animals suggest that wildfire smoke is likely to affect the health of large mammals in the wild. Air pollution (specifically ozone, PM₁₀, and nitrogen dioxide) was linked to increased mortality of dairy cows (*Bos taurus*) on a farm in Belgium (Cox et al. 2016). In contrast, for cattle in the Netherlands, no consistent effect of air pollution (ozone, PM₁₀, nitrogen dioxide, or ammonia) on mortality was observed (Egberts et al. 2019). Other health metrics provide a more nuanced picture of the effects of smoke in particular on large animal health. For example, a recent study directly linked exposure to PM_{2.5} from wildfire smoke to negative health effects in dairy cows, including reduced milk production, altered metabolism, and changes in blood immune cell composition (Anderson et al. 2022), and a study of captive rhesus macaque monkeys (*Macaca mulatta*) found that exposure to smoke as infants led to reduced lung volume as adolescents (Black et al. 2017). Case studies from veterinary medicine indicate respiratory and neurological effects of smoke exposure for cats (*Felis catus*) and dogs (*Canis familiaris*) (Drobatz et al. 1999a, b). While studies of domestic and captive animals are useful in considering potential impacts of smoke exposure for wildlife, animal behaviors in the wild often differ from those in captivity.

Smoke may also drive behavioral changes that are unrelated to health effects. For example, wildfire smoke alters the visual and olfactory cues that wildlife use for foraging (Jetz et al. 2003), navigation and migration (Hegedüs et al. 2007), and predator/prey detection (Apfelbach et al. 2005), which can also lead to behavioral changes. Research has shown that smoke prompts some mammals to exhibit energy-conserving behaviors, such as torpor, that presumably help animals avoid hostile fire and post-fire environments (Dickinson et al. 2009; Matthews et al. 2017; Geiser et al. 2018). Other animals adjust their behavior to take advantage of resources available in post-fire landscapes; for example, predators have been known to hunt animals that flee fire and smoke (Hovick et al. 2017). Wildlife use odors and chemosensory cues to detect prey or predators (Apfelbach et al. 2005; Garvey et al. 2017; Hughes et al. 2010; Kats and Dill 1998), forage, or find mates (Finnerty et al. 2022). Thus, the disruption of these cues and odors by the chemical composition of smoke can alter the mechanisms that animals use in foraging, risk aversion, and mating behavior which impacts their movement patterns (Finnerty et al. 2022). Smoke also affects sky polarization used for navigation in wildlife (Hegedüs et al. 2007); in fact, elevated PM_{2.5} levels were associated with longer foraging trips for honeybees (*Apis mellifera*, Cho et al. 2021). Similarly, high concentrations of smoke were related to tule greater white-fronted geese

(*Anser albifrons*) stopping their migration or changing direction resulting in longer migration times and distances (Overton et al. 2022). Though the specific mechanism for this changed behavior is unknown, the result was energetic deficits (Overton et al. 2022). Thus, while responses to smoke may vary by species, these behavioral and physiological effects could compound to impact population-level rates such as changes in survival or fecundity, with consequences for the conservation and management of wildlife (Sanderfoot et al. 2022).

Monitoring the health of wild animals, especially large animals, is expensive and invasive, making it difficult to directly examine the effects of wildfire smoke and subsequent population-level impacts. However, behavioral responses are more easily observed and can serve as a proxy for underlying health effects, as demonstrated in a study of orangutans (*Pongo pygmaeus*; Erb et al. 2018). Erb et al. (2018) documented the behavior of four orangutans in Indonesia during a severe smoke event and found that they rested more and traveled less when it was smoky. Additionally, ketones in the orangutans' urine were elevated during and after the smoke event, indicating fat burning from elevated calorie expenditure—likely due to an immune response to smoke inhalation (Erb et al. 2018). During the same severe fire season, Lee et al. (2017) documented rapid declines in acoustic activity in bird and Orthoptera communities in Singapore in response to air pollution associated with wildfires, although they were unable to determine the mechanisms driving this response. Similarly, gibbons (*Hylobates albibarbis*) were observed to sing less on smoky days in Borneo, despite otherwise good weather conditions, an effect hypothesized to be related to poorer health (Cheyne 2008). While valuable examples of behavioral responses to wildfire smoke, these studies are limited in their spatial and temporal extent. With the increasing use of non-invasive monitoring devices such as camera traps that can sample over broad spatial and temporal scales, it is possible to study impacts of smoke on wildlife at much larger scales (O'Connell and Bailey 2011).

Camera traps are widely used to study wildlife habitat use and activity and provide an opportunity to connect data on smoke exposure with wildlife behavioral data (Burton et al. 2015). Frequency of photo-captures of animals at camera traps is the result of several underlying processes, including animal density, activity, and habitat selection (Parsons et al. 2017; Neilson et al. 2018; Hofmeester et al. 2019). Occupancy models can explain variation in photo-capture data by separating the ecological process of species occurrence from the observational processes of whether or not a species is detected, given that it is present (MacKenzie et al. 2002). Occupancy models also provide a flexible framework to explore

how environmental covariates influence species occurrence versus species detection (MacKenzie et al. 2002). While estimating occupancy is often the primary goal of occupancy models, estimating detection can also provide ecological insights. The detection process has been used to investigate the intensity of habitat use at a camera site (Stewart et al. 2018). Detection may also indicate frequent transit past the camera trap, implying that camera trap detections can be used to quantify activity (Stewart et al. 2018). Therefore, decreased activity due to wildfire smoke may be observable via decreased camera trap detection probabilities. Given the widespread use of camera traps in wildlife research (Burton et al. 2015) and their ability to detect changes in wildlife activity (Stewart et al. 2018), researchers may be able to leverage established camera trap networks to study the effects of wildfire smoke on wildlife.

In this study, we explored impacts of wildfire smoke on mammalian activity and aimed to provide proof of concept that camera trap data can be used as a tool for exploring smoke effects on wildlife. We studied camera trap detections of eight large mammal species in Eastern Washington, a mixed-severity, fire-adapted system (Perry et al. 2011) with more severe than average fire seasons in 2018 and 2020, and less severe than average fire season in 2019, providing an opportunity to test for effects of wildfire smoke on wildlife activity. We used hierarchical occupancy models (MacKenzie et al. 2002) to test whether daily detection probability was related to fire-specific $PM_{2.5}$ forecasts. We also applied Poisson regression to test whether $PM_{2.5}$ influenced the number of detections per day, a proxy for activity at a finer temporal

scale. We hypothesized that wildlife behavior would be affected by smoke events, in terms of reduced activity, and we predicted that this would be indicated by lower daily detection probabilities and fewer detections per day when fire-specific $PM_{2.5}$ levels increased.

Methods

Study area

We deployed camera traps in two study areas in eastern Washington (Fig. 1). The Northeast study area (4535 km²) is predominantly owned and managed by private individuals and industrial timber companies (77%), with a smaller portion managed by the US Forest Service (USFS; 16%) and other federal and state agencies (Esri 2018). The Northeast supports populations of white-tailed deer (*Odocoileus virginianus*) and elk (*Cervus canadensis*) that occur in relatively high densities along with smaller populations of mule deer (*O. hemionus*) and moose (*Alces alces*). The predator community is primarily comprised of cougars (*Puma concolor*), black bears (*Ursus americanus*), coyotes (*Canis latrans*), bobcats (*Rufus lynx*), and gray wolves (*C. lupus*, Bassing et al. 2023; Ganz et al. 2023; Washington Department of Fish and Wildlife 2016; Washington Department of Fish and Wildlife et al. 2019). This region lies between the Selkirk and Huckleberry Mountains (elevation ranging 378–2079 m) and is dominated by mixed-conifer forests of grand fir (*Abies grandis*), Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), western hemlock (*Tsuga heterophylla*), and western red cedar (*Thuja plicata*; Williams et al. 1995). Agriculture and extensive timber harvest occur throughout the area. Lower-elevation dry forests of

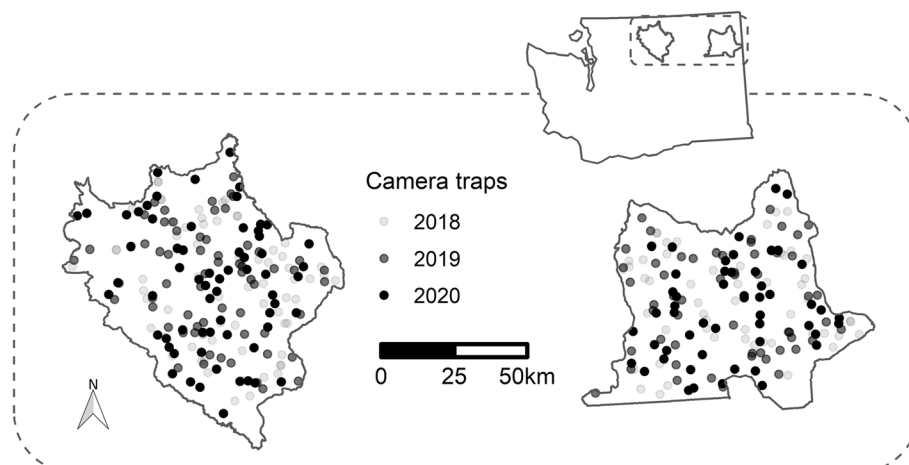


Fig. 1 Outlines of the Okanagan (left) and Northeast (right) study areas, located in the northeast corner of Washington state (top). Camera traps (dots) were placed on roads or trails in a random sampling design and were redeployed using the same design each year. Dots are shaded to represent the locations of camera traps deployed in each year of the study. Figure designed using ggplot2 (Wickham 2016), cowplot (Wilke 2020), ggson (Santos Baquero 2019), and spData (Bivand et al. 2021)

Douglas fir have a historic fire regime of frequent, low-severity fire (USDA Forest Service 2019). Current conditions after a century of fire suppression have led to closed canopy forests that are prone to stand-replacing events. At higher elevations and cooler microclimates, stands of western red cedar and western hemlock were historically and are currently typified by stand-replacing fire (USDA Forest Service 2019). During our study, one large wildfire burned near the study area: the Williams Flat Fire (44,446 acres burned) in 2019 (BLM and USFS 2018; WADNR 2019, 2020a, b).

