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RESEARCH ARTICLE

Monitoring wolverine (*Gulo gulo*) distribution across the western United States for regional and national assessment

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Abstract

Population monitoring of at-risk species is fundamental to directing effective and timely conservation actions. For wide-ranging threatened species, such as the wolverine (*Gulo gulo*), monitoring across multiple jurisdictions is necessary to track their distribution to inform collaborative regional and national management and policy. We repeated a landscape-scale, multi-jurisdictional remote camera survey first completed in 2017 to evaluate wolverine occupancy throughout the western United States in 2022. Our objectives were to 1) expand the sampling frame to include areas of potential recolonization (Colorado, Oregon, Utah, USA), 2) evaluate whether overall and state-specific occurrence has changed from 2017 in the common sampling frame of Idaho, Montana, Washington, and Wyoming, USA, and 3) evaluate spatial drivers of wolverine occurrence in 2022. From a sampling frame of 770 sites (15 × 15-km cells)

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identified as potential wolverine habitat, 229 sites were surveyed in 2022; no wolverines were detected in Colorado, Oregon, or Utah. We predicted wolverine occupancy and 95% highest posterior density intervals (HPDI) in states with detections to be 0.47 (0.37–0.58) in Idaho, 0.35 (0.21–0.52) in Montana, 0.29 (0.09–0.54) in Washington, and 0.35 (0.27–0.47) in Wyoming. We found weak to moderate evidence of a small decline in overall occupancy (ψ) from the common sampling frame (2017: 0.44 [0.37–0.52]; 2022: 0.39 [0.30–0.49]; $P(\psi_{2022} < \psi_{2017}) = 0.81$), driven by lower occurrences in Montana and Washington. However, this finding is complicated by a change in detection methodology that may have contributed to lower occurrences in Montana and Washington. Lastly, we found strong support (probability of an effect >0.95) that within areas of predicted wolverine habitat, increasing habitat connectivity and the proportion of a site that was previously burned (2001–2015) were associated with increased wolverine occupancy, while increasing normalized difference vegetation index (NDVI) was associated with decreased wolverine occupancy. Our expanded sampling frame provides the means to track wolverine occupancy and range extent—including recolonizations and contractions—across the western United States, providing insights at both the state and national scales.

KEYWORDS

carnivore, monitoring, multi-state, mustelidae, occupancy, rare species, spatially explicit, wolverine

Monitoring at-risk species or populations is critical for tracking changes and making informed conservation decisions (Lyons et al. 2008). Monitoring can also be challenging for widely distributed, rare species that exist over large geographies where it may be difficult to gain inference at appropriate scales to inform effective conservation (Inman et al. 2013, Ellis et al. 2014). Doing so often requires substantial investments of resources and coordination in data collection, management, and processing among multiple jurisdictions (Robinson et al. 2018). Mammalian carnivores are one such taxon that often present monitoring and coordination challenges (Bischof et al. 2020) owing to their low density, wide-ranging nature, and disproportionately threatened status (Fernández-Sepúlveda and Martín 2022, Santini et al. 2022, Steenweg et al. 2023). The North American wolverine (*Gulo gulo*), recently designated as threatened under the United States Endangered Species Act (U.S. Fish and Wildlife Service [United States Fish and Wildlife Service USFWS 2023*a*), has emerged as a focal species for one of the broadest multi-jurisdictional mammal monitoring programs in the western United States (Lukacs et al. 2020).

Wolverines are long-lived (up to 15 years), cold-adapted mustelids that have a circumboreal distribution across the Northern Hemisphere (Pasitschniak-Arts and Larivière 1995, Copeland and Whitman 2003, Inman et al. 2012*a*, *b*). In North America, wolverines inhabit tundra, boreal, and montane biomes, where they occur at low densities, exhibit low reproductive rates, and have high annual adult survival (Copeland and Whitman 2003; Krebs et al. 2004; Inman

et al. 2007, 2012*a*). Adult wolverines generally maintain consistent territories year-to-year (Aronsson and Persson 2018). Past human pressures, such as broad-scale predator poisoning and unregulated fur trapping, led to the extirpation of wolverines from the conterminous United States by the early 1900s (Aubry et al. 2007). However, in the 1930s, wolverines began recolonizing alpine and subalpine forests in high mountain ranges across multiple states (Newby and Wright 1955, Newby and McDougal 1964, Cegelski et al. 2003, Aubry et al. 2007). The current known distribution of reproductive wolverines in the conterminous western United States includes areas of Idaho, Montana, Washington, and Wyoming (Copeland 1996, Inman et al. 2007, Anderson and Aune 2008, Aubry et al. 2010, Lukacs et al. 2020). The recolonization of unoccupied habitat in other states may still be happening, as evidenced by observed long-distance dispersal events (Moriarty et al. 2009, Packila et al. 2017), and is likely being shaped by land cover, snow, and human activity (Day et al. 2024).

In their 2023 decision regarding wolverines, the United States Fish and Wildlife Service suggested the current conterminous United States wolverine population is likely secure in the short term but ultimately threatened because of limited genetic connectivity with populations in Canada and habitat loss due to climate change (United States Fish and Wildlife Service USFWS 2023*b*). A monitoring program that can facilitate investigation of these threats by tracking realized distribution of the species through time is an essential tool for conservation decision-making and for informing periodic federal status assessments. Additionally, affected state wildlife agencies sought a program that could simultaneously facilitate status assessment at the state and national scale, provide insight into potential management-influenced drivers of wolverine occurrence such as recreation, silviculture, fire management, or connectivity, and provide the means to evaluate a multi-state goal of maintaining wolverines throughout suitable habitat, all within a context of collaboration and shared knowledge across domains. Such a program was designed and implemented by Lukacs et al. (2020) during the winter of 2016 to 2017 (herein referred to as the 2017 survey). This initial survey was highly successful, as it demonstrated that a collaborative, multi-jurisdictional, and repeatable survey was attainable and could produce rigorous, high-quality estimates of wolverine distribution. However, the initial survey targeted only Idaho, Montana, Washington, and Wyoming, where wolverines were known or suspected to occur. As such, the design was not capable of delineating the edge of the wolverines' distribution (which requires sampling beyond the suspected occupied range), documenting colonization of previously unoccupied habitat, or associating colonization with management actions such as restorations to historical range. The initial design also limited inference to a 4-state region of the wolverine population in the conterminous United States. Expanding the sampling frame to include all contemporary habitat within the historical wolverine range would allow better delineation of the current distribution of the species, allow opportunity to observe and model colonization events of currently unoccupied regions, and enable national-scale (rather than regional) assessment for the species across all mapped habitat.

Here we report on the second recurring survey to the foundational West-wide wolverine survey work of Lukacs et al. (2020). To do so, we sampled the same cells using the same protocols as the initial 2017 survey. We also expanded the sampling frame to more fully capture the distribution of wolverine habitat (both occupied and assumed unoccupied) in the western United States and potentially detect wolverine recolonizations. Our objectives were to 1) estimate wolverine distribution in 2022 across the expanded sampling frame, 2) evaluate potential changes in overall and state-based occupancy since the 2017 survey, and 3) examine potential drivers of wolverine occupancy in 2022.

We hypothesized that because of the wolverine's life history, behavior, and demography (i.e., high survival, high degree of annual fidelity to a territory), there would be little to no change in occurrence in the common sampling frame between 2017 and 2022. We did not expect to detect wolverines in the expanded sampling areas in Colorado, Oregon, and Utah, which are beyond the known established range, but we considered detections possible because of documented dispersals over the last decade (Packila et al. 2017, United States Fish and Wildlife Service USFWS 2023*c*; Oregon Department of Fish and Wildlife [ODFW], personal communication; Utah Division of Wildlife Resources [UDWR] unpublished data). Lastly, we hypothesized that in areas of predicted wolverine habitat, wolverine occupancy in 2022 would be structured by a combination of environmental factors, human modification, and habitat connectivity.

