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Erratum

Ausband, D. E., S. J. Thompson, B. A. Oates, S. B. Roberts, M. A. Hurley, and M. A. Mumma. 2023. Examining dynamic occupancy of gray wolves in Idaho after a decade of managed harvest. Journal of Wildlife Management 87:e22453.

In Ausband et al. (2023), we wrote in the abstract that "[t]he single-season occupancy model demonstrated a positive relationship between harvest and occupancy at low to moderate levels of harvest (10–30%), but there was also evidence that high levels of harvest (>30%) reduce occupancy." Similarly, in the discussion, we wrote "[t]he relationships of low to moderate levels of harvest (10–30%) to colonization (positive), extinction (negative), and occupancy (positive) might also be explained by the ability of wolves to redistribute into cells…"

The inclusion of parenthesized harvest rates in these sentences is incorrect and misleading. We did not have information on cell-specific abundance to calculate a harvest rate in our study but instead characterized harvest as the number of individuals harvested within an occupancy cell. The parenthesized rates are based on an analysis in Adams et al. (2008) showing human-caused mortality rates <29% generally do not cause wolf populations to decline. Our use of the rate from Adams et al. (2008) in these sentences, however, suggests that a harvest rate of >30% can cause changes in wolf occupancy. This was not assessed and is therefore not supported by our study. In sum, our paper should have stated:

1) [t]he single-season occupancy model demonstrated a positive relationship between harvest and occupancy at lower and intermediate levels of harvest, but there was also evidence that higher levels of harvest reduced occupancy.
2) [t]he relationships of lower to intermediate levels of harvest to colonization (positive), extinction (negative), and occupancy (positive) might also be explained by the ability of wolves to redistribute into cells…

REFERENCE

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RESEARCH ARTICLE

Examining dynamic occupancy of gray wolves in Idaho after a decade of managed harvest

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Abstract

Gray wolves (*Canis lupus*) were reintroduced to Idaho, USA, in 1995–1996. The removal of Endangered Species Act protections in 2011 transferred wolf management to the state where wolves were subsequently classified as a harvested (i.e., hunted, trapped) big game species. We implemented a camera-based survey across Idaho from 2016–2021 as part of a population monitoring program. We used the resulting camera images in multi-year, dynamic and single-season occupancy models to examine potential changes in the asymptotic proportion of area occupied by wolves and assess the effect of cumulative wolf harvest from 2016–2021 on occupancy in the last year of the study, 2021. We also wanted to understand how habitat, prey, humans, harvest, livestock, and prey-related wolf removals affected wolf occupancy through their effects on colonization and extinction of occupancy cells through time. Statewide wolf occupancy did not change appreciably over the course of our study, with the proportion of survey cells occupied at an estimated high of 0.44 ± 0.03 (SE) in 2018 and a low of 0.39 ± 0.03 in 2020. Wolf colonization (i.e., probability that a cell switched from unoccupied to occupied between years) was positively associated with forest cover, images of humans, and the percent of neighboring cells that were occupied. Cell extinction (i.e., probability of switching from occupied to unoccupied between years) was negatively associated with neighboring cell occupancy. There were nonlinear relationships between wolf harvest, colonization, and extinction. The single-season occupancy model demonstrated a positive relationship between harvest and occupancy at low to moderate levels of harvest (10–30%), but there was also evidence that high levels of harvest (>30%) reduce occupancy. Our results indicate that although harvest might influence wolf occupancy at local scales, wolf occupancy remained relatively constant across the state and wolves remained well distributed across Idaho during the study.

KEYWORDS
Canis lupus, distribution, gray wolf, harvest, hunting, Idaho, occupancy, trapping

Gray wolves (*Canis lupus*) were reintroduced to Yellowstone National Park and central Idaho, USA, in 1995 and 1996 (Bangs and Fritts 1996). The reintroduced population quickly grew in abundance and its distribution expanded to other parts of Idaho, western Montana, northwestern Wyoming, Oregon, Washington, and California, USA. In 2009, wolves were removed from the Endangered Species Act list and management authority returned to the states.

The Idaho Department of Fish and Game (IDFG) designated wolves as a big game species and the first state-regulated wolf hunting season began in the fall of 2009. In 2010, reinstatement of Endangered Species Act protections paused the hunting season, but annual hunting and trapping resumed in fall 2011 after the second removal of Endangered Species Act protections. Although generally supported by Idaho residents at the time (IDFG 2008), the establishment of a wolf harvest (i.e., hunting and trapping) season in Idaho (and simultaneously in Montana) continues to be controversial. Some expressed concern that the levels of wolf harvest might be unsustainable (Creel and Rotella 2010, Creel et al. 2015, Vucetich and Nelson 2017), while others argued that the number of wolves harvested did not threaten the long-term viability of wolves in the region (Gude et al. 2012). Ultimately, only reliable data on the wolf population will provide clarity about the potential effects of hunting and trapping on Idaho's wolves.

As the Idaho statewide wolf population grew after reintroduction, it became increasingly difficult to adequately monitor the population via captures and radio-collaring. Idaho largely shifted to noninvasive data collection in 2015 for wolf occupancy models, which estimate the proportion of area overlapped by ≥1 wolf territories. Occupancy models are particularly useful for monitoring many species because they rely on relatively easy to collect detection and non-detection data and incorporate imperfect detection (i.e., species present but not detected; MacKenzie et al. 2006). In Idaho, wolf occupancy models were initially populated using data from hunters and labor-intensive, noninvasive scat surveys (Ausband et al. 2014). Cameras can also provide such detection and non-detection data and advances in technology have made cameras more reliable and the processing of large datasets of images more efficient (Tabak et al. 2019, Norouzzadeh et al. 2021). Pairing motion-sensitive cameras and occupancy models provided a logical framework for statewide monitoring of wolves in Idaho.