The Okanogan study area (5300 km²) is predominantly managed by the USFS (64%), although approximately one-third is privately owned and managed by individual landowners (32%; Esri 2018). Mule deer are the primary ungulate species in this region, although white-tailed deer, moose, and elk are also present. The predator community is similar to that in the Northeast study area (Bassing et al. 2023; Ganz et al. 2023; Washington Department of Fish and Wildlife 2016; Washington Department of Fish and Wildlife et al. 2019). This region is characterized by the steep, high elevation terrain of the North Cascade Range (elevation ranging 225–2790 m; Williams and Lillybridge 1983). Forests are dominated by stands of grand fir, Douglas fir, and ponderosa pine, and open regions are dominated by big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*; Williams and Lillybridge 1983). Timber harvest and agriculture occur within the Okanogan study area, particularly in the southeastern region. Fire regimes in this region vary: dry forests of ponderosa pine were historically open and park-like, and characterized by frequent, low-intensity fires, but after a century of fire suppression have been filled in with shade-tolerant species like grand and Douglas fir which create dense stands that promote lethal crown fires (Townsend et al. 2004). Cold, moist forests in higher elevations and microclimates such as riparian areas historically had infrequent, stand-replacing wildfires (Townsend et al. 2004). This regime is still in place, but higher fuel buildups in adjacent dry forests have created the potential for unusually large crown fires (Townsend et al. 2004). Open areas of big sagebrush have moderate fire frequencies, and as fire kills sagebrush, are stand-replacing (Innes and Zouhar 2018). Compared to nearby forests, the Okanogan burns more frequently due to drier vegetation and terrain conducive to wildfire spread (Townsend et al. 2004). During our 3-year study, there were four large fires near the Okanogan study area: the Crescent Mountain Fire (21,290 hectares burned) and the McLeod Fire (9878 hectares) in 2018 which occurred within the study area boundary, and the Cold Spring Fire (76,859 hectares)

and the Pearl Hill Fire (90,540 hectares) in 2020 which occurred just east of the study area (BLM and USFS 2018; WADNR 2019, 2020a, b). The fire season in the Pacific Northwest can be as long as May–October (Bureau of Land Management n.d.), although this varies annually.

Camera trap data collection

Starting in June 2018, we deployed 120 Reconyx HyperFire2 trail cameras (Reconyx Inc., Holmen, WI) across the Northeast and Okanogan study areas (Fig. 1). Full camera deployment and image processing details are reported in Bassing et al. (2023), but briefly, we implemented a stratified random sampling design to select camera trap locations (O’Connell and Bailey 2011) by stratifying each study area into four elevation bands. To avoid sampling alpine habitat, we capped the maximum elevation in the Okanogan study area at approximately 2100 m. We randomly selected 55 and 65 one-km² grid cells within the Northeast and Okanogan study areas, respectively, by area-weighting each stratum and selecting the number of grid cells proportional to the land area within each stratum per study area. We deployed a single, unbaited camera trap within 250 m of the centroid of each selected grid cell. Following this same random sampling design, we redeployed the 120 cameras at new randomly selected locations in June 2019 and again in June 2020. Cameras were maintained for a full year before being moved to a new location.

Camera traps were placed on secondary (unpaved) roads, human-use trails, or game trails to target linear features that would funnel animal movement and increase the likelihood of detecting rarer species that occur at low densities (Cusack et al. 2015). We recorded the geographic location of each camera, as well as site-specific data including the type of linear feature monitored (road, human-use trail, or game trail), habitat type (agriculture, burned, grassland, mixed conifer, and shrub-steppe), land management type, distance to linear feature monitored, and height of camera from the ground. The cameras recorded the date and time when each photo was taken.

We processed photo-capture data using the program Timelapse2 (Greenberg et al. 2019) and the Microsoft AI for Earth machine learning algorithm (“MegaDetector”; Beery et al. 2019). We used a three-tiered approach to process images (Bassing et al. 2023). First, the MegaDetector classified the primary object in each image. Then, two independent reviewers recorded the species in each image in Timelapse2. Finally, a third expert reviewer compared the independent datasets and made corrections as needed.

Covariates

To estimate exposure to smoke at camera trap locations, we used forecasts from the High-Resolution Rapid Refresh Smoke (HRRR-Smoke) model, developed and run by the National Oceanic and Atmospheric Administration (NOAA) Global Systems Laboratory (Ahmadov et al. 2017; James et al. 2018; Dowell et al. 2022). HRRR-Smoke is a chemical transport model that uses satellite detections of fire radiative power to simulate $PM_{2.5}$ from fires at a 3-km resolution across the contiguous US. We used forecasted fire-specific $PM_{2.5}$ initialized at 00 and 12 UTC in our analysis. From these forecasts, we first extracted near-surface, fire-specific $PM_{2.5}$ at an hourly timestep. Next, we averaged these hourly smoke predictions to calculate the daily mean concentration of fire-specific $PM_{2.5}$ for each grid cell across the contiguous US, following the methods of Marlier et al. (2022). We averaged the forecasts in Python 3.7 (Van Rossum and Drake 1995) and extracted the daily mean concentrations at the location of our camera traps for each day of the study period in Google Earth Engine (Principe 2016; Gorelick et al. 2017). This approach allowed us to match the smoke data to the temporal resolution (i.e., daily) of our camera trap data. Camera traps were spaced on average 4478 m apart each year, but across the 3 years, 19 $PM_{2.5}$ grid cells were sampled more than once. We removed fire-specific $PM_{2.5}$ forecasts above the 99.9th percentile (267.9 $\mu g/m^3$) from our analysis ($n=42$), which we considered to be outliers. The $PM_{2.5}$ concentrations were extremely right-skewed, with a maximum value of 4213.3 $\mu g/m^3$. These extreme values may represent exceptionally high smoke exposure. However, as validating the extreme values was not within the scope of our study and the extreme values were sparse and large compared with other forecasts (EPA 2020), we removed them so that they did not have undue influence on parameter estimation.

We also considered the effect of daily mean air temperature, as temperatures can affect animal activity (van Beest et al. 2012). We used data from the North American Regional Reanalysis (NARR; Mesinger et al. 2006), run by the National Oceanic and Atmospheric Administration (NOAA) National Centers for Environmental Prediction (NCEP), to characterize daily weather conditions at each monitoring site. NARR data have a spatial resolution of about 32 km². NCEP reanalysis data were provided by the NOAA Physical Sciences Laboratory (PSL) in Boulder, CO, USA, from their website at <https://psl.noaa.gov/data/gridded/data.narr.html> (Mesinger et al. 2006). We used the *ncdf4* package (Pierce 2019) to extract the daily mean air temperature for each day at each site included in our analysis, following the methods

of Sanderfoot and Gardner (2021). We also included the day of the fire season to control for seasonality in animal movement and activity.

We considered several variables known to influence detection probability in our study areas (Bassing et al. 2023). Specifically, we considered the type of linear feature each camera was monitoring to control for species' preferential use of certain types of linear features. Some species, especially carnivores, prefer to use human-made linear features for transit, whereas other species avoid them (Cusack et al. 2015). The types of linear feature were simplified to "road" and "trail" for our analysis. In addition, camera height and distance to the linear feature on which the camera was placed may have differentially affected the detection of study species, as species varied substantially in body size. As a result, we included camera height and distance to linear feature to control for inherent differences in the probability that a specific species would trigger a camera trap (Hofmeester et al. 2019).

Finally, we included several additional covariates — habitat type, elevation, and distance to nearest road — to account for differences in species' preferred landscape features. We included habitat type ("conifer" or "other", recorded in the field when camera traps were deployed) and land management type ("public" or "private"). We also extracted the elevation at which each camera trap was located, using the 30-m Digital Elevation Models provided by the USGS National Map Collection (Farr et al. 2007). Distance to nearest road (major or minor) was extracted from the Washington Department of Natural Resources roads database for each study area and represented isolation from human disturbance (Washington State Department of Natural Resources 2020a). We examined the correlation between all continuous covariates and did not include variables in the same model with $|r| > 0.7$. Data management was conducted in R (R Core Team 2021), using several packages: *tidyverse* (Wickham et al. 2019), *sf* (Pebesma 2018), *raster* (Hijmans 2022), and *sp* (Pebesma and Bivand 2005).

Modeling

We used two modeling approaches to address our question: (1) a single-species, single-season occupancy model (MacKenzie et al. 2002) to test if detection probability was related to fire-specific $PM_{2.5}$ at the daily temporal scale, and (2) a Poisson regression to test if the number of detections per day (a proxy for activity at a finer temporal scale) was related to $PM_{2.5}$. For both modeling approaches, we created species-specific models and discarded observations of the same species that occurred within 30 min at an individual camera trap to reduce temporal correlation between sequential images of an animal, generating independent detection events greater

than 30 min apart (Burton et al. 2015; Sollmann 2018). For the Poisson model, we used the number of independent detections per day as the response variable. For the occupancy model, we consolidated detection data to indicate whether the species was detected at a camera trap on a daily basis. For both approaches, we combined all 3 years of data, considering each camera location to be independent. We standardized all continuous covariates by subtracting the mean and dividing by the standard deviation to allow for direct comparison of effect sizes.