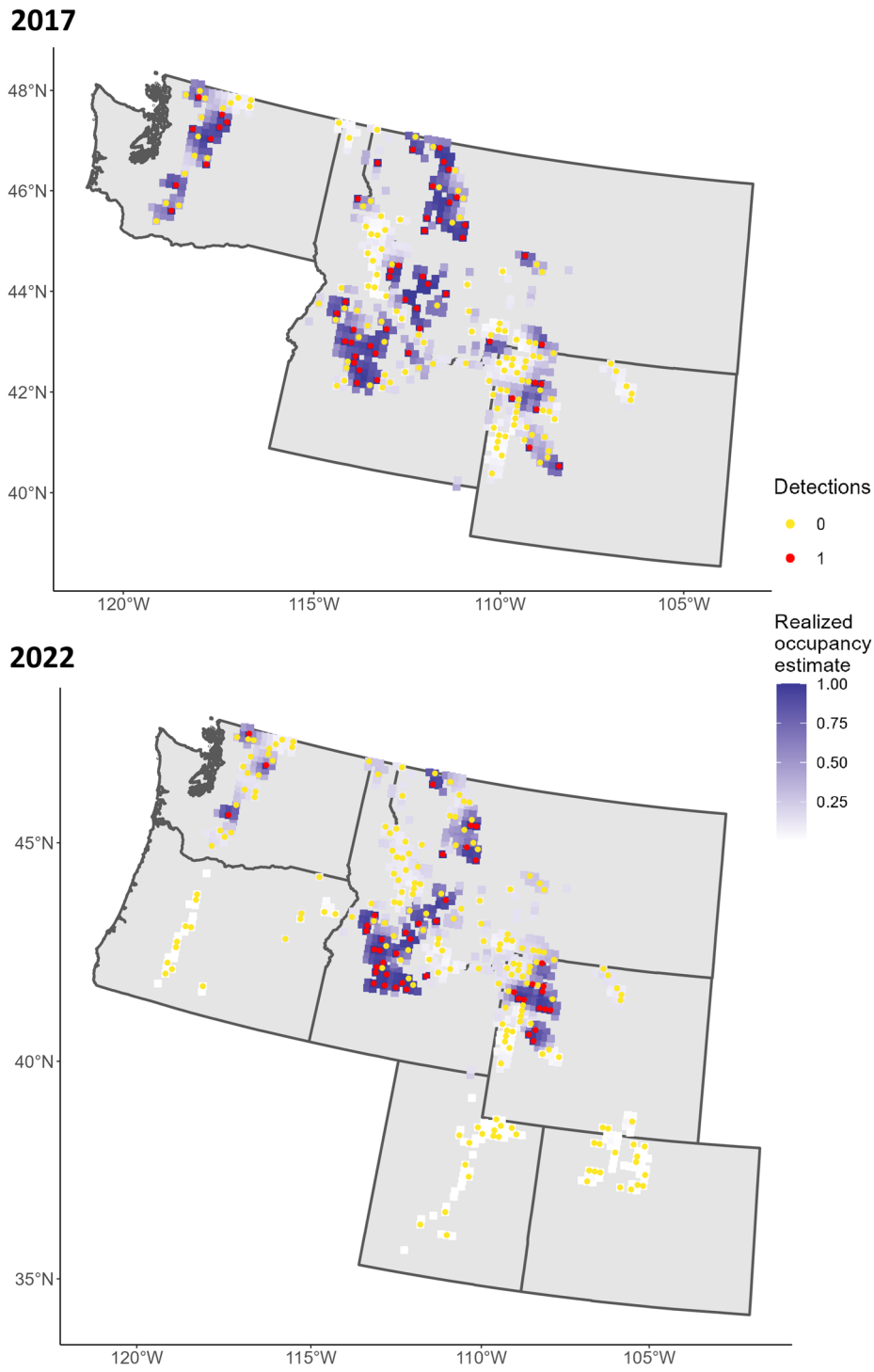

FIGURE 1 Sampling frame, detections, and spatially explicit realized occupancy estimates (i.e., accounts for each surveyed site's detection history) for the 2017 (top; Idaho, Montana, Washington, Wyoming) and 2022 (bottom; Colorado, Idaho, Montana, Oregon, Utah, Washington, Wyoming) wolverine (*Gulo gulo*) surveys throughout the western United States.

STUDY AREA

Our sampling frame included most of the predicted wolverine habitat throughout the western United States (Figure 1). This frame included the 4 states surveyed in 2017 (Idaho, Montana, Washington, and Wyoming) and 3 new states (Colorado, Oregon, and Utah). The fundamental sampling units were 15×15-km cells (n_{2017} = 633; n_{2022} = 770; also referred to below as sites). The cell size was designed to be roughly the average home-range size of female wolverines within the Greater Yellowstone Ecosystem (Inman et al. 2012*a*). Cells either comprised ≥50% predicted wolverine habitat (Lukacs et al. 2020) or were added or dropped from the frame via expert opinion (e.g., cells on the Olympic Peninsula of Washington were dropped because wolverines were never documented there historically, while n = 42 cells in Idaho, Montana, and Wyoming were added to include island mountain ranges of interest). Wolverine habitat was defined as the union of wolverine habitat models developed by Copeland et al. (2010) and Inman et al. (2013). These models were based on variables such as the frequency of late-spring snow (Copeland et al. 2010), or variables representing temperature, vegetation structure, snow, alpine meadows, ungulate escape terrain, and human presence as related to fundamental wolverine needs (see Table S1 in Inman et al. 2013). As such, most cells available to sample included large areas of alpine and subalpine land cover types with specific vegetative species varying by region. Spruce (*Picea* spp.), fir (*Abies* spp.), pine (*Pinus* spp.), and aspen (*Populus tremuloides*) were common overstory species in subalpine forests. Precipitation generally increased with elevation across the study area; mean winter snow accumulation over all cells per year was 1.4 m, although accumulations exceeded 3.5 m in many cells (National Operational Hydrologic Remote Sensing Center 2004). The highest elevations included cirque basins where boulders and talus were common.

METHODS

Surveys

We sampled 184 cells (n_{Idaho} = 59, $n_{Montana}$ = 48, $n_{Washington}$ = 26, and $n_{Wyoming}$ = 51) in 2017 out of 633 potential cells (n_{Idaho} = 200, $n_{Montana}$ = 188, $n_{Washington}$ = 93, and $n_{Wyoming}$ = 152). In 2022, we sampled 229 cells, which included nearly all the 2017 cells plus an additional 51 cells from the areas beyond the expected current range of wolverines ($n_{Colorado}$ = 16, n_{Oregon} = 16, $n_{SouthernWyoming}$ = 4, n_{Utah} = 15). The total cells that could be sampled from these areas were $n_{Colorado}$ = 45, n_{Oregon} = 33, $n_{SouthernWyoming}$ = 12, and n_{Utah} = 48. We selected most sampled cells from the sampling frame using the generalized random tessellation stratified sampling procedure (Stevens and Olsen 2004) with additional (n_{2022} = 12) cells added to the sample via expert opinion.

In each cell, we deployed a single detection station following a standardized ruleset that "prioritized centrality within the cell, access throughout the winter [for baited sites only; see below], high-quality wolverine microsite, outside designated wilderness, greater distance from adjacent stations, and greater distance from roads and trails" (Lukacs et al. 2020). Detection stations consisted of 1) a passive infrared camera (Reconyx PC800 Hyperfire or HyperFire 2 Professional Covert IR, Reconyx, Inc., Holmen, WI, USA) secured to a tree 3–4 m above the ground, and 2) an attractant deployed 4–6 m from the camera, centered in the camera's viewshed (Figures S1–S2). Attractants were 1 of 2 types. Bait stations were deployed in areas that were accessible by project personnel all winter and consisted of a 7–9-kg piece of meat (e.g., elk, deer, beaver) wired to the attractant tree 2.5–3 m above the ground, along with a sponge soaked in long-call scent-lure (same or similar lure as described by Long et al. 2024) wired above the bait. For these stations, the camera was setup in the standard horizontal orientation. Lure stations were deployed at sites that were inaccessible throughout the winter or wherever desired to reduce logistical effort and costs (Lukacs et al. 2020). At such stations, a scent dispenser (Long et al. 2024) was deployed in place of meat and sponges. Dispensers contained the same long-call lure described above and were programmed to drip approximately 3 mL of liquid lure, every 24–48 hours, onto a cow femur mounted below the dispenser (Long et al. 2024).