We wanted to assess the stability of wolf occupancy in Idaho through time and the potential effects of environmental and human-related covariates on the probabilities of an area becoming occupied (i.e., colonization) or being vacated (i.e., extinction) by wolves from one year to the next. We used images from motion-sensitive cameras to build a multi-year, dynamic occupancy model for gray wolves across potential wolf habitat in Idaho, accounting for the effects of human-caused mortality and other anthropogenic and natural influences on occupancy and colonization and extinction rates. We predicted that occupancy would be positively affected by the abundance of ungulates (elk [*Cervus canadensis*], deer [*Odocoileus* spp.], and moose [*Alces alces*]), forest cover, topographic features that enhance the cursorial hunting success of wolves, proportion of wolf rendezvous site (i.e., pup-rearing) habitat, and the occupancy of adjacent areas. Additionally, we predicted that occupancy would be negatively affected by the density of public roads, presence of domestic livestock (because of increased risk of human mortality), and the number of humans observed at a survey site. We also explored how harvest was associated with colonization and extinction of surveyed cells and whether local robustness of the wolf population (adjacent cell occupancy) or security cover (forest cover) modulated that relationship. Finally, we explored whether wolf harvest was associated with higher extinction and lower colonization probabilities of surveyed cells that contained greater numbers of livestock, where targeted wolf removal efforts were likely more common (DeCesare et al. 2018), and whether greater cumulative harvest over the course of the study resulted in lower occupancy in the final year of monitoring.

STUDY AREA

We conducted our study from 2016–2021 in Idaho (152,292 km^2; Figure 1). Habitat varied widely across our study area, from mesic forests in the north to montane forest and sage-steppe moving south across the state. Most of our study area was in montane forests. Elevation ranged from 216–3,859 m, annual precipitation ranged from 33 cm in southern Idaho to 76 cm in north Idaho, and average temperatures ranged from a low of −51°C in winter to a high of 47°C in summer. Much of Idaho (62%) is in federal ownership and is managed largely by the United States Forest Service and Bureau of Land Management.

METHODS

Data collection

We used images from motion-sensitive cameras to build a multi-year, dynamic occupancy model for gray wolves across potential wolf habitat in Idaho, accounting for the effects of human-caused mortality and other anthropogenic and natural influences on initial occupancy at the beginning of the study and colonization and extinction rates. We projected a grid of 686-km^2 survey cells ($n = 334$) across Idaho (Figure 1). We selected this cell size to approximate the mean size of a single wolf pack territory (Ausband et al. 2014). We excluded cells in the southern portion of Idaho where high levels of human habitation and agricultural cultivation make the landscape generally unsuitable for wolves (Nadeau et al. 2009). We placed 1 motion-sensitive camera (Reconyx® PC900 or Hyperfire 2 cameras, Holmen, WI, USA) in each of 222 remaining cells (Figure 1) set to motion-trigger, taking 3 images per trigger event with no pause between triggers. During 2016–2021, IDFG personnel deployed motion-sensitive cameras along roads and trails within 500 m of wolf rendezvous sites (identified in prior monitoring) or within highly suitable wolf rendezvous site habitat predicted using a previously developed model (Ausband et al. 2010, Jacobs and Ausband 2018*a*). In cells without identified wolf rendezvous sites, we selected locations for camera deployment by choosing the largest, most contiguous patch of predicted highly suitable (i.e., model predicted a high probability of selection) wolf rendezvous site habitat. We included a 500-m buffer around each point to allow field personnel the flexibility to select camera deployment locations that were perceived as likely to be encountered by wolves (e.g., junction of 2 low-use or decommissioned roads). We deployed most cameras by 1 July (snow conditions influenced timing of camera deployments) and retrieved them after 15 September each year. We did not bait motion-sensitive cameras and set them at heights >2.5 m when possible, to avoid damage from wildlife and deter theft (Jacobs and Ausband 2018*b*). In 2016, we angled cameras relative to the road (or trail) to maximize the length of the road in each camera's viewshed (e.g., viewshed facing down the trail), whereas during 2017–2021, we attempted to set cameras perpendicular to the road or trail to have animals move through more of each camera's motion-sensor array and increase the likelihood of detection.

We examined the resulting images using Timelapse2 software (S. Greenberg, University of Calgary, Alberta, Canada). For images collected 2019–2021, we used the MegaDetector object detection algorithm to identify