We used camera trap data from July 1 to October 31 for 2018, 2019, and 2020. We did not observe any smoke events during May and June and thus did not include them to reduce seasonal variation in animal movement. We focused on large mammals with >150 detections over the course of the study which included black bears, bobcats, cougars, coyotes, elk, moose, mule deer, and white-tailed deer, but excluded wolves. 93% of mule deer detections were in the Okanagan study area, while 90% of white-tailed deer detections were in the Northeast study area. Thus, we only used detection data from those respective study areas for these two species.

We used a binary response variable for the occupancy model that indicated whether a given species was detected at least once per day during the study period (July 1–Oct 31). We created species-specific detection histories with 123 one-day sampling occasions at each camera site and combined data across all 3 years. We used R packages *camtrapR* (Niedballa et al. 2016) and *unmarked* (Fiske and Chandler 2011) to organize the data and fit the occupancy models. For each species, we specified the full model for detection probability at site i and occasion j (p_{ij}) such that:

$$\begin{aligned} \text{logit}(p_{ij}) = & \gamma_0 + \gamma_1 \times \text{day}_{ij} + \gamma_2 \times \text{day}_{ij}^2 + \gamma_3 \times \text{roadType}_i \\ & + \gamma_4 \times \text{camHeight}_i + \gamma_5 \times \text{camHeight}_i^2 \\ & + \gamma_6 \times \text{camDist}_i + \gamma_7 \times \text{camDist}_i^2 + \gamma_8 \times \text{temp}_{ij} \\ & + \gamma_9 \times \text{temp}_{ij}^2 \end{aligned}$$

where *day* is the day of the fire season, *roadType* is the type of linear feature the camera was placed on (road or trail), *camHeight* is the measured camera height, *camDist* is the distance to linear feature, and *temp* is the mean daily temperature at a site. Similarly, for each species, we specified the full model for occupancy probability at site i , ψ_i , such that:

$$\begin{aligned} \text{logit}(\psi_i) = & \alpha_0 + \alpha_1 \times \text{habType}_i + \alpha_2 \times \text{landMgmt}_i \\ & + \alpha_3 \times \text{elev}_i + \alpha_4 \times \text{elev}_i^2 + \alpha_5 \times \text{roadDist}_i \\ & + \alpha_6 \times \text{roadDist}_i^2 \end{aligned}$$

where *habType* and *landMgmt* refer to the habitat and land management types, respectively, *elev* is the elevation,

and *roadDist* is the distance to the nearest road. For model selection, we first used backwards selection from a full model without $\text{PM}_{2.5}$ to remove variables of least importance, resulting in a parsimonious model, and then added $\text{PM}_{2.5}$ to test whether wildfire smoke was significant in the resulting final model. We used this approach in order to account for other relevant variables without overfitting (Burnham and Anderson 2002). More specifically, for each species, we determined the top model by starting with a full model that did not include $\text{PM}_{2.5}$ and eliminated variables with p -values greater than 0.05 one at a time, retaining base terms for squared terms, until a model with only significant covariates and base terms emerged ($p < 0.05$). We then added $\text{PM}_{2.5}$ to the detection portion of the model and determined whether it was significant based on a 0.05 significance level. When a model did not converge, we switched optimizers in *unmarked*. We used the “BFGS” optimizer for bobcats, elk, and moose. BFGS did not result in convergence for the black bear, cougar, or coyote models, so we used “L-BFGS-B” instead. White-tailed deer and mule deer had occupancy rates near one, so we did not include occupancy models for these species.

For the Poisson model, we used the number of detections per day as the response variable. For each species, we included all covariates in the full model for the expected number of detections, λ_{ij} , for each site i and occasion j :

$$\begin{aligned} \log(\lambda_{ij}) = & \beta_{0,i} + \beta_1 \times \text{day}_{ij} + \beta_2 \times \text{day}_{ij}^2 + \beta_3 \times \text{roadType}_i \\ & + \beta_4 \times \text{camHeight}_i + \beta_5 \times \text{camHeight}_i^2 \\ & + \beta_6 \times \text{camDist}_i + \beta_7 \times \text{camDist}_i^2 \\ & + \beta_8 \times \text{temp}_{ij} + \beta_9 \times \text{temp}_{ij}^2 + \beta_{10} \times \text{habType}_i \\ & + \beta_{11} \times \text{landMgmt}_i + \beta_{12} \times \text{elev}_i + \beta_{13} \times \text{elev}_i^2 \\ & + \beta_{14} \times \text{roadDist}_i + \beta_{15} \times \text{roadDist}_i^2 \end{aligned}$$

We included a random intercept ($\beta_{0,i}$, where $\beta_{0,i} \sim \text{Normal}(\beta_0, \sigma^2)$) by camera trap site to account for site variability and repeated observations at the site; however, we did not include a year effect, as cameras sampled different locations each year. We used the “bobyqa” optimizer from the *lme4* package in R to fit models (Bates et al. 2015). We used the same model selection process as in the occupancy models.

Results

The mean fire-specific $\text{PM}_{2.5}$ level at our camera traps during our study period was $6.597 \mu\text{g}/\text{m}^3$, with a standard deviation of $21.247 \mu\text{g}/\text{m}^3$. Sharp spikes in $\text{PM}_{2.5}$ concentrations highlight the acute nature of wildfire smoke events (Fig. 2). On 3.6% of camera trap days, for which

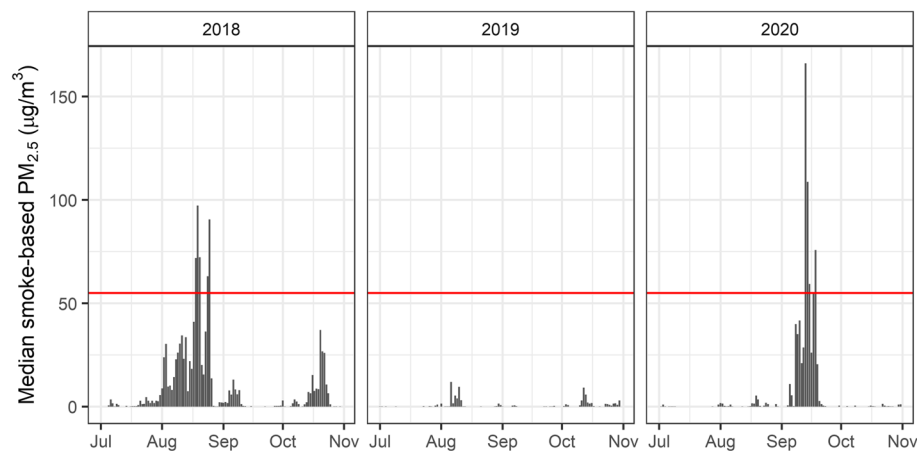


Fig. 2 Daily median fire-specific surface-level $\text{PM}_{2.5}$ concentration ($\mu\text{g}/\text{m}^3$) at active camera traps during the eastern Washington fire season. Forecasts were generated by the High-Resolution Rapid Refresh Smoke (HRRR-Smoke) chemical transport model, which uses satellite detection of fire radiative power to simulate $\text{PM}_{2.5}$ from fires at a 3-km radius. Twice-daily forecasts were averaged to arrive at a daily mean concentration of fire-specific $\text{PM}_{2.5}$ at each camera trap location. The median of the daily mean $\text{PM}_{2.5}$ value at each camera trap is presented here. For reference, we included the $\text{PM}_{2.5}$ threshold considered unhealthy by public health standards (red line, $55.5 \mu\text{g}/\text{m}^3$). Note that our study area is primarily rural and not highly developed; as such, sources of $\text{PM}_{2.5}$ other than smoke are negligible. Figure designed using `ggplot2` (Wickham 2016)

25% of camera traps were represented, $\text{PM}_{2.5}$ concentrations were greater than the concentration classified as unhealthy by the US Environmental Protection Agency ($55.5 \mu\text{g}/\text{m}^3$, EPA 2012).

The effect of fire specific $\text{PM}_{2.5}$ differed among species and between the two temporal scales of the detection response variables (Table 1). While we found no evidence that $\text{PM}_{2.5}$ was related to the probability of daily detection in the occupancy models for any species, we did find evidence that $\text{PM}_{2.5}$ influenced number of detections per day in the Poisson models for bobcats, moose, and mule deer (Table 1). We found a marginally significant, 12.9% decrease in the expected number of bobcat detections per day for each standard deviation increase in $\text{PM}_{2.5}$ ($21.247 \mu\text{g}/\text{m}^3$, $p=0.066$, Table 1, Fig. 3, Supplementary table 4). For moose, we found an 11.2% decrease in the expected number of moose detections per day for each standard deviation increase in $\text{PM}_{2.5}$ ($p=0.043$, Table 1, Supplementary table 12, Fig. 3). Lastly, for mule deer, we found a 5.8% increase in the expected number of detections per day for each standard deviation increase in $\text{PM}_{2.5}$ ($p=0.007$, Table 1, Supplementary table 13, Fig. 4). However, the size of the effect of $\text{PM}_{2.5}$ was small for all species and models, except in the Poisson model for bobcats, where it was comparable to other covariates in the top model—the coefficient for $\text{PM}_{2.5}$ was -0.138 , while other coefficients ranged from -0.081 (temperature) to -0.859 (habitat type, Supplementary table 4).

We found a number of significant effects of covariates other than $\text{PM}_{2.5}$ on occupancy and detection for the daily detection (Supplementary Tables 1, 3, 5, 7, 9, and

11) and number of detections per day (Supplementary Tables 2, 4, 6, 8, 10, 12, 13 and 14) response variables. In the occupancy models, elevation was a statistically significant predictor of occupancy for all species except cougars (Table 1), although the direction and magnitude varied by species. Road type was an important predictor of detection for all species except elk and, consistently, detection was lower on trails than on roads. In the Poisson regression models, elevation and day of the fire season were both important predictors of number of detections per day for the majority of species (Table 1).