Sampling devices for DNA, consisting of 0.30-caliber gun brushes affixed to corrugated polypropylene collars (Figura and Knox 2008), were also attached to the tree bole 30–45 cm beneath the bait or femur at all sites during the 2017 survey and most sites in 2022; these genetic data were not used in this study. At the lure stations, the camera was rotated 90 degrees from the standard orientation, such that the sensor was aligned vertically. We revisited baited sites monthly over winter to refresh the meat, replace gun brushes, and swap memory cards; we did not revisit scent dispenser sites until we retrieved the equipment. The distribution of bait and lure sites varied by survey year ($n_{2017,\ Bait} = 141$, $n_{2017,\ Lure} = 43$; $n_{2022,\ Bait} = 62$, $n_{2022,\ Lure} = 167$) and by state (Table S1).

We standardized camera settings (e.g., 5 photos/trigger, 1-second quiet period between triggers, high sensor sensitivity) across all sites to the same settings from the 2017 wolverine survey (Lukacs et al. 2020). Cameras that were located within wilderness areas followed a Minimum Requirements Decision Guide analysis approved by United States Forest Service Regional Foresters. We deployed all sites in late fall and retrieved equipment in late spring or summer, spanning the primary period of interest, winter. For the 2017 survey data, this period mostly occurred between 1 December 2016 and 31 March 2017. The exceptions were cells in Wyoming, half of which were sampled in that time period and half in the winter of 2015–2016. The 2022 survey followed similarly with the primary sampling period between 1 December 2021 and 31 March 2022.

Detection data

Photographs from the 2017 and 2022 surveys were imported into the CPW PhotoWarehouse software (Ivan and Newkirk 2016) or Wildlife Insights (https://www.wildlifeinsights.org/) to facilitate data organization and animal species identification. Each state classified animals using 2 independent observers (one potentially being artificial intelligence [AI], e.g., Wildlife Insights), flagging images when there was disagreement. A referee, usually the project manager for the state, then reviewed the image to make a final classification. Detection and non-detections of wolverines were then summarized into site detection histories to be analyzed in an occupancy modeling framework (MacKenzie et al. 2017) to estimate species occurrence while accounting for false absences (i.e., wolverines were undetected at a site that they occupied). For each survey, we used a 1-month interval for a sampling occasion such that there were 4 occasions for each survey. Wolverines typically make extensive use of their home range over a relatively short time frame (e.g., 1 month; Inman et al. 2012*a*), providing opportunity for the species to be available for detection within each occasion and allowing for repeat detections at occupied sites.

Occupancy meaning

Surveying a highly mobile species by fixed-point sampling (e.g., camera traps) does not allow for a strict definition of species occurrence (i.e., the species is only present or absent). The system is not closed, which is an assumption of the occupancy modeling approach taken here. As such, throughout we interpret occupancy as the probability wolverines use a site during the sampling period (asymptotic occupancy; Efford and Dawson 2012), and detection probability is technically the product of the probability of availability and detection, given the species uses the site. Despite this needed shift in language, point-based sampling has been shown to provide robust inference to species occurrence or use across species (Steenweg et al. 2018). Furthermore, wolverines are also highly territorial and occur at low densities, such that home range-sized cells are expected to be used by one or a few individuals. As such, trends in wolverine occupancy may be a reasonable surrogate for trends in abundance (i.e., via the occupancy-abundance relationship; Ellis et al. 2014, Fuller et al. 2016, Linden et al. 2017). More importantly, our design aims to evaluate changes in conterminous United States and regional wolverine distribution.

Predictive occupancy modeling: wolverine distribution

To estimate wolverine distribution in 2022, we fit a Bayesian spatial occupancy model (Johnson et al. 2013), as was previously done with the 2017 survey data (Lukacs et al. 2020). We used this predictive model to generate a map of spatial predictions of occupancy, which allowed us to summarize wolverine occupancy across the sampled region and by state, and compare occupancy between the 2017 and 2022 surveys. The fundamental parameters of this model are the probability that the species will be detected at a site that is occupied (p) and the probability the site is occupied by the species (ψ). The parameter ψ can be informed by covariates as well as a spatial process, which leverages the spatially explicit information of detections and non-detections at each camera location, incorporating the intuitive notion that nearby cells' occupancy probabilities are likely more similar than cells farther away; this process can thereby improve occupancy predictions of nearby unsampled cells. The spatial structure was specified as a Gaussian spatial process, in which we estimated spatial random effects, governed by the spatial scale parameter (τ). Specifically, we used a restricted spatial regression parameterization (Hughes and Haran 2013). We controlled the extent of the spatial process' influence by defining a neighborhood within a threshold distance of 23 km from any given cell centroid; this distance allowed occupancy estimates of all cells directly adjacent to each other, including the diagonals, to influence each other. This aligns well with our home-range-sized sampling cells, where we assumed a wolverine in one cell can move through adjacent cells but less commonly would move beyond that.

In addition to the spatial process, we modeled ψ as an additive effect of the proportion of a cell containing predicted habitat (as used in defining the sampling frame; Copeland et al. 2010, Inman et al. 2013, Lukacs et al. 2020) and a categorical variable that separated cells into disparate mountain ranges (i.e., North Cascades, South Cascades, Northern Rockies, Southern Rockies, and Utah Mountains; Figure S3). We hypothesized that habitat is a limiting factor of wolverine occupancy, and that the more habitat in a cell would lead to higher wolverine occupancy. Further, we hypothesized that occupancy differed across the entire sampling frame, especially considering that the new mountain ranges added to this survey (southern Rocky Mountains [Colorado, Wyoming], South Cascades [Oregon], and Utah Mountains [Utah]) were not expected to have wolverines. Inclusion of the mountain range variable was important to prevent overprediction of occurrence in mountain ranges with no detections of wolverines. We modeled p using a site-level covariate (bait) indicating whether the site had bait and lure or only lure. Our hypothesis was that sites with bait would be more attractive because of the food reward or some other aspect of a large bait, leading to more revisits or more opportunity to obtain a photograph of an animal when at a camera, and would thus increase detection probability compared to sites with only a scent lure.

We also refit the 2017 survey data (Lukacs et al. 2020) using a separate spatial occupancy model to ensure comparability with the model fit to the 2022 data. Specifically, changes included 1) setting the spatial neighborhood threshold to 23 km instead of 20 km, which was the previous threshold and did not incorporate diagonal cells, 2) using the same predicted habitat variable to model occupancy as used to define the sampling frame instead of an older version of a habitat variable used by Lukacs et al. (2020), 3) using the bait variable to model detection probability, which was previously not used, 4) defining state designations of each cell based on the centroid of the cell to ensure consistent designations, rather than the field team that collected the data as was done previously (e.g., Montana field researchers surveying a cell primarily in Idaho), 5) using the restricted spatial regression parameterization rather than an intrinsic conditional autoregressive model to reduce confounding with the predicted habitat variable, which led to poor parameter convergence of the occupancy intercept, and 6) using a prior probability distribution on τ such that it was more diffuse and led to improved posterior parameter convergence.