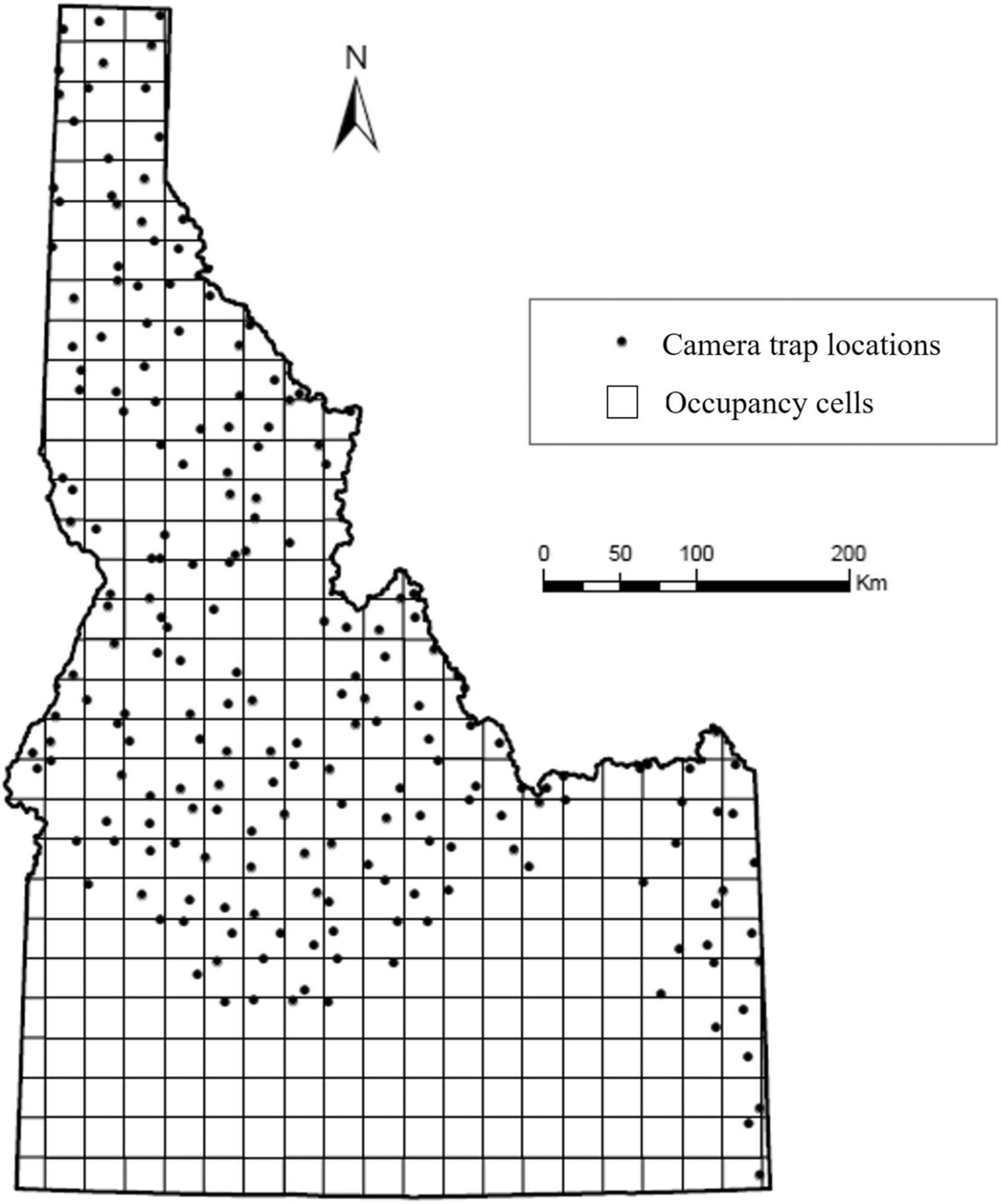

FIGURE 1 Statewide occupancy grid and locations of motion-sensitive cameras used to collect images for wolf occupancy modeling in Idaho, USA, 2016–2021. We did not deploy cameras in some survey cells because of private land access or restrictions on installations in federal-designated Wilderness Areas.

pictures with >0.80 probability of containing animals and avoid human review of empty images (Beery et al. 2019). Trained staff reviewed all remaining images, recording species and the number of individuals present, and noted events that rendered a camera inoperable (e.g., wildlife or wind moving the camera viewshed, resulting in an obstructed view). We divided each primary sampling period (15 Jun–31 Sep) into 2-week, secondary sampling intervals. The first and final periods occurred while cameras were being deployed and retrieved and often recorded much of the 2-week interval. We used images of wolves to generate detection histories for the 6-year duration of the study. For example, a 6-year detection history at a camera that only captured images of wolves during the third sampling period in year 1 and the second sampling period in year 3 would take the following format: 0010000 0000000 0100000 0000000 0000000 0000000.

Covariate preparation

We considered covariates known to affect wolf occupancy from previous studies, such as percent forest cover, road density (km/km^2), elevation, slope, and terrain roughness (Table 1; Rich et al. 2013, Ausband et al. 2014). We generated several additional covariates from image data, assuming that cameras could provide an index of activity at each camera for 2 timescales (annually and over each 2-week sampling interval). We considered images of ungulate prey (moose, elk, and deer), human activity (humans and vehicles), and livestock activity (cows and sheep) as covariates that might describe initial wolf occupancy, detection, colonization, or extinction. Because a single individual could be photographed repeatedly over a short time period (e.g., a grazing cow), we calculated image-based covariates as the number of hours within each timescale (i.e., 2-week interval, summer study period) where the species of interest (e.g., prey, human, livestock) was recorded at least once, instead of tallying the number of images of each species. For example, we looked at each hour, and if there were any cow images during an hour, that hour registered as a 1. Thus, the maximum value was capped at 24 per day. In addition to the image-based livestock index, we used livestock grazing allotment boundaries and permitted grazing records to generate a summer index of cattle abundance on lands managed by the Bureau of Land Management, United States Forest Service, and Idaho Department of Lands. For each cell by study year, we summed the billed (Bureau of Land Management), authorized (U.S. Forest Service), and permitted (Idaho Department of Lands) livestock animal-unit-months (AUM) during 15 June through 30 September across all livestock allotments managed by these agencies. For allotments that crossed occupancy cell boundaries, we partitioned and allocated AUMs based on the area of the allotment in each cell.

Idaho Department of Fish and Game has a mandatory reporting requirement for all hunted or trapped wolves in Idaho. These records are maintained in a combined database with information on wolves removed for livestock and prey-related conflict management and all other wolf mortalities in Idaho documented by IDFG. For our assessment of human-caused mortality, we used all documented mortalities that contained precise enough location information to assign to an occupancy cell (i.e., harvest) and summed those mortalities within the year prior to each sampling period for each cell. For example, the wolf harvest value for the 2016 sampling period included all reported harvest that occurred from 15 June 2015 through 14 June 2016. Most wolf harvest occurred in winter, outside of the summer sampling period. Further, even if a cell was unoccupied during summer, we assumed that harvest could still occur during the following winter because of the potential for wolves to colonize an unoccupied cell during fall and winter following our summer survey period. Lastly, we used the area (km^2) of highly suitable rendezvous site habitat in each cell and the proportion of neighboring cells that were occupied by wolves as predictive covariates of occupancy.