Discussion

This study is the first to use camera trap data to link population-level activity patterns with wildfire smoke events. We hypothesized that mammals would exhibit reduced activity as smoke intensified, due to underlying health effects, which would be observable via decreased camera trap detection rates. Contrary to our expectations, we found little to no evidence of this for most species; however, we did find support for our hypothesis for detections per day for bobcat and moose. Surprisingly, mule deer showed small, positive effects of $\text{PM}_{2.5}$ on detections per day. Fire-specific $\text{PM}_{2.5}$ did not influence the detection of five of our eight species: black bears, cougars, coyotes, elk, or white-tailed deer. Known drivers of mammalian distributions (i.e., elevation) and detection probabilities (i.e., day of fire season, road type, and camera height) were consistently included in our top models. While effects of $\text{PM}_{2.5}$ from smoke were often smaller than the effects of other covariates, this was not always

Table 1 Summary of results for top models plus $PM_{2.5}$, with $PM_{2.5}$ coefficient, standard error, and p -value for each species and model. One standard deviation in $PM_{2.5}$ is equivalent to $30.0 \mu g/m^3$. Ψ refers to occupancy covariates, and p refers to detection covariates for the occupancy model. $camDist$ indicates the distance from the camera to the linear feature it was placed on, while $roadDist$ indicates the distance from the camera to the nearest road in the WADNR roads database. Significant p -values (< 0.05) for the effect of $PM_{2.5}$ are indicated with a **, while marginally significant p -values (< 0.1) are indicated with a *. N refers to number of detections for each species in our dataset; ST indicates the number of the Supplementary table containing the parameter estimates for the model. All Poisson models include the camera site ID as a random intercept

Species	Model type	Covariates	$PM_{2.5}$	SE	P -value
Bear, $n = 902$	Occupancy ST 1	$\Psi(elev + elev^2)$, $p(day + day^2 + roadType + camHeight + temp + PM_{2.5})$	-0.057	0.039	0.142
	Poisson ST 2	$day + day^2 + roadType + elev + elev^2 + PM_{2.5}$	-0.031	0.036	0.388
Bobcat, $n = 400$	Occupancy ST 3	$\Psi(habType + elev + roadDist + roadDist^2)$, $p(day + day^2 + roadType + camHeight + camHeight^2 + camDist + temp + temp^2 + PM_{2.5})$	-0.067	0.063	0.289
	Poisson ST 4	$day + day^2 + roadType + camDist + camDist^2 + temp + temp^2 + habType + elev + PM_{2.5}$	-0.138	0.075	0.066*
Cougar, $n = 293$	Occupancy ST 5	$\Psi(habType)$, $p(roadType + camDist + PM_{2.5})$	-0.043	0.066	0.519
	Poisson ST 6	$roadType + habType + PM_{2.5}$	-0.005	0.057	0.936
Coyote, $n = 1825$	Occupancy ST 7	$\Psi(habType + elev + elev^2 + roadDist + roadDist^2)$, $p(roadType + camHeight + camHeight^2 + PM_{2.5})$	0.003	0.026	0.903
	Poisson ST 8	$day + day^2 + roadType + habType + elev + elev^2 + roadDist + PM_{2.5}$	-0.011	0.024	0.634
Elk, $n = 279$	Occupancy ST 9	$\Psi(habType + elev + elev^2)$, $p(camHeight + camHeight^2 + camDist + camDist^2 + temp + PM_{2.5})$	0.052	0.050	0.298
	Poisson ST 10	$day + day^2 + habType + landMgmt + elev + elev^2 + PM_{2.5}$	0.052	0.043	0.227
Moose, $n = 584$	Occupancy ST 11	$\Psi(elev + elev^2 + roadDist)$, $p(roadType + camHeight + camHeight^2 + camDist + camDist^2 + PM_{2.5})$	-0.064	0.055	0.241
	Poisson ST 12	$roadType + elev + elev^2 + roadDist + PM_{2.5}$	-0.119	0.059	0.043**
Mule deer, $n = 2710$	Poisson ST 13	$day + day^2 + temp + temp^2 + PM_{2.5}$	0.056	0.021	0.007**
White-tailed deer, $n = 4019$	Poisson ST 14	$day + camDist + camDist^2 + temp + temp^2 + elev + elev^2 + PM_{2.5}$	-0.018	0.018	0.300

the case, as the effect for bobcats was comparable to the effects of other significant variables. Our results demonstrate that mammals exhibit species-specific behavioral responses to wildfire smoke which can be observed via changes in detection rates, suggesting smoke is an environmental stressor in mammalian communities.

Moose detections per day exhibited a negative response to $PM_{2.5}$, implying that their known sensitivity to environmental extremes may extend to wildfire smoke. Moose are at the edge of their geographic range in Eastern Washington and are known to be sensitive to other environmental extremes, namely high temperatures. Captive moose can become heat stressed above $17\text{--}24^\circ\text{C}$ (McCann et al. 2013) and wild moose likely have similar thermal limitations. Moose tend to modify their activity during times of excessive heat by becoming less active during the hottest part of the day, more active during twilight and night, and selecting thermal refuges in hot

afternoons (Dussault et al. 2004; Street et al. 2016; Montgomery et al. 2019). During our study, the average temperature was above the range in which moose become heat stressed for 3.8–33.8% of days across camera trap sites, although we observed no effect of temperature on moose detections. Temperature and $PM_{2.5}$ levels were not correlated (Pearson's correlation coefficient = 0.099), indicating that the $PM_{2.5}$ effect we observed was independent of any heat sensitivity effects. Since moose are already thermally stressed at the southern range of their distribution, it is plausible they may be more sensitive to other environmental stressors, like wildfire smoke, leading to behavioral responses that reduce their detection rates.

We used detection rate as a proxy for mammalian activity, with lower detection rates indicating a decrease in activity. However, some animals may increase their activity to engage in fire or smoke avoidance behaviors

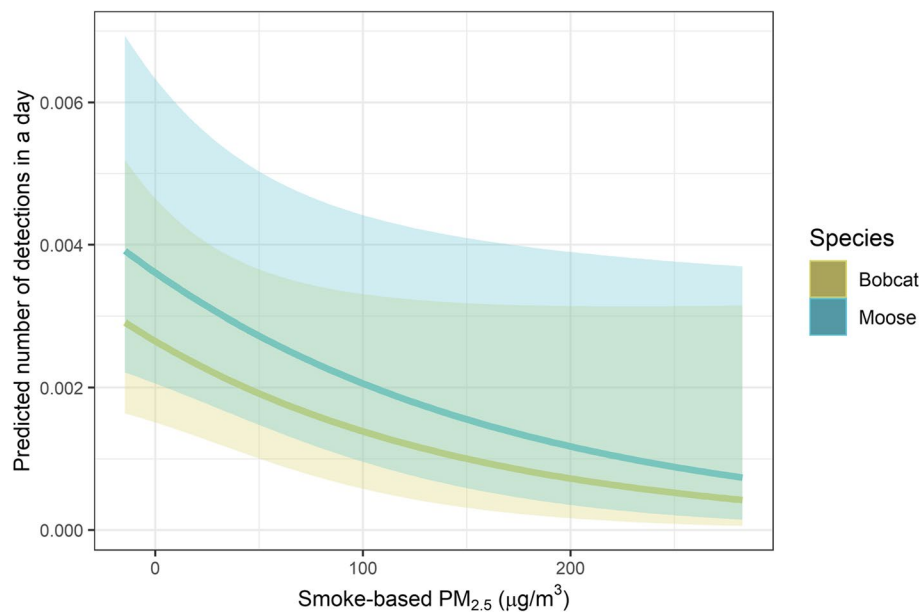


Fig. 3 Predicted number of detections per day for a range of $PM_{2.5}$ concentrations ($\mu g/m^3$) for bobcat and moose. Solid lines represent mean values predicted by the top model, accounting for variance from fixed effects only. All covariates were held at their averages and estimates were averaged across factor levels. Shaded ribbons represent 95% confidence intervals. Figure designed using *ggplot2* (Wickham 2016); color palette provided by Pedersen and Cramer (2021)

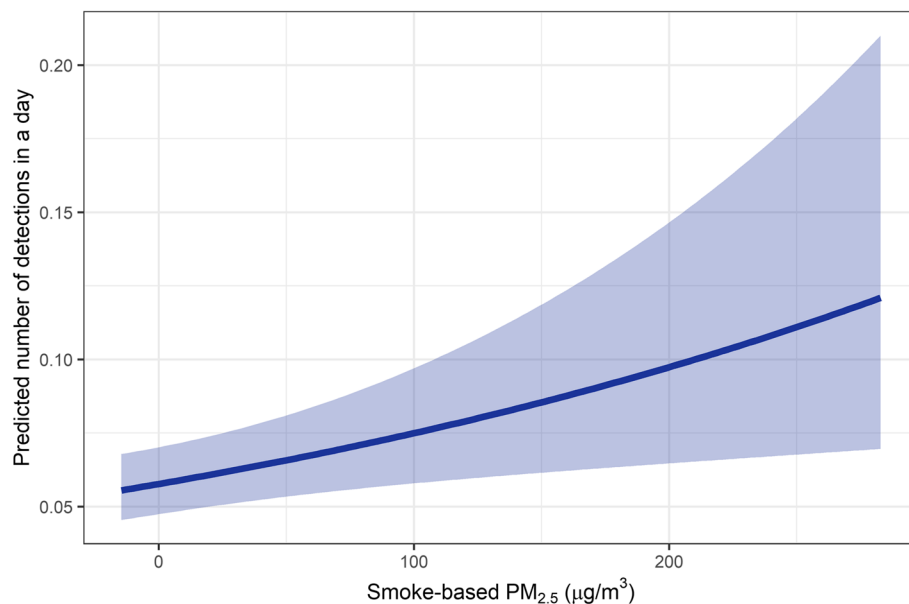


Fig. 4 Predicted number of detections per day for a range of $PM_{2.5}$ concentrations ($\mu g/m^3$) for mule deer. The solid line represent mean values predicted by the top model, accounting for variance from fixed effects only. All covariates were held at their averages and estimates were averaged across factor levels. The solid ribbon represent 95% confidence intervals. Figure designed using *ggplot2* (Wickham 2016); color palette provided by Pedersen and Cramer (2021)

(Sanderfoot et al. 2022), which could increase detection rates. For example, we found a small positive effect of $PM_{2.5}$ on detections per day of mule deer. Mule deer

migrate to lower elevations in the fall (Kucera 1992), which typically occurs from mid-October to mid-November in the Okanogan study area (Ganz et al. 2023).