We fit models in the R programming language (v4.4.2; R Core Team 2025) using the stocc R package (Johnson et al. 2013). To summarize parameter posterior distributions, we used a Markov chain Monte Carlo (MCMC) algorithm, burning in 5,000 iterations, thinning to every twentieth iteration, and saving 95,000 iterations. We evaluated parameter convergence by examining traceplots and using the Gelman-Rubin statistic ($\hat{R}$; Gelman and Rubin 1992) based on 4 chains with random initial values. We set prior probability distributions to be diffuse over realistic values of the parameters ($\tau \sim$ Gamma(5, 1000), $\beta_\psi \sim$ Normal(0, 3.2), $\beta_p \sim$ Normal(0, 3.2); note that β

indicates linear model coefficients on the probit scale), except for the partial occupancy intercepts for the mountain range variable in the 2022 model that were expected to be unoccupied ($\beta_{\psi,mtn.ranges}$ ~ Normal(-15, 0.44)).

We summarized state and regional occupancy by deriving posterior distributions from the latent state occurrences for each site *i* (z_i) across MCMC iterations. We evaluated changes in occupancy between the 2017 and 2022 surveys by summarizing differences in the latent state occurrences in only the common sampling frame (i.e., Montana, Idaho, Washington, and nearly all cells in Wyoming) between the 2 spatial occupancy models. We did not explicitly model the dynamic changes (i.e., site colonization and extirpation) in occupancy, as 2 surveys are inappropriate to capture these processes. We report posterior median occupancy and coefficient estimates along with 95% high posterior density intervals (HPDI). We also report measures of evidence for an increase or decrease in occupancy from the common sampling frame and within states by a Bayesian measure of a probability of direction (e.g., $P(\psi_{2022} < \psi_{2017})$; measured as the proportion of a posterior distribution on one side of zero; Makowski et al. 2019). This measure is not explicit about the magnitude of change; it is only explicit about the support of the evidence of a change. For reference, a value of 0.90 corresponds (excluding much philosophical context) to a frequentist one-sided *P*-value of 1 − 0.90 = 0.10 (Makowski et al. 2019). We follow the same approach in evaluating statistical support of estimated coefficients by deriving the probability of the direction of an effect (pd = $P(\beta>0)$). Together, we interpret a high probability (≥0.90) as strong evidence of a change (increase or decrease, depending on the inequality sign) in occupancy or a positive effect of a coefficient, while a low probability (≤0.10) as strong evidence of a negative effect of a coefficient. Further, we interpret the probabilities between 0.80–0.90 as weak to moderate evidence of a change in occupancy or positive effect of a coefficient and the probabilities between 0.10–0.20 as weak to moderate evidence of a negative effect of a coefficient.

Inferential occupancy modeling: variables driving wolverine occupancy

In addition to the spatial occupancy model used to predict and map wolverine distribution, we investigated spatial factors influencing the distribution of wolverine occupancy in 2022 by fitting a single-season Bayesian occupancy model (MacKenzie et al. 2017). We conducted this analysis separately from the spatial occupancy model, as the spatial random effect confounds inference with spatial predictors (Hodges and Reich 2010). We limited the sampling frame for this analysis to only states that had wolverine detections. Including states beyond their current range would be mixing sites that have no wolverines because they are not present (e.g., sites in Utah), and thus cannot choose sites to occupy and not occupy, and sites that are available to wolverines but are not used (e.g., sites in Montana). Because of how we defined our sampling frame (cells with ≥50% predicted habitat), our investigation does not consider all possible ranges of spatial factors throughout the western United States. We are likely excluding many areas (and their associated covariate values) that have a low probability of wolverine occurrence.

We hypothesized that wolverine occupancy would fundamentally be affected by environmental features, human activity or land cover modification, and habitat connectivity (Figure S4; Table S2-S4). We considered environmental features to include snow characteristics, the extent of previous wildfires, and vegetation greenness (i.e., a measure of vegetation density and health). We hypothesized that average spring snowpack over the 5 years leading up to the survey could be a determinant of wolverine occurrence (Copeland et al. 2010, Barrueto et al. 2022, Schepens et al. 2023). We initially summarized snow characteristics for each cell in terms of the mean and standard deviation of snow depth on 1 May for the 5 years leading into and including the 2022 survey, along with the mean and standard deviation of snow water equivalent (SWE; National Operational Hydrologic Remote Sensing Center 2004); however, snow depth and SWE were highly correlated ($|r| > 0.55$; Figure S5) and thus we only used the mean snow depth in fitted models. We predicted increasing mean snow depth in May would positively affect wolverine occupancy, up to a point. Beyond some amount of snow depth, there is likely little additional gain realized; thus, we considered mean snow depth as a quadratic. We hypothesized that fire could

negatively and positively influence wolverine occupancy depending on whether the fire was recent or not. A recent fire could remove cover for wolverines and their prey, while older fires may ultimately lead to increased cover and prey availability. Accordingly, we constructed 2 covariates for fire: the proportion of a cell that had burned recently (2016–2021; recent fire) and the proportion that burned during older fires (2001–2015; Vanderhoof et al. 2025). The last environmental feature we considered was vegetation greenness, as measured by the normalized difference vegetation index (NDVI; mean per cell from 2010–2020; U.S. Geological Survey 2025). We hypothesized that greener areas represented more productive areas within predicted wolverine habitat, which could provide increased cover and prey availability. Therefore, we predicted that increasing NDVI would positively affect wolverine occupancy, up to some point; similar to mean snow depth, we considered NDVI as a quadratic.

We considered human activity and land cover modification as forms of anthropogenic disturbance that wolverines would attempt to avoid (Fisher et al. 2013, 2022; Milanesi et al. 2022). We measured the combined effect as a derived value of human modification from a global dataset (Theobald et al. 2025) and predicted that higher values would lead to decreased wolverine occupancy. Lastly, we hypothesized that large blocks of connected habitat, as indexed by contiguous cells with similar values of the predicted habitat covariate would facilitate wolverine settlement and occupancy of the landscape; wolverines tend to use large expanses of less disturbed habitat (Fisher et al. 2013, Milanesi et al. 2022). We used the spatially constrained multivariate clustering tool in ArcGIS Pro 3.1.2 (ESRI, Inc. Redlands, CA, USA) with a specified maximum of 50 clusters for the 7-state area (but only used those clusters in the 4-state analysis area), to divide all cells in the sampling frame into clusters based on their respective proximity and values of the predicted habitat variable. Our choice to specify a maximum of 50 clusters was subjective. We iterated through several possibilities for this specification and noted that values < 50 tended to result in groupings that seemed ecologically implausible (e.g., the Greater Yellowstone Ecosystem and central ID were included in the same cluster). Similarly, values > 50 tended to split ecosystems into implausibly separated clusters (e.g., the Northern Continental Divide Ecosystem split into 2 or 3 clusters). Values near 50 balanced 1) permitting an algorithm to produce objectively derived clusters with 2) resulting clusters that appeared ecologically plausible. The covariate cluster count for any given cell was the size of the cluster to which that cell belonged (size = cell count). We predicted that increasing cluster count would positively affect wolverine occupancy.

We fitted 3 models using our hypothesized variables affecting wolverine occupancy. The first was an environmental model that included the quadratic terms for mean snow depth and NDVI, and linear terms for recent fire and older fire. The second was a habitat-focused model that included an interaction between human modification and cluster count; this model captured the notion that human modification in a cell was different depending on whether there was more or less habitat connectivity. The third was a combined simplified environmental and habitat model that included the linear terms for all hypothesized variables.

We fitted the 3 models using the ubms R package (Kellner et al. 2021), which provides functions to fit occupancy models using MCMC algorithms from stan via the rstan package (Stan Development Team 2025). All continuous covariates were scaled and centered to a mean of 0 and standard deviation of 1; this improves posterior convergence and allows direct comparison among coefficients (each coefficient is scaled in terms of 1 standard deviation of the variable). Prior probability distributions for all parameters were diffuse, specified as Logistic distributions centered at 0 with scale parameter 1 (Northrup and Gerber 2018). We interpreted statistical support of estimated coefficients following the same process outlined in the 'Predictive occupancy modeling' section. We compared models using the expected log pointwise predictive density (Vehtari et al. 2017) implemented in the loo R package (Vehtari et al. 2024). We evaluated model fit using a posterior predictive check, simulating 1,000 datasets, summarizing the proportion of detections in each dataset, and calculating a Bayesian *P*-value (Hobbs and Hooten 2015) as the probability a simulated proportion is greater than the observed; values near 0 and 1 indicate a lack of fit. We evaluated parameter convergence by visually examining parameter traceplots of 3 chains and using the Gelman-Rubin statistic (Gelman and Rubin 1992).