We prepared covariates for analysis by truncating outlier values following a visual assessment of each covariate (Table 1) and then standardizing (i.e., 1 SD around a mean of zero) continuous covariates to improve model convergence (Fiske and Chandler 2011). We checked for correlations between covariates using Spearman's correlation coefficient (r) and considered any pair of variables with $r > 0.60$ values to be collinear (Dormann et al. 2013) and retained the collinear variable that was easier to interpret.

Model development and selection

We used a multi-season (i.e., multi-year), dynamic occupancy model (Mackenzie et al. 2003) to assess the probabilities of detection (p), initial occupancy (ψ_{2016}), colonization (γ; i.e., transition from unoccupied to occupied in the next year), and

TABLE 1 Covariates used to model dynamic occupancy and the 4 sub-models of a dynamic occupancy model (detection [p], initial occupancy [ψ_{2016}], colonization [γ], and extinction [ε]) of gray wolves in Idaho, USA, 2016–2021. Non-dynamic (site) covariates were static over the duration of the study, annually varying (year) covariates had a different value for each study year, and interval-level covariates varied for each 2-week detection interval within each year. Some covariates can be parsed to be a 2016 only value for ψ_{2016}, annual totals for γ and ε, or 2-week totals for p (e.g., ungulate image-hours). If a covariate was not considered in a sub-model, it is left blank.

Covariate	Form[a]	Source	p	ψ_{2016}	γ	ε
Proportion forest (cell)	L and Q	Gap analysis project[b]	Site	Site	Site	Site
Proportion forest (100-m radius)	L and Q	Gap analysis project[b]	Site			
Rendezvous site habitat	L and Q	Ausband et al. (2010)	Site	Site	Site	Site
Elevation	L and Q	Digital Elevation Model (30-m), cell average		Site	Site	Site
Slope	L and Q	Digital Elevation Model (30-m), cell average		Site		
Roughness	L and Q	Digital Elevation Model (30-m), cell average		Site		
Road density	L and Q	km/km^2 of open roads within cell[c]	Site	Site		
Livestock stocking rate	L and Q	Sum of cattle animal unit months (AUMs) based on grazing data from major land management agencies[d]		2016	Year	Year
Ungulate image-hours	L	Number of hours with ≥1 ungulate image (truncated 13 high annual values to 140)		2016	Year	Year
Livestock image-hours	L	Number of hours with ≥1 cow or sheep image (truncated 14 high annual values to 200)		2016	Year	Year
Human image-hours	L	Number of hours with ≥1 human or vehicle image (truncated 17 high annual values to 350)		2016	Year	Year
Occupied neighboring cells	L	Percent of total neighboring cells that had ≥1 wolf image taken during that study season		2016	Year	Year
Year	Categorical	Variable for each year ($n = 5$)				
Year 2016	Categorical	Variable for year 2016 versus all other years ($n = 2$)				
Wolf harvest[e]	L and Q	Number of wolves harvested in occupancy cell during previous year			Year	Year
Functioning days	Log	Log of operational days to account for cameras that did not operate for entire interval				Interval

[a] L = linear relationship considered, Q = quadratic relationship considered.

[b] U.S. Geological Survey Gap Analysis Project (2016).

[c] Idaho Department of Parks and Recreation trails and roads layer.

[d] U.S. Forest Service, Bureau of Land Management, and Idaho Department of Lands grazing allotments.

[e] Wolf harvest not included during development of base model but added and tested in final model selection step.

extinction (ε; i.e., transition from occupied to unoccupied in the next year). The approach involved 2 sub-models: a detection model, which estimates p as a function of site-level covariates, and a state model, which describes relationships of ψ_{2016}, γ, and ε with static covariates that vary only among sites, dynamic covariates, which vary across years, and interval-level covariates that vary among sampling periods within years (MacKenzie et al. 2003). We also directly tested the effects of human-caused mortality on occupancy (ψ_{2021}) by examining the effect of cumulative human-caused mortality over the course of the study on the last year of detection and non-detection data using a single-season occupancy model. Given the duration of our sampling periods each year and the ability of wolves to move considerable distances, our occupancy estimates are best defined as the proportion of area (survey cells) occupied by ≥1 wolf at some time during the 2-month sampling period (asymptotic occupancy; Efford and Dawson 2012, Neilson et al. 2018). Given our methodology was consistent throughout the study and that we were not interested in absolute occupancy, this approach was suitable to address our primary objective of examining yearly changes in wolf occupancy. To account for sampling periods where a camera did not operate for the entire period, and thus would have a lower probability of detecting wolves, we included the log of operational days for that camera and sampling period in the detection sub-model. We implemented all models in program R (version 4.0.5; R Core Team 2021) using the colext function in package unmarked (Fiske and Chandler 2011).

To assess potential covariate combinations, we selected covariates in a multi-stage process. We began with a highly parameterized model that included linear relationships of every covariate in every sub-model of the dynamic occupancy model (p, ψ_{2016}, γ, ε). To account for a potential influence of the change in camera angle in relation to roads and trails on the probability of detection, we compared a 6-categorical structure for year (i.e., detection different in each year) to a 2-categorical structure (i.e., 2016 vs. all other years) in the detection sub-model, retaining the better-supported structure as determined by Akaike's Information Criterion adjusted for small sample sizes (AIC_c; Burnham and Anderson 2002). Next, for continuous covariates (Table 1), we compared linear versus quadratic relationships of each covariate separately, retaining the better-supported relationship. We conducted each comparison while modeling all other covariates in their linear form. We then combined the better-supported structure for year and relationship (i.e., linear or quadratic) for each covariate to build a saturated model (Table 1). Using the saturated model as a starting point, we moved to a stepwise, covariate-removal process, sequentially removing the least-supported covariates until removals no longer resulted in a lower AIC_c value to form our base model (Arnold 2010). We then tested the effect of wolf harvest on occupancy by building 4 additional models that incorporated wolf harvest and removals as a covariate in the extinction and colonization models. The 4 models incorporated the numbers of wolves harvested with linear and quadratic relationships, and as an interactive term with forest cover and an interactive term with occupancy of neighboring cells.