Given that our study period (July 1–October 31) partially overlapped with fall migration, it is possible the $PM_{2.5}$ effect was confounded with migratory behaviors. However, we think this is unlikely, as day of the fire season and smoke $PM_{2.5}$ were not correlated (Pearson's correlation coefficient = -0.018). Instead, it is likely that mule deer are responding to their environment changing as a result of smoke, for example, moving more potentially to avoid predators if visual or olfactory cues of predation risk are affected by smoke. As wildfire activity increases, wildlife may be forced to engage in smoke avoidance behaviors more often, resulting in higher costs of navigation (Hegedüs et al. 2007; Overton et al. 2022), foraging (Cho et al. 2021), vigilance, and other behaviors.

Modeling the effect of $PM_{2.5}$ on both daily detection and detections per day allowed us to consider which scale may be most useful in assessing impacts of wildfire smoke on mammalian behavior. We observed responses to smoke in the number of detections per day for bobcats, moose, and mule deer in the Poisson regression, but we observed no response to smoke in daily detection probabilities, suggesting that monitoring animal activity at finer temporal resolutions may be necessary to evaluate effects of smoke on animal behavior. Our occupancy models, which reduced data to just a binary indicator of whether a species was detected at least once per day, may have been too temporally coarse to reveal changes in behavioral activity for most of our focal species. Instead of detection/non-detection data at the daily scale, numbers of individuals, travel speed, or behaviors such as climbing or vigilance could be estimated from camera trap photos (Rowcliffe et al. 2016; Stewart et al. 2016; Schuttler et al. 2017). Additionally, other sources of animal movement data, such as GPS tracking, may enable ecologists to directly tie smoke exposure to changes in animal behavior at a finer scale (Stewart et al. 2018).

One challenge, particularly for wildlife research which is often conducted in remote areas, is acquiring reliable smoke ($PM_{2.5}$) data. Our study area had very few EPA Air Quality System monitors, which are a commonly used, high-quality source of $PM_{2.5}$ concentrations (Diao et al. 2019). The monitors ranged from 4 to 450 km from our camera locations. Thus, we needed another way to characterize smoke levels during our study. HRRR-Smoke is a relatively new tool for real-time smoke monitoring that supports high-quality forecasts of $PM_{2.5}$ from fires at a fine spatial (3 km) and temporal (hourly) resolution. It has been used to inform public health (Marlier et al. 2022) and wildlife science (Overton et al. 2022) applications. While HRRR-Smoke only provides simulated values of smoke $PM_{2.5}$, existing comparisons to ground-based measurements demonstrate that HRRR-Smoke effectively captures the distribution and intensity

of smoke plumes (Chow et al. 2022). However, HRRR-Smoke may underestimate $PM_{2.5}$ due to the limited availability of sub-daily measurements of fire radiative power collected by polar-orbiting satellites (Chow et al. 2022). Therefore, by relying on forecasts from HRRR-Smoke, we may have underestimated the effect of smoke in our analysis. There were also some unvalidated extreme values in the HRRR smoke forecasts which we removed but may have represented high $PM_{2.5}$ concentrations. It is likely that wildlife responses are more extreme in the rare but increasingly common cases when $PM_{2.5}$ is catastrophically high during the fire season. For example, when tule geese encountered average $PM_{2.5}$ concentrations of $161 \mu\text{g}/\text{m}^3$ during migration, they stopped or went in other directions (Overton et al. 2022). Additionally, the small number of camera-trap days with very high $PM_{2.5}$ levels likely limited our ability to detect a relationship between animal activity and wildfire smoke, despite the extensive camera-trap dataset we used. Model development for simulating fire behavior and smoke plumes is an active area of research in atmospheric science, with different products designed to meet specific stakeholder needs and minimize diverse types of uncertainty.

Our results show that multiple study species exhibited changes in detection rates on smoky days; however, our hypothesis that animal activity would be reduced with increasing smoke levels was generally not supported. While we noted some issues in detecting responses to $PM_{2.5}$ concentrations in our dataset above, it is also possible that we did not observe responses because the animals in our study did not change their movement and behavior in response to smoke. This suggests that the immediate effects of increased smoke (e.g., health effects or changes to olfactory cues) do not impact these species' behavior. This could be a result of tradeoffs with factors such as dietary requirements or predator-prey interactions that prevent wildlife from modifying their behavior in response to smoke events. Alternatively, this could indicate that smoke is not as important of a factor for wildlife populations as other direct and indirect effects of fire (Engstrom 2010; Jolly et al. 2022). However, we caution that while we did not find much support for our hypothesis, which focused on short-term effects of smoke exposure, the long-term effects of increased $PM_{2.5}$ levels on wildlife populations which were not observable in this study may be of greater consequence. Smoke exposure has been found to be energetically costly for free-living wildlife species including orangutans (Erb et al. 2018), geese (Overton et al. 2022), and bees (Cho et al. 2021) and is likely to increase susceptibility to disease (Albery et al. 2021). In addition, Black et al. (2017) found that captive rhesus macaque monkeys exposed to elevated smoke levels (about 2 weeks during infancy) developed

immune dysfunction, which resulted in reduced lung volume and capacity in adulthood (Bassein et al. 2019). We recommend that future studies directly examine fitness outcomes that result from smoke exposure by connecting survival or reproductive success to individual, marked animals' exposure to smoke pollution.

Wildlife responses to wildfire smoke is an emerging question in ecology (Sanderfoot et al. 2022), and for most of our study species, we were unable to find research to contextualize our results. For example, we did not find relevant literature on bobcat responses to wildfire smoke even though this was the species where we observed the largest effect size. Even studies looking at direct effects of fire on wildlife mortality are lacking (Jolly et al. 2022). Climate change is expected to intensify fire and thus smoke, influencing the health and behavior of wildlife in myriad ways (Engstrom 2010; Erb et al. 2018; Overton et al. 2022; Cho et al. 2021; Sanderfoot et al. 2022), and more research is urgently needed to quantify the magnitude of these effects and to inform conservation.

Conclusions

Our results suggested that some mammals alter their behavior in response to smoke exposure, possibly due to underlying health effects or changes in environmental cues. Importantly, we demonstrated how combining relatively inexpensive wildlife sampling methods (i.e., camera traps) with large-scale smoke data (i.e., fire-specific PM_{2.5} concentrations) can be effective for studying some of the effects of smoke on wildlife populations. Finally, our study adds to limited research on smoke impacts on wildlife and emphasizes the need to rapidly expand research in this area to inform wildlife conservation (Lee et al. 2017; Erb et al. 2018; Sanderfoot and Gardner 2021).

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-023-00207-1>.

Additional file 1: Supplementary tables.

Acknowledgements

Many thanks to Morgan Delgado, Brielle Jaglowski, Parker Levinson, Nate Rice, and Trent Roussin, who deployed and maintained camera traps, and to the 111 undergraduate students at the University of Washington who assisted in processing images collected by camera traps. We also thank the Washington Predator-Prey Project, as well as biologists with the WDFW, the Washington Department of Natural Resources, and the US Forest Service, for facilitating data collection. We also acknowledge the large team which contributed to the development and operational implementation of the HRRR-smoke model during 2016–2020. We also acknowledge two anonymous reviewers whose feedback greatly improved this paper.

Authors' contributions

JA analyzed and interpreted the data, wrote the initial manuscript, and reviewed and edited drafts. RLE, SBB, OVS, and BG conceptualized and designed the study, planned methodology, reviewed and edited drafts, and

provided advice. SBB also performed camera trap fieldwork and managed image processing. AK, SR, EJ, and RA acquired and processed the HRRR-Smoke data and reviewed and edited drafts.

Authors' information

RLE's contributions to this manuscript occurred while he was employed by the University of Washington and Illinois Natural History Survey, prior to his employment by the US Department of Agriculture, National Agricultural Statistics Service.

Funding

Funding was provided by the Washington Department of Fish and Wildlife (WDFW), the Washington State Legislature, Federal Aid in Wildlife Restoration Grant no. F16AF00910, WDFW Aquatic Lands Enhancement Account no. 19-13500, the McIntire-Stennis Cooperative Forestry Research Program (Grant No. NI19MSCFRXXG035/Project Accession No. 1020586) from the USDA National Institute of Food and Agriculture, and the Carleton Class of 1963 fellowship. Support for the development of the HRRR-smoke was provided by the NOAA Joint Polar Satellite System (JPSS) Proving Ground and Risk Reduction Program.