RESULTS

Detections

In 2022, we detected wolverines in 44 cells (out of 229) compared to 55 cells (out of 184) in 2017 (Figure 1). No wolverines were detected in the expanded southern sampling frame of Colorado, Oregon, southern Wyoming, or Utah. The naive occupancy (proportion of cells with detections/total cells available) for Idaho was similar in both years ($Idaho_{2017}$: 0.32, $Idaho_{2022}$: 0.34), lower in Montana and Washington ($Montana_{2017}$: 0.44 and $Montana_{2022}$: 0.17, $Washington_{2017}$: 0.35 and $Washington_{2022}$: 0.16), and higher in Wyoming ($Wyoming_{2017}$: 0.16 and $Wyoming_{2022}$: 0.25). Montana and Washington lost the most sites with detections between surveys (11 and 6, respectively; Figure S6). The number of sites surveyed with bait, compared to only lure, decreased overall between surveys for the same states (Table S1); notably, Montana and Washington were the only states surveyed in both years that transitioned to only lure in 2022.

Predictive occupancy modeling: wolverine distribution

Spatial occupancy models fit to the 2017 and 2022 survey data were well converged ($\hat{R} < 1.05$; Figure S7). In agreement with our hypothesis, we found strong support that detection probability was lower at lure-only sites compared to baited sites in both years (2017: −0.49, 95% HPDI = [−1.00, 0.03], pd = 0.05; 2022: −1.24, 95% HPDI = [−1.67, −0.80], pd = 0.00), while our hypothesis about the effect of predicted habitat on predicted occupancy was weak to moderately supported (2017: 1.17, 95% HPDI = [−1.74, 3.20], pd = 0.88; 2022: 1.82 95% HPDI = [−1.53, 5.18], pd = 0.87). We found wolverine occupancy to vary across the western United States (Figure 1; Figure S8); point estimates for overall occupancy (Figures 1 and 2) in 2017 were 0.44 (95% HPDI = [0.37, 0.52]) and in 2022 were 0.39 (95% HPDI = [0.30, 0.49]). Summarizing across the common sampling frame from both years, we found weak to moderate evidence that wolverine occupancy declined from 2017 to 2022 (Figures 1 and 2; $P(\psi_{2022} < \psi_{2017}) = 0.81$). Median posterior difference in total predicted occupied sites was −35 (95% HPDI = [−115, 42]) and for only the sampled sites was −6 (95% HPDI = [−27, 13]).

Central Idaho had a large collection of cells with high estimated occupancy probabilities in both years with no evidence of a decline (Figures 1 and 3). Glacier National Park and the Northern Continental Divide Ecosystem in northwestern Montana had a large collection of cells with high occupancy probabilities in 2017, but estimated occupancy decreased in 2022 (Figures 1 and 3; $P(\psi_{MT,\ 2022} < \psi_{MT,\ 2017}) = 0.97$). The Greater Yellowstone

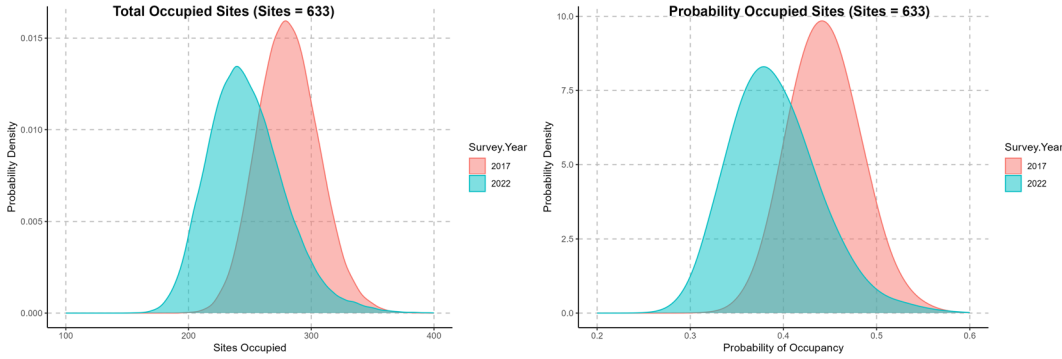

FIGURE 2 Posterior distributions of the total predicted sites occupied by wolverines (*Gulo gulo*; left) and the probability of occupancy by wolverines compared across the 2 surveys (2017, 2022) and only in the common sampling frame (Idaho, Montana, Washington, Wyoming, USA). The probability of a decline between surveys ($P(\psi_{2022} < \psi_{2017})$) was 0.81.