We tested model fit of the saturated model (i.e., incorporating all covariates initially considered) using a parametric bootstrap goodness-of-fit test based on Pearson's χ^2 where $P > 0.05$ indicates adequate model fit (Fiske and Chandler 2011). We derived annual occupancy probability (ψ_{2017}–ψ_{2021}) for years after 2016 using model estimates of ψ_{2016}, p, γ, and ε and projecting forward for each study year. We calculated standard errors for these derived values using a bootstrap method (Kéry and Chandler 2012). To generate model-based predictions, we fixed all covariates at their mean value and varied the covariate of interest from observed minimum to maximum values. Unless otherwise specified, we drew figure axes with original, unstandardized covariate values.

To directly test the effects of wolf harvest on occupancy, we calculated cumulative wolf harvest within each survey cell by summing all human-caused wolf mortalities from 2016 through spring 2021. We then included cumulative wolf harvest as a covariate in the occupancy ($\psi_{2021\text{single-season}}$) submodel of a single-season occupancy model that used motion-sensitive camera data collected from 15 June 2021–31 September 2021. We also included covariates from ψ_{2016} and p sub-models of the dynamic occupancy base model. We excluded covariates from the base model that were not applicable (e.g., year) or those that prevented model convergence (e.g., road density).

RESULTS

After accounting for private land and restrictions on installations in federally designated Wilderness Areas, we deployed 206–209 cameras each summer from 2016–2021. We collected image data from 191–197 cameras each year after accounting for cameras that were damaged, lost, or stolen (Figure 1; Table 2). We observed wolves at 31–39% of operable cameras and juveniles (i.e., <6 months old) at 2–11% of operable cameras per year (Table 2). We assigned 2,484 documented wolf mortalities to occupancy cells from 15 June 2015–14 June 2021 (97% of all mortality records; IDFG, unpublished data). Sources of mortality cumulatively considered as harvest in this study were 43.8% hunting, 36.1% trapping, 17.7% control actions for conflict management, 0.9% illegal kill, 0.8% roadkill, 0.5% unknown cause, and 0.3% other (e.g., train kill, accident; K. E. Oelrich, IDFG, unpublished data). Statewide annual harvest totals ranged from 288 in the year prior to the 2017 summer sampling period (i.e., 15 Jun 2016 to 14 Jun 2017) to 579 in the year prior to the 2020 summer sampling period (i.e., 15 Jun 2019 to 14 Jun 2020). Within each survey cell (i.e., 686-km^2 cells), harvest ranged from 0–23 wolves annually ($\bar{x}$ = 1.8, SD = 2.9).

In preliminary assessments, we retained linear relationships for all covariates in the sub-models, except road density in the detection sub-model, which was better supported as a quadratic relationship on detection probability (Figure 2A). The 6-category structure for the effect of year on detection probability (Figure 2B) was better supported than the 2-category structure in the detection sub-model ($\Delta AIC_c = 8.6$). The saturated model indicated adequate model fit ($P = 0.85$).

Our stepwise covariate removal process reduced the saturated model from 44 parameters to a base model of 25 parameters (Table S1 and Figure S1, available in Supporting Information). The majority of covariates in our base model were stationary through time (Figures S1A–S1E) and the lone annually varying covariate (livestock AUMs) demonstrated considerably greater spatial variability than temporal (Figure S1F). In our final model selection step, where we assessed wolf harvest covariates (Figure S1G) in colonization and extinction sub-models, only 1 model garnered similar support as the base model (<2.0 AIC_c; Table 3). This model included quadratic relationships for wolf harvest in the colonization and extinction sub-models (Figures 3 and 4; Table S1).

The best-supported model indicated a positive relationship between detection probability and percent forest cover within 100 m of the camera ($\beta = 0.08$, SE = 0.05), percent forest cover within the survey cell ($\beta = 0.16$, SE = 0.06), and log of functioning camera days ($\beta = 0.96$, SE = 0.16), although forest cover within the survey cell was not strongly predictive. Detection probability was negatively associated with the amount of rendezvous site habitat ($\beta = -0.10$, SE = 0.05). The probability of detecting wolves increased with road density up to roughly 0.6 km/km^2 after which it declined (Figure 2A). With all other covariates held at mean values, detection ranged from a low of 0.24 (95% CI = 0.18–0.30) in 2020 to a high of 0.38 (95% CI = 0.32–0.43) in 2017 (Figure 2B).

TABLE 2 Summary of motion-sensitive camera deployment and images captured for gray wolf occupancy estimation in Idaho, USA, 2016–2021.

	2016	2017	2018	2019	2020	2021
Cameras deployed	207	207	209	209	206	206
Cameras contributing data[a]	194	194	191	197	195	194
Total wolf images[b]	1,860	1,233	2,084	2,079	1,372	1,993
Cameras with ≥1 adult wolf	67	76	72	74	60	64
Cameras with ≥1 wolf juvenile	4	22	16	11	10	10

[a] Difference in the number of cameras deployed versus those contributing data resulted from camera failure due to damage from weather or wildlife or human theft.

[b] Includes repeated images of the same individual(s) taken in the same 3-image, trigger event.