Availability of data and materials

The following data supporting this research are sensitive and not available publicly: coordinates of camera trap locations. Complete data are available to qualified researchers from the Wildlife Chief Scientist of the Washington Department of Fish and Wildlife by contacting (360) 902-2515. Final datasets used for modeling, as well as code used in data cleaning, model construction, and model selection, and raw data with specific locations of camera traps removed, are available on GitHub at <https://github.com/jayars99/wildfire-smoke-camera-traps-public>.

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.

Author details

¹Department of Biology, University of New Mexico, Albuquerque, NM, USA. ²National Agricultural Statistics Service, US Department of Agriculture, Washington, DC, USA. ³School of Environmental and Forest Sciences, University of Washington, Seattle, WA, USA. ⁴Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA, USA. ⁵Department of Environmental Health Sciences, Fielding School of Public Health, University of California, Los Angeles, Los Angeles, CA, USA. ⁶Northeast States for Coordinated Air Use Management, Boston, MA, USA. ⁷Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, Boulder, CO, USA. ⁸NOAA Global Systems Laboratory, Boulder, CO, USA.

Received: 24 August 2022 Accepted: 20 July 2023

Published online: 24 August 2023

References

- Abatzoglou, John T., and A. Park Williams. 2016. Impact of anthropogenic climate change on wildfire across Western US forests. *Proceedings of the National Academy of Sciences* 113 (42): 11770–11775. <https://doi.org/10.1073/pnas.1607171113>.
- Ahmadov, Ravan, Georg Grell, Eric James, Ivan Csiszar, M. Tsidulko, B. Pierce, S. McKeen, et al. 2017. Using VIIRS fire radiative power data to simulate biomass burning emissions, plume rise and smoke transport in a real-time air quality modeling system. In *2017 IEEE International Geoscience*

- and Remote Sensing Symposium (IGARSS) 2806–8. <https://doi.org/10.1109/IGARSS.2017.8127581>.
- Albery, Gregory F., Isabella Turilli, Maxwell B. Joseph, Janet Foley, Celine H. Frere, and Shweta Bansal. 2021. From flames to inflammation: How wildfires affect patterns of wildlife disease. *Fire Ecology* 17 (1): 23. <https://doi.org/10.1186/s42408-021-00113-4>.
- Anderson, Ashly, Pedram Rezamad, and Amy L. Skibiel. 2022. Effects of wildfire smoke exposure on innate immunity, metabolism, and milk production in lactating dairy cows. *Journal of Dairy Science* 105 (8): 7047–7060. <https://doi.org/10.3168/jds.2022-22135>.
- Apfelbach, Raimund, Caroline D. Blanchard, Robert J. Blanchard, R. Andrew Hayes, and Iain S. McGregor. 2005. The effects of predator odors in mammalian prey species: A review of field and laboratory studies. *Neuroscience & Biobehavioral Reviews* 29 (8): 1123–1144. <https://doi.org/10.1016/j.neubiorev.2005.05.005>.
- Bassein, Jed, Ganesh, Sandya, Pena-Ponce, Myra Dela, Backer, Jan De, Lanclus, Maarten, Belmans, Dennis, Holsbeke, Cedric Van, and Miller, Lisa. 2019. Wildfire Smoke Exposure During Infancy Results in Impaired Lung Function. *European Respiratory Journal* 54(suppl 63). <https://doi.org/10.1183/13993003.congress-2019.PA2830>.
- Bassing, Sarah B., Melia DeVivo, Taylor R. Ganz, Brian N. Kertson, Laura R. Prugh, Trent Roussin, Lauren Satterfield, Rebecca M. Windell, Aaron J. Wirsing, and Beth Gardner. 2023. Are we telling the same story? Comparing inferences made from camera trap and telemetry data for wildlife monitoring. *Ecological Applications* In Press. <https://doi.org/10.1002/eap.2745>.
- Bates, Douglas, Martin Mächler, Ben Bolker, and Steve Walker. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67(October): 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Beery, Sara, Dan Morris, and Siyu Yang. 2019. Efficient pipeline for camera trap image review. *arXiv:1907.06772*. *arXiv*. <https://doi.org/10.48550/arXiv.1907.06772>.
- Bivand, Roger, Jakub Nowosad, and Robin Lovelace. 2021. *spData: Datasets for spatial analysis. R package version 2.0.1*. <https://CRAN.R-project.org/package=spData>.
- Black, Carolyn, Joan E. Gerriets, Justin H. Fontaine, Richard W. Harper, Nicholas J. Kenyon, Fern Tablin, Edward S. Schelegle, and Lisa A. Miller. 2017. Early life wildfire smoke exposure is associated with immune dysregulation and lung function decrements in adolescence. *American Journal of Respiratory Cell and Molecular Biology* 56 (5): 657–666. <https://doi.org/10.1165/rcmb.2016-0380OC>.
- Bureau of Land Management and USDA Forest Service. 2018. *2018 Pacific Northwest wildland fire season summary of key events and issues*. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fseprd611322.pdf. Accessed 27 Nov 2021.
- Bureau of Land Management. 2017. *Programs: Public Safety and Fire: Fire: State Info*. Oregon/Washington Fire Service | Bureau of Land Management. Retrieved July 7, 2023, from <https://www.blm.gov/orwafire>.
- Burnham, Kenneth P., and David R. Anderson. 2002. *Model selection and multimodel inference: A practical information-theoretical approach*, 2nd ed. New York: Springer-Verlag.
- Burton, A. Cole, Eric Neilson, Dario Moreira, Andrew Ladle, Robin Steenweg, Jason T. Fisher, Erin Bayne, and Stan Boutin. 2015. REVIEW: Wildlife camera trapping: A review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology* 52 (3): 675–685. <https://doi.org/10.1111/1365-2664.12432>.
- Chen, Gongbo, Yuming Guo, Xu Yue, Shilu Tong, Antonio Gasparrini, Michelle L. Bell, Ben Armstrong, et al. 2021. Mortality risk attributable to wildfire-related PM_{2.5} pollution: A global time series study in 749 locations. *The Lancet Planetary Health* 5 (9): e579–87. [https://doi.org/10.1016/S2542-5196\(21\)00200-X](https://doi.org/10.1016/S2542-5196(21)00200-X).
- Cheyne, Susan M. 2008. Effects of meteorology, astronomical variables, location and human disturbance on the singing apes: *Hylobates albibarbis*. *American Journal of Primatology* 70 (4): 386–392. <https://doi.org/10.1002/ajp.20502>.
- Cho, Yoori, Sujong Jeong, Dowon Lee, Sang-Woo Kim, Rokjin J. Park, Luke Gibson, Chunmiao Zheng, and Chan-Ryul Park. 2021. Foraging trip duration of honeybee increases during a poor air quality episode and the increase persists thereafter. *Ecology and Evolution* 11 (4): 1492–1500. <https://doi.org/10.1002/ece3.7145>.
- Chow, Fontini K., Katelyn A. Yu, Alexander Young, Eric James, Georg A. Grell, Ivan Csiszar, Marina Tsidulko, Saulo Freitas, Gabriel Pereira, Louis Giglio, Mariel D. Friberg, and Ravan Ahmadov. 2022. High-resolution smoke forecasting for the 2018 Camp Fire in California. *Bulletin of the American Meteorological Society* 103 (6): e1531–1552. <https://doi.org/10.1175/BAMS-D-20-0329.1>.
- Cox, Bianca, Antonio Gasparrini, Boudewijn Catry, Frans Fierens, Jaco Vangronsveld, and Tim S. Nawrot. 2016. Ambient air pollution-related mortality in dairy cattle: Does it corroborate human findings? *Epidemiology* 27 (6): 779–786. <https://doi.org/10.1097/EDE.0000000000000545>.
- Cusack, Jeremy J., Amy J. Dickman, J. Marcus Rowcliffe, Chris Carbone, David W. Macdonald, and Tim Coulson. 2015. Random versus game trail-based camera trap placement strategy for monitoring terrestrial mammal communities. *PLoS One* 10 (5): e0126373. <https://doi.org/10.1371/journal.pone.0126373>.
- Diao, Minghui, Tracey Holloway, Seohyun Choi, Susan M. O'Neill, Mohammad Z. Al-Hamdan, Aaron Van Donkelaar, Randall V. Martin, et al. 2019. Methods, availability, and applications of PM_{2.5} exposure estimates derived from ground measurements, satellite, and atmospheric models. *Journal of the Air & Waste Management Association* 69 (12): 1391–1414. <https://doi.org/10.1080/10962247.2019.1668498>.
- Dickinson, Matthew B., Michael J. Lacki, and Daniel R. Cox. 2009. Fire and the endangered Indiana bat. *Proceedings of the 3rd Fire in Eastern Oak Forests Conference; 2008 May 20–22; Carbondale, IL. Gen. Tech. Rep. NRS-P-46*, ed. Todd F. Hutchinson, 51–75. Newtown Square: U.S. Department of Agriculture, Forest Service, Northern Research Station. p-46. <https://www.fs.usda.gov/treesearch/pubs/17291>.
- Dowell, David C., Curtis R. Alexander, Eric P. James, Stephen S. Weygandt, Stanley G. Benjamin, Geoffrey S. Manikin, Benjamin T. Blake, et al. 2022. The High-Resolution Rapid Refresh (HRRR): An hourly updating convection-allowing forecast model. Part I: Motivation and system description. *Weather and Forecasting* 37 (8): 1371–95. <https://doi.org/10.1175/WAF-D-21-0151.1>.
- Drobatz, Kenneth J., L.M. Walker, and Joan C. Hendricks. 1999a. Smoke exposure in cats: 22 cases (1986–1997). *Journal of the American Veterinary Medical Association* 215 (9): 1312–1316.
- Drobatz, Kenneth J., L.M. Walker, and Joan C. Hendricks. 1999b. Smoke exposure in dogs: 27 cases (1988–1997). *Journal of the American Veterinary Medical Association* 215 (9): 1306–1311.
- Dussault, Christian, Jean-Pierre Ouellet, Réhaume Courtois, Jean Huot, Laurier Breton, and Jacques Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. *Écoscience* 11 (3): 321–328. <https://doi.org/10.1080/11956860.2004.11682839>.
- Egberts, V., G. van Schaik, B. Brunekreef, and G. Hoek. 2019. Short-term effects of air pollution and temperature on cattle mortality in the Netherlands. *Preventive Veterinary Medicine* 168 (July): 1–8. <https://doi.org/10.1016/j.prevetmed.2019.03.021>.
- Engstrom, R. Todd. 2010. First-order fire effects on animals: Review and recommendations. *Fire Ecology* 6 (1): Article 1. <https://doi.org/10.4996/fireecology.0601115>.
- Erb, Wendy M., Elizabeth J. Barrow, Alexandra N. Hofner, Sri Suci Utami-Atmoko, and Erin R. Vogel. 2018. Wildfire smoke impacts activity and energetics of wild Bornean orangutans. *Scientific Reports* 8 (1): 7606. <https://doi.org/10.1038/s41598-018-25847-1>.
- Esri. 2018. National Atlas of the United States, and United States Geological Survey. Redlands: Washington State Public Lands.
- Farr, Tom G., Paul A. Rosen, Edward Caro, Robert Crippen, Riley Duren, Scott Hensley, Michael Kobrick, et al. 2007. The shuttle radar topography mission. *Reviews of Geophysics* 45 (2). <https://doi.org/10.1029/2005RG000183>.
- Finnerty, Patrick B., Clare McArthur, Peter Banks, Catherine Price, and Adrian M. Shrader. 2022. The olfactory landscape concept: A key source of past, present, and future information driving animal movement and decision-making. *BioScience* 72 (8): 745–752. <https://doi.org/10.1093/biosci/biac039>.
- Fiske, Ian, and Richard Chandler. 2011. *Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance*. *Journal of Statistical Software* 43 (August): 1–23. <https://doi.org/10.18637/jss.v043.i10>.