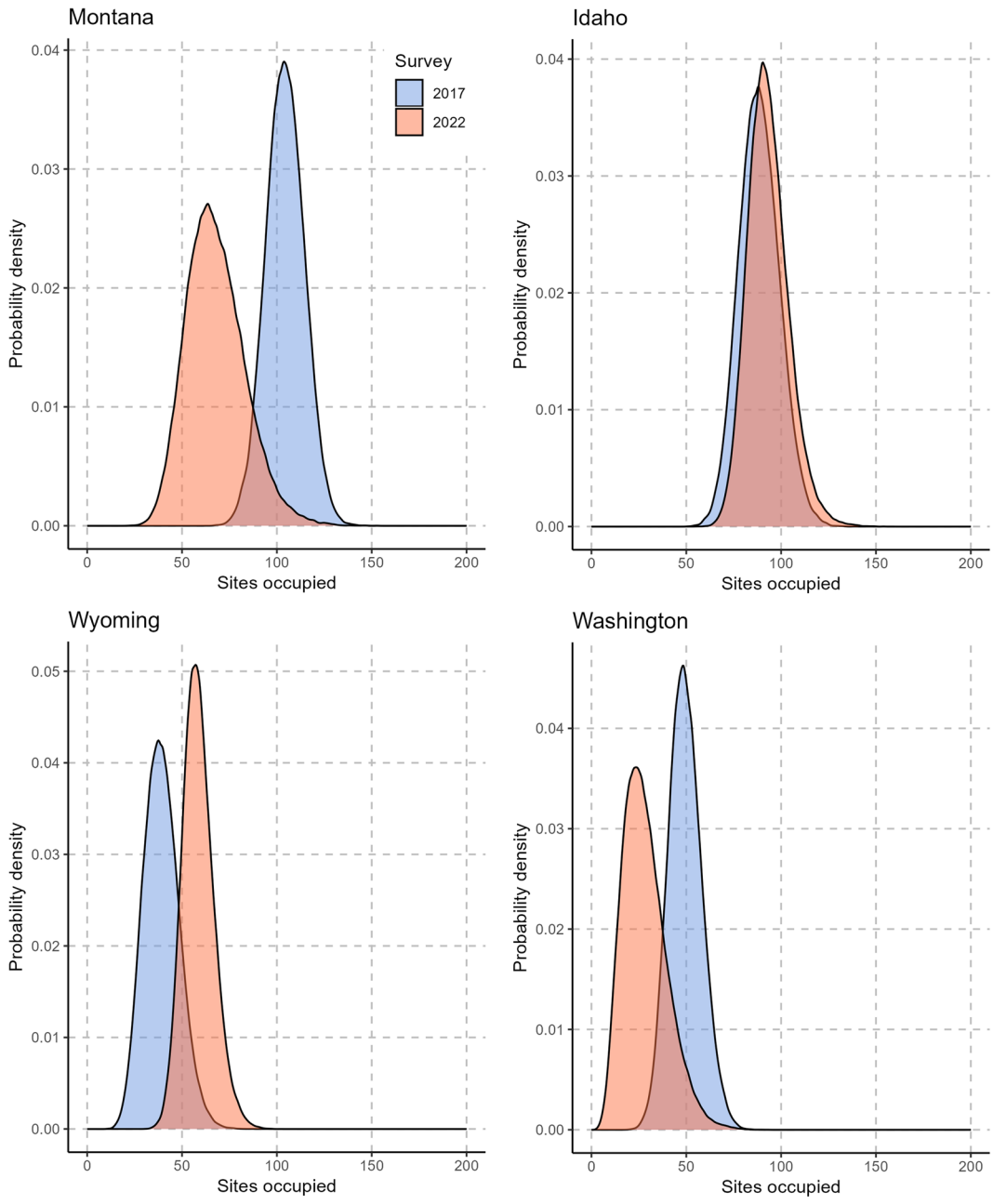

FIGURE 3 Posterior distributions of the predicted proportion of wolverine (*Gulo gulo*) sites occupied by state (Idaho, Montana, Washington, Wyoming, USA) in the common sampling frame between the 2017 and 2022 surveys.

Ecosystem of northwest Wyoming had highly variable occupancy probabilities; overall, the probability of occupancy in Wyoming increased between surveys (Figures 1 and 2; $P(\psi_{WY,\ 2022} > \psi_{WY,\ 2017}) = 0.95$). The northern Cascade mountains of Washington also had high variability in occupancy probabilities in 2017 and showed a decline in 2022 (Figures 1 and 3; $P(\psi_{WA,\ 2022} < \psi_{WA,\ 2017}) = 0.92$). Given that wolverines were not detected in the southern portion of the expanded sampling frame in 2022 (southern Rocky Mountains, south Cascades, and Utah Mountains), occupancy predictions were zero in Colorado, Oregon, and Utah (Figure 1).

Inferential occupancy modeling: variables driving wolverine occupancy

We found each model fit the data (Bayesian *P*-values near 0.5) and the combined environmental and habitat occupancy model was most supported (Table S5); posterior distributions were well converged ($\hat{R}$ < 1.01; Figure S7). Within the context of our sampling frame, which were areas expected to be good habitat for wolverines, we found mixed results for our hypotheses. We found strong support for our hypothesis that the food reward of bait, or some other aspect of using a large piece of meat, led to a higher probability of detecting wolverines compared to using lure only (Figure 4; pd = 0.00; p_{Bait} = 0.65, 95% HPDI = [0.56, 0.0.74]; p_{Lure} = 0.17, 95% HPDI = [0.09, 0.29]). In effect, the probability of detecting a wolverine at a baited site over the 4-month sampling period was near 1 (Figure 5), thus eliminating parametric uncertainty from the detection process of the occupancy model; this high probability of detection was not the case at sites where only lure was used.

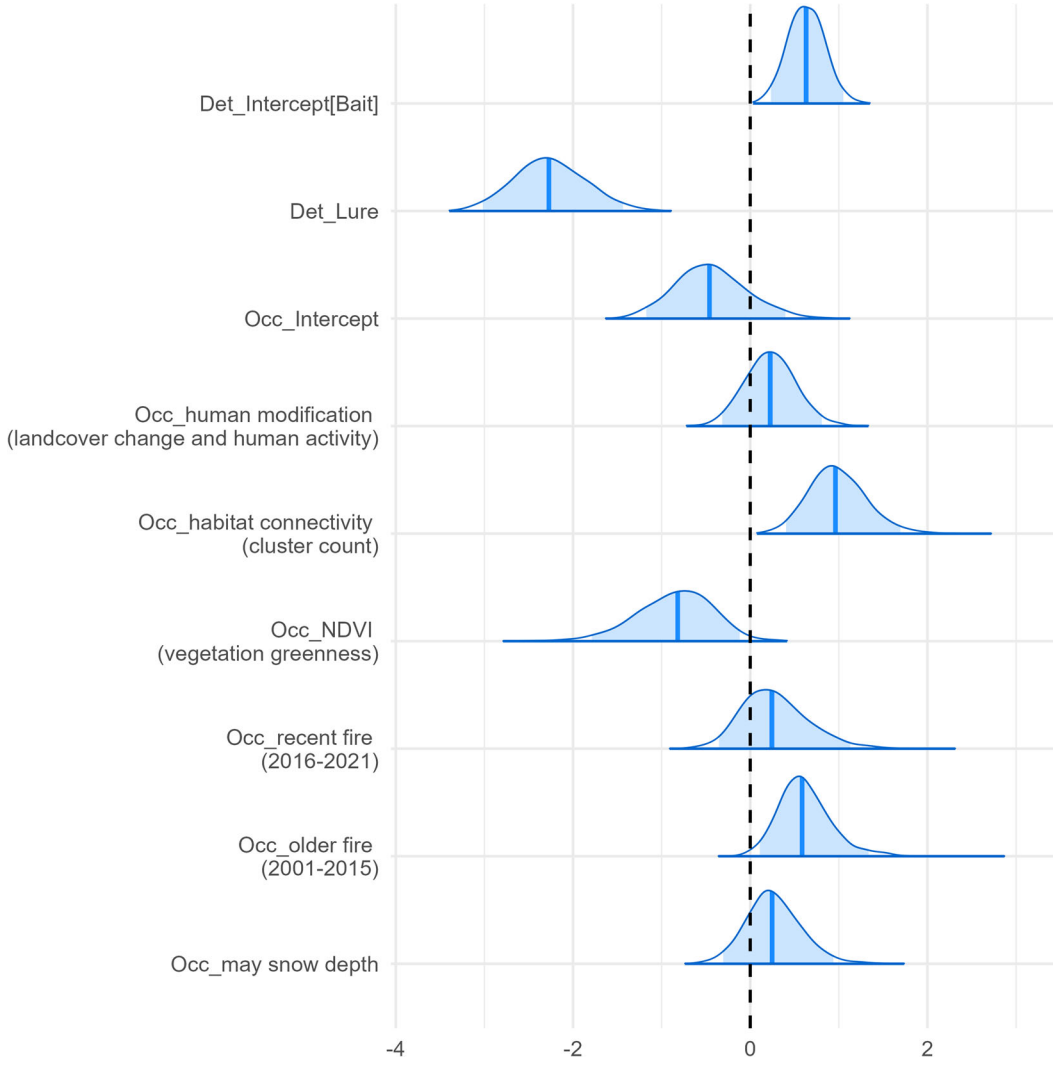

FIGURE 4 Posterior distributions of wolverine (*Gulo gulo*) occupancy (Occ) and detection (Det) coefficients from the most supported model (by expected pointwise log density) using survey data collected in 2022 from Idaho, Montana, Washington, and Wyoming, USA. The thick solid line within each posterior distribution is the posterior median and the shaded region indicates the 95% credible intervals.