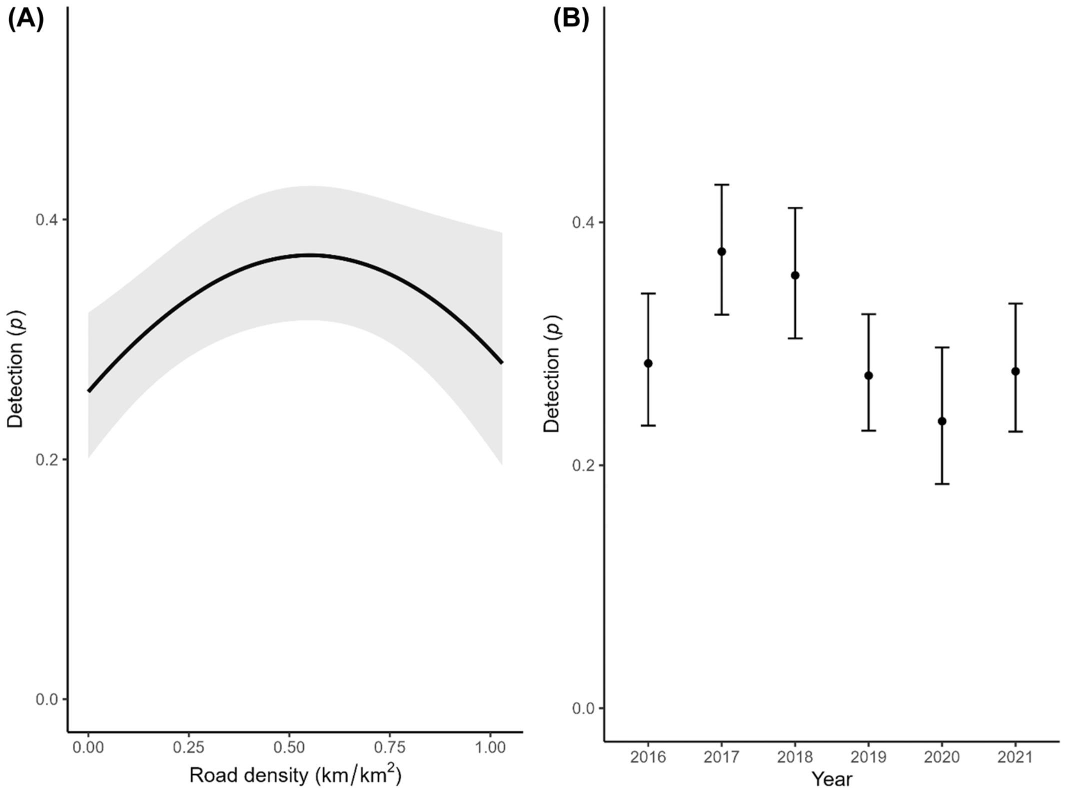

FIGURE 2 Partial effects of road density (km/km^2) and year on detection probability (*p*) of gray wolves from the best supported dynamic occupancy model using motion-sensitive camera images collected each summer in Idaho, USA, 2016–2021. Shaded polygons (A) and bars (B) represent 95% confidence intervals.

The top model for initial occupancy (ψ_{2016}) included a positive relationship with cell forest cover ($\beta = 0.80$, SE = 0.22), mean elevation ($\beta = 0.47$, SE = 0.21), and images of livestock in the initial year ($\beta = 0.34$, SE = 0.19), although images of livestock were not strongly predictive. Initial occupancy (ψ_{2016}) was negatively related to mean slope ($\beta = -0.31$, SE = 0.20; Figure 4).

The best-supported model indicated that local colonization had a positive relationship with cell forest cover ($\beta = 0.56$, SE = 0.18). Colonization was negatively associated with annual livestock AUM values ($\beta = -0.45$, SE = 0.20). Colonization exhibited a non-linear relationship with wolf harvest, with the probability of colonization increasing until harvest reached approximately 5 wolves per cell and then declining with further harvest; confidence intervals were wide, however, suggesting that colonization probability was not well-predicted at higher levels of harvest (Figure 3A). The probability of local extinction was negatively associated with neighboring cell occupancy ($\beta = -0.48$, SE = 0.16) and elevation ($\beta = -0.32$, SE = 0.17), although elevation was not strongly predictive. The probability of local extinction also exhibited a non-linear relationship with wolf harvest (Figure 3B), but where extinction probability decreased as wolf harvest increased from 0 to 8 wolves and increased thereafter. With all covariates set at their mean values, the predicted probability of colonization was 0.25 (SE = 0.03) and was slightly lower than the predicted probability of extinction (0.30, SE = 0.04) although 95% confidence intervals overlapped between the 2 estimates. Projected statewide occupancy (ψ_{2016}–ψ_{2021}) was not significantly different across the duration of the 6-year study, with an estimated high of 0.44 ± 0.03 in 2018 and a low of 0.39 ± 0.03 in 2020 (Figure 5). A comparison of mapped, cell-specific probabilities of occupancy between 2016 and 2021 showed that wolves remained widely distributed within Idaho across the duration of the study (Figure 6).

TABLE 3 Model selection results for dynamic occupancy models using summer camera trap images to examine the effects of wolf harvest on wolf detection (p), occupancy (ψ), colonization (γ), and extinction (ε) in Idaho, 2016–2021. We included the null model (no covariates in any sub-model) for comparison. We ranked models using Akaike's Information Criterion adjusted for small sample size (AIC_c). The base model for p included percent forest cover in the cell and forest cover in the surrounding 100-m radius, road density as a linear and quadratic term, ungulate photos, year, and log of functioning days. The base model for ψ included forest cover, mean elevation, mean slope, and livestock images; γ included forest cover, livestock AUMs, and livestock images; ε included mean elevation and whether the neighboring cell was occupied. Wolf harvest^2 was included in colonization and extinction models and indicates the inclusion of a quadratic relationship.