- Garvey, Patrick M., Alistair S. Glen, Margaret N. Clout, Sarah V. Wyse, M. Nichols, and Roger P. Pech. 2017. Exploiting interspecific olfactory communication to monitor predators. *Ecological Applications* 27 (2): 389–402. <https://doi.org/10.1002/eap.1483>.
- Ganz, Taylor R., Melia T. DeVivo, Ellen M. Reese, and Laura R. Prugh. 2023. Wildlife whodunnit: forensic identification of predators to inform wildlife management and conservation. *Wildlife Society Bulletin* 47(1) <https://doi.org/10.1002/wsb.v47.110.1002/wsb.1386>.
- Geiser, Fritz, Clare Stawski, Anna C. Doty, Christine E. Cooper, and Julia Nowack. 2018. A burning question: what are the risks and benefits of mammalian torpor during and after fires? *Conservation Physiology* 6 (1). <https://doi.org/10.1093/conphys/coy057>.
- Gorelick, Noel, Matt Hancher, Mike Dixon, Simon Ilyushchenko, David Thau, and Rebecca Moore. 2017. Google Earth Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*. <https://doi.org/10.1016/j.rse.2017.06.031>.
- Greenberg, Saul, Theresa Godin, and Jesse Whittington. 2019. Design patterns for wildlife-related camera trap image analysis. *Ecology and Evolution* 9 (24): 13706–13730. <https://doi.org/10.1002/ece3.5767>.
- Hegedűs, Ramón, Susanne Åkesson, and Gábor Horváth. 2007. Anomalous celestial polarization caused by forest fire smoke: Why do some insects become visually disoriented under smoky skies? *Applied Optics* 46 (14): 2717–2726. <https://doi.org/10.1364/AO.46.002717>.
- Hijmans, Robert J. 2022. *raster*: geographic data analysis and modeling. R package version 3.5-15. <https://CRAN.R-project.org/package=raster>.
- Hofmeester, Tim R., Joris P.G.M. Cromsigt, John Odden, Henrik Andrén, Jonas Kindberg, and John D.C. Linnell. 2019. Framing pictures: A conceptual framework to identify and correct for biases in detection probability of camera traps enabling multi-species comparison. *Ecology and Evolution* 9 (4): 2320–2336. <https://doi.org/10.1002/ece3.4878>.
- Hovick, Torre J., Devan A. McGranahan, R. Dwayne Elmore, John R. Weir, and Samuel D. Fuhlendorf. 2017. Pyric-carnivory: Raptor use of prescribed fires. *Ecology and Evolution* 7 (21): 9144–9150. <https://doi.org/10.1002/ece3.3401>.
- Hughes, Nelika K., Catherine J. Price, and Peter B. Banks. 2010. Predators are attracted to the olfactory signals of prey. *PLoS One* 5 (9): e13114. <https://doi.org/10.1371/journal.pone.0013114>.
- Innes, Robin J., and Kris Zouhar. 2018. Fire regimes of mountain big sagebrush communities. In *Fire effects information system*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory (Producer). Available: https://www.fs.usda.gov/database/feis/fire_regimes/mountain_big_sagebrush/all.html [2023, June 22].
- James, Eric, Ravan Ahmadov, and Georg A. Grell. 2018. Realtime wildfire smoke prediction in the United States: The HRRR-Smoke model. In *Proceedings of the EGU General Assembly Conference*, 19526.
- Jetz, Walter, Jan Steffen, and Karl E. Linsenmair. 2003. Effects of light and prey availability on nocturnal, lunar and seasonal activity of tropical nightjars. *Oikos* 103 (3): 627–639. <https://doi.org/10.1034/j.1600-0706.2003.12856.x>.
- Jolly, Chris J., Chris R. Dickman, Tim S. Doherty, Lily M. van Eeden, William L. Geary, S.M. Legge, John C.Z. Woinarski, and Dale G. Nimmo. 2022. Animal mortality during fire. *Global Change Biology* 28 (6): 2053–2065. <https://doi.org/10.1111/gcb.16044>.
- Kats, Lee B., and Lawrence M. Dill. 1998. The scent of death: Chemosensory assessment of predation risk by prey animals. *Écoscience* 5 (3): 361–394. <https://doi.org/10.1080/11956860.1998.11682468>.
- Kollanus, Virpi, Pekka Tiittanen, Jarkko V. Niemi, and Timo Lanki. 2016. Effects of long-range transported air pollution from vegetation fires on daily mortality and hospital admissions in the Helsinki metropolitan area, Finland. *Environmental Research* 151 (November): 351–358. <https://doi.org/10.1016/j.envres.2016.08.003>.
- Kucera, Thomas E. 1992. Influences of sex and weather on migration of mule deer in California. *The Great Basin Naturalist* 52 (2): 122–130.
- Lee, Benjamin P.Y.-H., Zoe G. Davies, and Matthew J. Struebig. 2017. Smoke pollution disrupted biodiversity during the 2015 El Niño fires in Southeast Asia. *Environmental Research Letters* 12 (9): 094022. <https://doi.org/10.1088/1748-9326/aa87ed>.
- Lelieveld, Johannes, John Stephen Evans, M. Fnais, Despina Giannadaki, and A. Pozzer. 2015. The contribution of outdoor air pollution sources to premature mortality on a global scale. *Nature* 525 (7569): 367–371. <https://doi.org/10.1038/nature15371>.
- MacKenzie, Darryl I., James D. Nichols, Gideon B. Lachman, Sam Droege, JAndrew Royle, and Catherine A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83 (8): 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWDJ\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWDJ]2.0.CO;2).
- Marlier, Miriam E., Katherine I. Brenner, Jia C. Liu, Loretta J. Mickley, Sierra Raby, Eric James, Ravan Ahmadov, and Heather Riden. 2022. Exposure of agricultural workers in California to wildfire smoke under past and future climate conditions. *Environmental Research Letters* 17 (September): 094045. <https://doi.org/10.1088/1748-9326/ac8c58>.
- Matthews, Jaya K., Clare Stawski, Gerhard Körtner, Cassandra A. Parker, and Fritz Geiser. 2017. Torpor and basking after a severe wildfire: Mammalian survival strategies in a scorched landscape. *Journal of Comparative Physiology B* 187 (2): 385–393. <https://doi.org/10.1007/s00360-016-1039-4>.
- McCann, Nicholas, Ron Moen, and T.R. Harris. 2013. Warm-season heat stress in moose (*Alces alces*). *Canadian Journal of Zoology* 91 (December). <https://doi.org/10.1139/cjz-2013-0175>.
- Mesinger, Fedor, Geoff DiMego, Eugenia Kalnay, Kenneth Mitchell, Perry C. Shafan, Wesley Ebisuzaki, Dušan Jović, et al. 2006. North American regional reanalysis. *Bulletin of the American Meteorological Society* 87 (3): 343–360. <https://doi.org/10.1175/BAMS-87-3-343>.
- Montgomery, Robert A., Kyle M. Redilla, Remington J. Moll, Bram Van Moorter, Christer M. Rolandsen, Joshua J. Millsaugh, and Erling J. Solberg. 2019. Movement modeling reveals the complex nature of the response of moose to ambient temperatures during summer. *Journal of Mammalogy* 100 (1): 169–177. <https://doi.org/10.1093/jmammal/gyy185>.
- Neilson, Eric W., Tal Avgar, A. Cole Burton, Kate Broadley, and Stan Boutin. 2018. Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere* 9 (1): e02092. <https://doi.org/10.1002/ecs2.2092>.
- Niedballa, Jürgen, Rahel Sollmann, Alexandre Courtiol, and Andreas Wilting. 2016. CamtrapR: An R package for efficient camera trap data management. *Methods in Ecology and Evolution* 7 (12): 1457–1462. <https://doi.org/10.1111/2041-210X.12600>.
- O'Connell, Allan F., and Larissa L. Bailey. 2011. Inference for occupancy and occupancy dynamics. In *Camera traps in animal ecology*, ed Allan F. O'Connell, J. D. Nichols, and K. U. Karanth, 191–204. Tokyo: Springer. https://doi.org/10.1007/978-4-431-99495-4_11.
- Overton, Cory T., Austen A. Lorenz, Eric P. James, Ravan Ahmadov, John M. Eadie, Fiona Mcduie, Mark J. Petrie, et al. 2022. Megafires and thick smoke portend big problems for migratory birds. *Ecology* 103 (1): e03552. <https://doi.org/10.1002/ecy.3552>.
- Parsons, Arielle Waldstein, Tavis Forrester, William J. McShea, Megan C. Baker-Whattton, Joshua J. Millsaugh, and Roland Kays. 2017. Do occupancy or detection rates from camera traps reflect deer density? *Journal of Mammalogy* 98 (6): 1547–1557. <https://doi.org/10.1093/jmammal/gyx128>.
- Pebesma, Edzer J. 2018. Simple features for R: Standardized support for spatial vector data. *The R Journal* 10 (1): 439–46. <https://doi.org/10.32614/RJ-2018-009>.
- Pebesma, Edzer J., and Roger S. Bivand. 2005. Classes and methods for spatial data in R. *R News* 5 (2). <https://cran.r-project.org/doc/Rnews/>.
- Pedersen, Thomas L., and Fabio Cramer. 2021. *scico: Colour palettes based on the scientific colour maps. R package version 1.2.0.9000*. <https://github.com/thomasp85/scico>.
- Perry, David A., Paul F. Hessburg, Carl N. Skinner, Thomas A. Spies, Scott L. Stephens, Alan Henry Taylor, Jerry F. Franklin, Brenda McComb, and Greg Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *Forest Ecology and Management* 262 (5): 703–717. <https://doi.org/10.1016/j.foreco.2011.05.004>.
- Pierce, David. 2019. *ncdf4: interface to unidata netCDF (version 4 or earlier) format data files. R package version 1.19*. <https://cran.r-project.org/package=ncdf4>.
- Principe, Rodrigo E. 2016. *Extracting pixel values by points and converting to table in Google Earth Engine? #265618*. Forum post. <https://gis.stackexchange.com/a/265618>.
- R Core Team. 2021. *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. URL <https://www.R-project.org/>.
- Rowcliffe, J. Marcus, Patrick A. Jansen, Roland Kays, Bart Kranstauber, and Chris Carbone. 2016. Wildlife speed cameras: Measuring animal travel speed