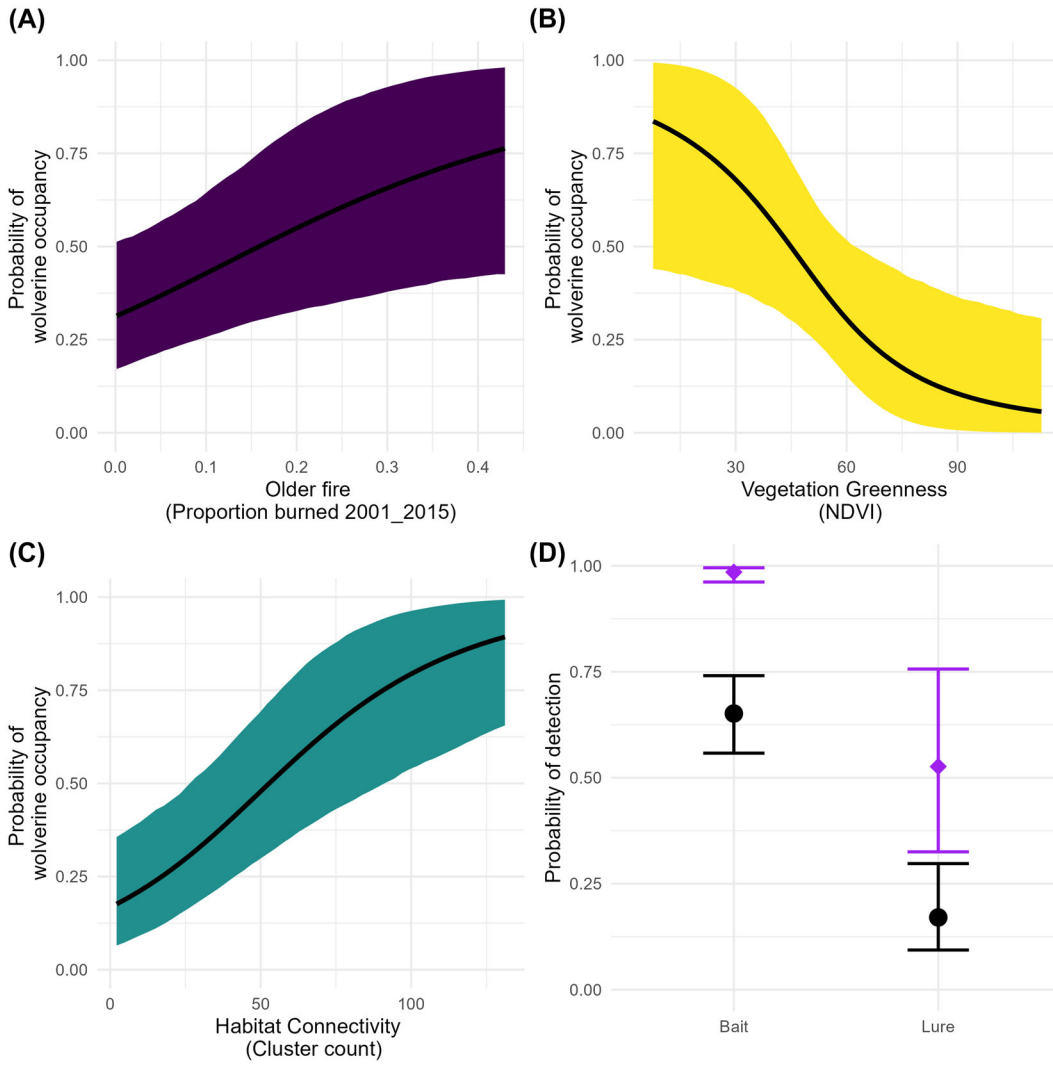

FIGURE 5 Predictions of wolverine (*Gulo gulo*) occupancy (A–C) and detection probabilities (D) in the western United States for the supported variables (older fire, normalized difference vegetation index [NDVI], cluster count, bait) using 2022 survey data (solid thick line is the posterior median and the shaded regions indicate the 95% credible intervals). The black circle and intervals indicate the probability of detection per 1-month occasion and the purple diamond symbol and intervals indicate the probability of detection of a wolverine at least once at an occupied site across 4 1-month sampling occasions (total sampling duration).

Among the environmental features we hypothesized to affect wolverine occupancy within predicted wolverine habitat, we found strong evidence that older fires (pd = 0.99) correlated positively with increased wolverine occupancy (Figures 4 and 5); the highest values of this covariate occurred in Idaho and Washington and, on average, were lowest in Montana and Wyoming (Table S3). In contrast to our hypothesis and prediction, we found strong evidence that vegetation greenness (NDVI) was negatively associated with wolverine occupancy (Figures 4 and 5; pd = 0.02); this covariate's values were well distributed across all the states (Table S4). We did not find clear supporting evidence that more recent fires (pd = 0.78), spring snowpack (mean snow depth; pd = 0.79), or human activity and land cover (human modification; pd = 0.77) affected wolverine

occupancy in our sampling frame. However, we did find strong evidence that habitat connectivity (cluster count; pd = 0.99) correlated with increased wolverine occupancy, supporting our hypothesis; the highest values of this covariate occurred in Wyoming and Montana and, on average, were lowest in Idaho (Table S3).

DISCUSSION

The monitoring program described here represents one of the most spatially extensive, highly coordinated surveys for a carnivore species in North America. Results from this collaborative, multi-jurisdictional survey confirm that as of winter 2021–2022 the current known distribution of wolverines in the western United States includes the North Cascades of Washington, the northern Continental Divide Ecosystem in northwest Montana, the Salmon-Selway Ecosystem of central Idaho (including the Idaho-Montana border), and the Greater Yellowstone Ecosystem in northwestern Wyoming. As such, there is currently no evidence of range expansion into non-core areas, at least for overwinter occupancy. This is despite sampling a higher proportion of available sites in the non-core states (0.31–0.48) compared to the core states (0.26–0.33). Individual dispersals beyond the core areas are known to have occurred in the southern Rocky Mountains (i.e., Colorado; Packila et al. 2017), the Utah Mountains (i.e., Utah; UDWR unpublished data, United States Fish and Wildlife Service USFWS 2023*c*), the Sierra Nevada Mountains (i.e., California; Moriarty et al. 2009), and the South Cascades (i.e., Oregon Department of Fish and Wildlife ODFW 2023). The continued monitoring of these areas of peripheral habitat is essential to identify future re-colonization of historical habitat. Equally important is the continued monitoring of wolverine distribution throughout their current known range. The monitoring program outlined in Lukacs et al. (2020), and expanded on here, sets the stage for continued rigorous and efficient range-wide monitoring of the wolverine.

We found weak to moderate evidence of a small decline from 2017 to 2022 in overall wolverine occurrence in the western United States, due mostly to lower occurrences in northern Montana (around Glacier National Park) and in the Washington Cascades. This estimated small decline was unexpected because of the wolverine's life history (e.g., highly territorial, high annual survival), the extensive high-quality habitat in these regions, and long-established occupation in Montana. We offer several possible explanations for this result.

First, the loss of detections in Montana and Washington coincided with both states moving from a mixture of mostly baited sites in 2017 ($n_{\text{Bait, Montana}} = 43$, $n_{\text{Lure, Montana}} = 5$, $n_{\text{Bait, Washington}} = 18$, $n_{\text{Lure, Washington}} = 8$) to exclusively lure-only sites in 2022 ($n_{\text{Lure, Montana}} = 46$, $n_{\text{Lure, Washington}} = 26$). This change was made because the initial comparison of bait versus lure suggested no difference in detection probability (Lukacs et al. 2020). The occupancy model we implemented attempted to correct potential differences in attractant type, but our approach was limited to information from sites in which a detection occurred at least once. If some lure sites had no success in detecting wolverines at all, that could have led to the results we observed. While the protocol used for lure sites has been proven effective in other applications (Long et al. 2024), recent studies (R. A. Long, Woodland Park Zoo, unpublished data) highlight that the single, rotated camera used in our protocol could fail to detect some animals visiting the station. Conversely, most baited sites deployed in 2022 were chosen specifically because they were accessible to personnel all winter and known to have wolverine occurrence from the previous survey (which provided opportunities to collect fresh DNA samples regularly, a secondary objective of this survey). Perhaps postulated differences in detection (lower, or no detection at lure sites) are artifacts of this non-random deployment of attractant type. Second, the potential decline in overall occupancy, especially in these 2 regions, may reflect a loss of individuals from these areas. The observed difference in estimated occupancy can be traced to an overall net loss of wolverine detections in 9 cells from one survey to the next. We can offer no definitive explanation for why this may have happened, but it is plausible that a combination of natural or human-caused events (e.g., increased incidence of avalanches, disease, fire, recreation) could have occurred in local areas, leading to extirpations in this relatively small number of cells. Third, it is plausible that the small observed difference is simply sampling variation. That is, even if wolverines were distributed exactly the same for each survey, chance events related to sampling

should be expected and can lead to differences in point estimates, like those observed here. Fourth, the observed changes may also be due to variation in habitat use causing transient dynamics in occurrence by this wide-ranging carnivore (e.g., Mayer et al. 2022). We know that this species maintains large home ranges and moves extensively, likely into and out of our sampled cells. Perhaps such movements, by chance, led to fewer individuals being available for detection within our sample cells in the 2022 survey compared to 2017. An understanding of transient dynamics would only be possible after many additional surveys. Lastly, some combination of the explanations provided above could all have been at play and resulted in the potential change in range-wide occupancy we observed.