Model	Parameters	ΔAIC_c	Model weight
Base; γ + wolf harvest^2 ε + wolf harvest^2	29	0.00	0.52
Base	25	1.27	0.27
Base; γ + wolf harvest ε + wolf harvest	27	3.85	0.08
Base; γ + wolf harvest × occupied neighbors ε + wolf harvest × occupied neighbors	30	3.94	0.07
Base; γ + wolf harvest × cell forest cover ε + wolf harvest × cell forest cover	30	4.28	0.06
Saturated	44	41.43	<0.01
Null	4	222.03	<0.01

Our single-season occupancy model indicated a relationship between cumulative wolf harvest and occupancy ($\psi_{2021\text{single-season}}$). There was similar support (<2.0 AIC_c) for models containing linear and quadratic relationships to cumulative wolf harvest, both of which outcompeted the base model (Table 4; Table S3, available in Supporting Information). The model containing the quadratic relationship indicated that at low and intermediate values, cumulative harvest was positively correlated with occupancy, but occupancy decreased at high harvest values (Figure 7A). The model containing the linear relationship indicated a positive correlation between wolf harvest and occupancy (Figure 7B).

DISCUSSION

We estimated occupancy (i.e., asymptotic proportion of area occupied) using motion-sensitive cameras across a large spatial scale (152,292 km^2) to examine potential changes in occupancy in a harvested population of wolves. Wolf occupancy did not significantly change during the 6 years of our study despite considerable harvest (e.g., ~500 wolves in 2021), and our estimates of colonization and extinction were likely offsetting (i.e., 95% confidence intervals overlapped). We did, however, observe non-linear relationships between wolf harvest and colonization and extinction, suggesting that higher levels of wolf harvest might affect occupancy at local scales. The probability of cell colonization decreased when >5 wolves were harvested per cell, whereas the probability of cell extinction increased when >8 wolves were harvested per cell. At lower levels of harvest, however, the predicted response curve means indicated opposite trends (i.e., increased colonization and decreased extinction when <5 or <8 wolves were harvested, respectively). The model including wolf harvest garnered similar support as our base model, suggesting a lesser influence of harvest in comparison to other covariates. We hypothesized that non-linear relationships in response to harvest might be explained by differences between the effects of hunter or trapper harvest and conflict-related wolf

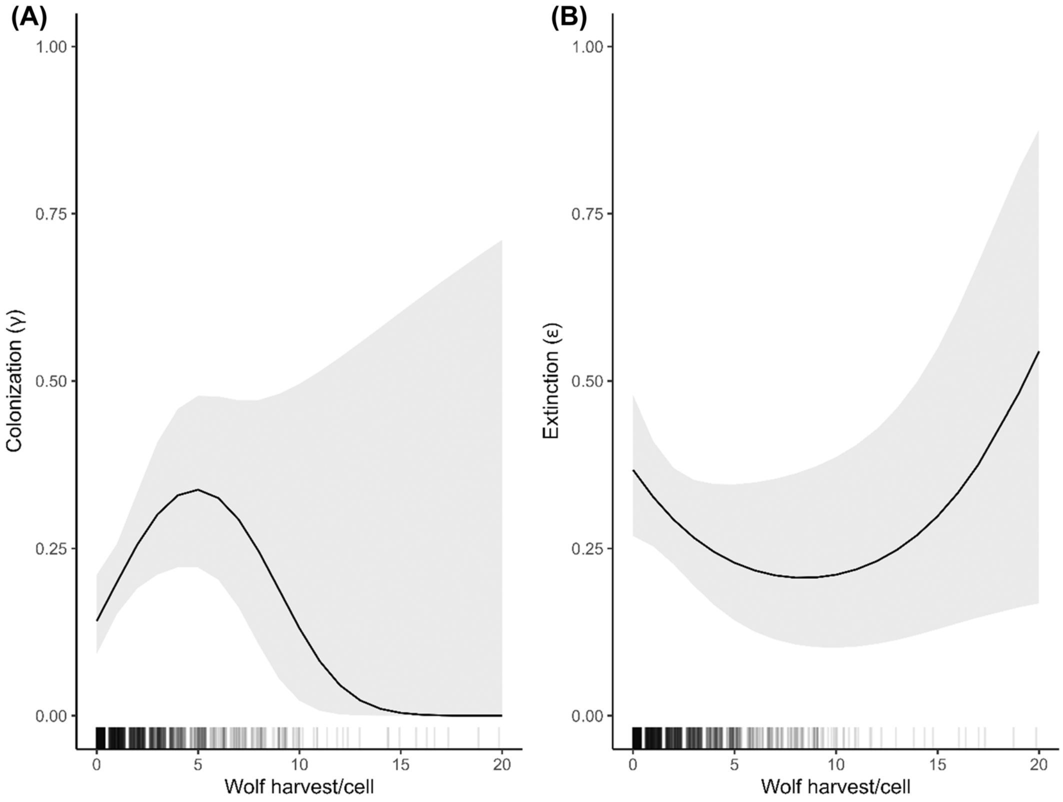

FIGURE 3 Partial effects of cell-specific gray wolf harvest on colonization (A) and extinction (B) probabilities estimated from the best supported dynamic occupancy model using motion-sensitive camera images collected each summer in Idaho, USA, 2016–2021. Shaded areas represent 95% confidence intervals. Tick marks along *x*-axis are values of wolf harvest by cell and year.

removals, given that conflict-related actions are intended to reduce wolf abundance in specific conflict areas and may have the goal of eliminating entire packs. Thus, we conducted a *post hoc* analysis where we considered a model that separated harvest-related mortality from conflict-related mortality. This model had less support than our model where the 2 types of wolf mortality were combined (Table S4, available in Supporting Information).