- and day range using camera traps. *Remote Sensing in Ecology and Conservation* 2 (2): 84–94. <https://doi.org/10.1002/rse2.17>.
- Sanderfoot, Olivia V., and Tracey Holloway. 2017. Air pollution impacts on avian species via inhalation exposure and associated outcomes. *Environmental Research Letters* 12 (8): 083002. <https://doi.org/10.1088/1748-9326/aa8051>.
- Sanderfoot, Olivia V., Sarah B. Bassing, Jamie L. Brusa, Robert L. Emmet, Sierra J. Gillman, K. Swift, and Beth Gardner. 2022. A review of the effects of wildfire smoke on the health and behavior of wildlife. *Environmental Research Letters* 16 (12): 123003. <https://doi.org/10.1088/1748-9326/ac30f6>.
- Sanderfoot, Olivia V., and Beth Gardner. 2021. Wildfire smoke affects detection of birds in Washington State. *Ornithological Applications* no. duab028 (June). <https://doi.org/10.1093/ornithapp/duab028>.
- Santos Baquero, Oswaldo. 2019. *ggsn: North symbols and scale bars for maps created with 'ggplot2' or 'ggmap'. R package version 0.5.0*. <https://CRAN.R-project.org/package=ggsn>.
- Schuttler, Stephanie G., A.W. Parsons, Tavis D. Forrester, M.C. Baker, W.J. McShea, Robert Costello, and R. Kays. 2017. Deer on the lookout: How hunting, hiking and coyotes affect white-tailed deer vigilance. *Journal of Zoology* 301 (4): 320–327. <https://doi.org/10.1111/jzo.12416>.
- Sollmann, Rahel. 2018. A gentle introduction to camera-trap data analysis. *African Journal of Ecology* 56 (4): 740–749. <https://doi.org/10.1111/aje.12557>.
- Stewart, Frances E C., Nicole A. Heim, Anthony P. Clevenger, John Paczkowski, John P. Volpe, and Jason T. Fisher. 2016. Wolverine behavior varies spatially with anthropogenic footprint: Implications for conservation and inferences about declines. *Ecology and Evolution* 6 (5): 1493–1503. <https://doi.org/10.1002/ece3.1921>.
- Stewart, Frances E.C., Jason T. Fisher, A. Cole Burton, and John P. Volpe. 2018. Species occurrence data reflect the magnitude of animal movements better than the proximity of animal space use. *Ecosphere* 9 (2): e02112. <https://doi.org/10.1002/ecs2.2112>.
- Street, Garrett, John Fieberg, Arthur Rodgers, Michelle Carstensen, Ron Moen, Seth Moore, Steve Windels, and James Forester. 2016. Habitat functional response mitigates reduced foraging opportunity: Implications for animal fitness and space use. *Landscape Ecology* 31 (9): 1939–1953. <https://doi.org/10.1007/s10980-016-0372-z>.
- Townsend, J., B. Gaines, J. Hadfield, R. Harrod, C. Mehmehl, and E. Leyda. 2004. *Forest health assessment for the Okanogan and Wenatchee national forests*. United States Department of Agriculture, Forest Service, Pacific Northwest Region.
- U.S. Environmental Protection Agency (EPA). 2012. *Revised air quality standards for particle pollution and updates to the air quality index (AQI)*. https://www.epa.gov/sites/default/files/2016-04/documents/2012_aqi_factsheet.pdf.
- U.S. Environmental Protection Agency (EPA). 2020. *Air quality system data mart*. <https://www.epa.gov/airdata>.
- USDA Forest Service. 2019. *Colville National Forest Land Management Plan*. Final Programmatic Environmental Impact Statement, United States Department of Agriculture, Forest Service, Colville National Forest.
- van Beest, Floris M., Bram van Moorter, and Jos M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Animal Behaviour* 84 (3): 723–735. <https://doi.org/10.1016/j.anbehav.2012.06.032>.
- Van Rossum, Guido, and Fred L. Drake Jr. 1995. *Python reference manual*. Centrum voor Wiskunde en Informatica Amsterdam.
- Washington Department of Fish and Wildlife. 2016. *Wildlife program 2015–2017 ungulate assessment*. <https://wdfw.wa.gov/publications/01948>.
- Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service. 2019. *Washington Gray Wolf Conservation and Management 2018 Annual Report*. Ellensburg: Washington Department of Fish and Wildlife.
- Washington State Department of Natural Resources. 2019. *Wildfire Division season summary*. https://www.dnr.wa.gov/publications/rp_fire_annual_report_2019.pdf. Accessed 14 July 2022.
- Washington State Department of Natural Resources. 2020a. *WADNR Active Roads*. <https://data-wadnr.opendata.arcgis.com/documents/wadnr-active-roads-download/about>. Accessed 30 Apr 2020a.
- Washington State Department of Natural Resources. 2020b. *Wildfire Division season summary*. https://www.dnr.wa.gov/publications/rp_fire_annual_report_2020b.pdf. Accessed 25 May 2022.
- Wickham, Hadley, Mara Averick, Jennifer Bryan, Winston Chang, Lucy D. McGowan, Romain François, Garrett Golemund, Alex Hayes, Lionel Henry, Jim Hester, Max Kuhn, Thomas L. Pedersen, Evan Miller, Stephan M. Bache, Kirrill Müller, Jeroen Ooms, David Robinson, Dana P. Seidel, Vitalie Spinu, Kohske Takahashi, Davis Vaughan, Claus Wilke, Kara Woo, and Hiroaki Yutani. 2019. Welcome to the tidyverse. *Journal of Open Source Software* 4 (43), 1686. <https://doi.org/10.21105/joss.01686>.
- Wickham, Hadley. 2016. *ggplot2: elegant graphics for data analysis*. New York: Springer-Verlag.
- Wilke, Claus O. 2020. *cowplot: Streamlined plot theme and plot annotations for 'ggplot2'. R package version 1.1.1*. <https://CRAN.R-project.org/package=cowplot>.
- Williams, Clinton K., and Terry R. Lillybridge. 1983. *Forested plant associations of the Okanogan National Forest*. Washington DC: U.S. Department of Agriculture, Forest Service.
- Williams, Clinton K., Brian F. Kelley, Bradley G. Smith, and Terry R. Lillybridge. 1995. *Forested plant associations of the Colville National Forest. Gen. Tech. Rep. PNW-GTR-360*. Portland: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. In Cooperation with: Pacific Northwest Region, Colville National Forest. 405 p 360. <https://doi.org/10.2737/PNW-GTR-360>.

Publisher's Note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Submit your manuscript to a SpringerOpen[®] journal and benefit from:

- Convenient online submission
- Rigorous peer review
- Open access: articles freely available online
- High visibility within the field
- Retaining the copyright to your article

Submit your next manuscript at ► [springeropen.com](https://www.springeropen.com)