Ultimately, we only have 2 snapshots of wolverine occurrence, such that drawing conclusions about trends is premature. For the next survey iteration (planned for winter 2026–2027), plans include pairing baited and lure-only stations within expected occupied sites to test for differences in occurrence and detection probability by attractant type. Additional considerations that are being investigated include how to improve wolverine detections at stations with lure dispensers, how to better track dispenser performance, and whether standardizing to a single attractant type (bait or lure) would be beneficial. Planned ensuing surveys will improve our understanding of temporal changes in wolverine occurrence, and ultimately whether there are consistent changes of decline (i.e., a negative trend) or increase (i.e., positive trend).

In addition to providing predictive distributions of wolverine occurrence, we evaluated hypotheses relevant to drivers of wolverine occurrence. Importantly, these findings are within the context of areas expected to be good habitat for wolverines, such that we are not capturing areas of unsuitable and likely unoccupied environments, which would likely result in higher magnitude spatial covariate effects. Notably, we found a strong correlation of higher wolverine occurrence in areas characterized by large, contiguous blocks of cells with high proportions of predicted habitat. This same effect was not found in modeling of the 2017 wolverine survey data (Lukacs et al. 2020), which may be due to a change in methodology here to better capture the clustering of contiguous habitat. This finding is consistent with previous characterizations of habitat requirements for this species (Fisher et al. 2022) and highlights the continued importance of conserving large, contiguous patches of habitat on the landscape. Fortunately, much of the current wolverine range in the western United States exists in protected areas. The largest 10 clusters of contiguous cells (range = 43–99 cells per cluster; median = 84% wolverine habitat per cell in these clusters) encompass 107,100 km^2. Of this, 84,355 km^2 (79%) are protected as federally designated wilderness, National Park, or federally designated roadless area. Moreover, this result highlights the potential value of other contiguous blocks of high-quality habitat that are as of yet unoccupied by wolverines in the contiguous United States. For example, a large cluster in Colorado could potentially support wolverines, and actions to promote recolonization there would likely speed the process of expanding wolverine distribution (Colorado Parks and Wildlife 2026).

The extent, severity, and frequency of wildfire have accelerated in recent decades and are projected to continue as effects of climate change continue to alter historical precipitation patterns (Abatzoglou and Williams 2016, Parks and Abatzoglou 2020, Wasserman and Mueller 2023). We found increasingly positive association between wolverine occurrence and time elapsed since wildfire; the association was strongest with older burns. A positive association in occurrence with decades-old burns is similar to other forest carnivores (e.g., Canada lynx [*Lynx canadensis*]; Vanbianchi et al. 2017, Lyons et al. 2023), and may be due to increases in prey populations associated with recovering, early successional vegetation. The overall impact of wildfire on the wolverine population in the conterminous United States seems likely to depend on how quickly, and to what extent, habitat is burned in the coming decades.

We hypothesized that NDVI would be positively correlated with wolverine occurrence based on the perceived relationship between vegetative cover and prey as described for fire. However, we found the opposite result. In hindsight, we suggest this negative correlation is reasonable given the high affinity of wolverines to use extensive alpine areas, which are characterized by low NDVI. More generally, the wolverine's ecological niche includes exploiting less productive areas (Inman et al. 2012*a*, *b*), which would also suggest they would use areas with relatively lower NDVI.

We did not find clear support for either of our hypotheses that wolverine occurrence would be positively correlated with spring snowpack (mean snow depth) or negatively with human activity and land cover change (human modification). However, these factors were integral in determining the sampling frame that was based on first-order (Johnson 1980) habitat selection at the level of species distribution (Copeland et al. 2010, Inman

et al. 2013). Thus, it is possible that they have already been accounted for and that variation in these variables within the sampling frame does not affect wolverine occupancy. Conversely, spring snowpack and human modification might be unrelated to wolverine occupancy at the scale of existing wolverine habitat across the contiguous United States. For example, recent work in more northern latitudes reported that spring snow cover does not limit the distribution of wolverine dens (e.g., Jokinen et al. 2019, Persson et al. 2023). While these studies focused on den locations and we focused on wolverine occupancy during winter, our sampling frame was defined in part based on an association between wolverine den locations (primarily in northern latitudes) and spring snow cover frequency to hypothesize that spring snow limits wolverine occurrence overall (Copeland et al. 2010). Our current results cannot fully elucidate the effect of spring snowpack on wolverine occurrence during winter because our sampling frame spanned only areas consistently covered by spring snow in the early 2000s (defined in Copeland et al. 2010), but future iterations of our survey may shed light on this topic as more of our sampling frame may lose spring snow cover in the coming decades. Also, protected status of habitat has been identified as a strong predictor of wolverine occurrence and density in other portions of wolverine range in North America (Kortello et al. 2019, Barrueto et al. 2020, Barrueto et al. 2022). Perhaps the lack of association we found between wolverine occupancy and human modification is due to the high proportion of wolverine habitat that occurs within protected landscapes in the contiguous United States. We also recognize that these covariates are imperfect measures that do not represent winter-long snow dynamics or all types of human disturbance.

MANAGEMENT IMPLICATIONS

Coordinating a multi-state wolverine survey requires strong, consistent communication among state wildlife agencies and partners. Regular communication not only facilitates a rigorous, spatially extensive survey capable of covering the distribution of the wolverine, it also fosters a shared understanding of the species' status, the factors and management actions that can affect wolverines, individual agency roles within the larger context, and a shared commitment to collectively managing this wide-ranging and low-density carnivore. The results from this monitoring program are useful for evaluating federal and state listing decisions, defining state wildlife action plan objectives, and identifying areas that may benefit from active restoration efforts. The continuation of this monitoring program can ultimately provide previously unavailable trends in occurrence of the wolverine in the contiguous United States that could be relevant to listing and delisting decisions. The program also has the potential to relate environmental and anthropogenic variables of management relevance to wolverine occupancy (e.g., recreation, fire, wilderness status, connectivity, and climate) over the large scale at which the wolverine population in western North America operates. It can also provide a better understanding of the factors governing their occurrence by ultimately estimating site dynamics and the effects of management actions to expand wolverine distribution or improve connectivity among habitat patches; these outcomes could be important for future federal status assessments for the species. Continued conservation of large, connected blocks of habitat will be important for maintaining and expanding the distribution of this species. The distribution of wolverines in the western United States would expand more quickly with assisted dispersal to currently unoccupied large patches of habitat beyond the current core range (Colorado Parks and Wildlife 2026). Lastly, wildfire management and mitigation have the potential to alter wolverine occurrence in some areas, necessitating considerations of potentially negative short-term and positive long-term effects on wolverine distribution.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

The non-invasive sampling of wolverines described in this manuscript was consistent with current Animal Welfare guidelines that govern such sampling in each of the participating states.

DATA AVAILABILITY STATEMENT

Data and code supporting this research can be found at https://github.com/bgerber123/Wolverine-WAFWA-Survey2022-Manuscript and archived at 10.5066/P14QNSOX. Note that the spatial locations have been rounded to 10 kilometers to buffer exact locations of wolverine detections.

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SUPPORTING INFORMATION

Additional supporting material may be found in the online version of this article at the publisher's website.

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