An alternative explanation for the non-linear relationships among wolf harvest and colonization and extinction is that wolf harvest (i.e., hunting, trapping, conflict-based removals) often occurs in areas where wolves are abundant or in areas of repeat conflict (e.g., areas where recolonizing wolves are repeatedly removed because of conflicts with livestock). Thus, harvest is linked with local wolf abundance at lower levels of mortality, but higher levels of mortality reduce the probability of colonization while increasing the probability of local extinction. We also observed some support for higher levels of mortality reducing occupancy in our single-season occupancy model. The relationships of low to moderate levels of harvest (10–30%) to colonization (positive), extinction (negative), and occupancy (positive) might also be explained by the ability of wolves to redistribute into cells, where wolves were harvested in the previous winter, before our summer camera surveys began. The potential for wolves to rapidly move into neighboring cells is evidenced by the negative relationship we observed between the proportion of occupied neighboring cells and the probability of extinction.

Despite the detected relationships between harvest and colonization and extinction, the addition of wolf harvest did not provide a significant improvement over the base model, thus suggesting a lesser influence of harvest in comparison to other covariates. Further, most covariates (e.g., forest cover, rendezvous site habitat) in our initial

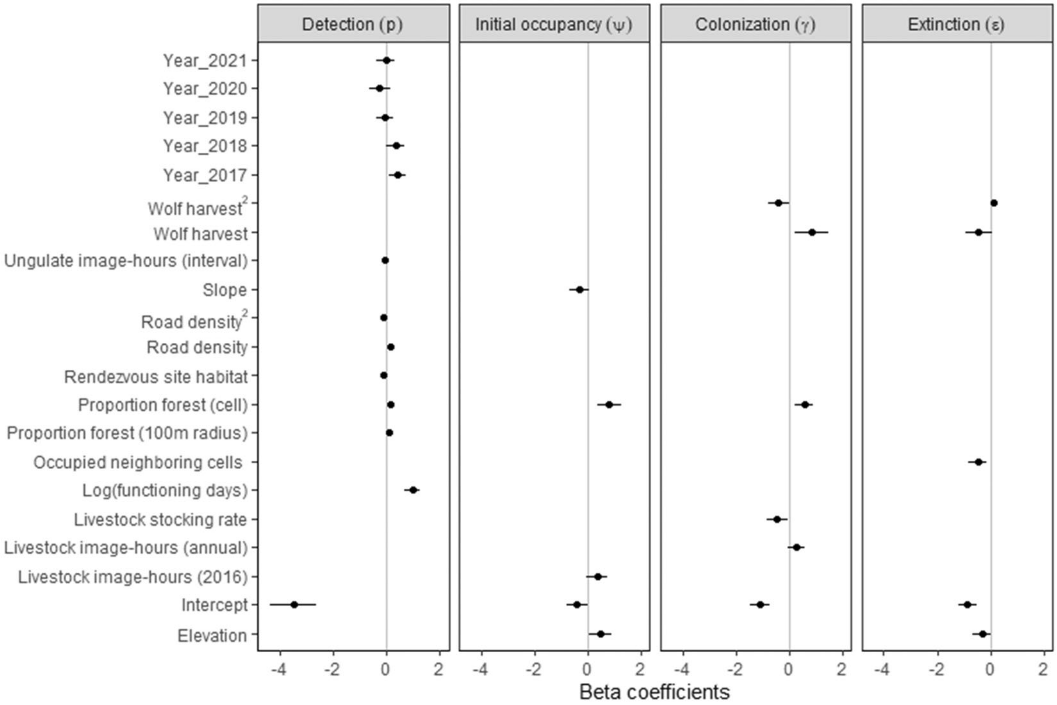

FIGURE 4 Beta coefficients (and 95% CI) for gray wolf detection probability (p), initial occupancy (ψ_{2016}), colonization (γ), and extinction (ε) probability sub-models from the best supported the top dynamic occupancy model in Idaho, USA, 2016–2021. Covariates raised to the second power (e.g., road density^2) indicate a quadratic relationship.

occupancy, colonization, and extinction sub-models were stationary and did not vary annually; thus, model predictions at the cell level were generally equivocal from year to year.

Similar to previous studies (Rich et al. 2013, Ausband et al. 2014, Bassing et al. 2019), there was a strong positive relationship between wolf occupancy and forest cover. Forest cover was strongly supported in the initial occupancy and colonization models and is likely indicative of areas in Idaho with higher productivity and more abundant prey, similar to relationships observed in Ontario, Canada (Kittle et al. 2015). Prey can influence wolf space use, which corresponds to wolf distribution and density elsewhere (Boitani 2003, Fuller et al. 2003, Sells et al. 2022). Likewise, survey cells with higher mean elevation were positively associated with occupancy and negatively associated with extinction and may represent areas of Idaho with greater preferred prey abundance on summer range. Images of ungulates, however, were not supported in the initial occupancy, colonization, or extinction sub-models, potentially because they were not representative of ungulate density of the survey cell but instead of the local area surrounding the camera.

Our camera-generated covariates for humans and livestock garnered little model support, and when they were supported, the relationships were often counter to our expectations. We assumed that more livestock images would be coupled with greater human activity that would discourage wolf activity in an area. Similar to images of ungulates, human and livestock images might not have been representative of human and livestock abundances at the scale of the cell, but this does not explain why livestock images were positively associated with initial occupancy and colonization. Livestock presence in a camera viewshed on summer livestock grazing allotments may not relate to the level of human presence but instead be positively related to the local habitat features that were desirable as forage for livestock and wild ungulates and were components of summer wolf rendezvous site habitat (i.e., wet, grassy areas with minimal topography; Ausband et al. 2010). In contrast, colonization was negatively associated with cell-scale livestock abundance, as enumerated by AUM stocking rates, which aligned with our expectations.

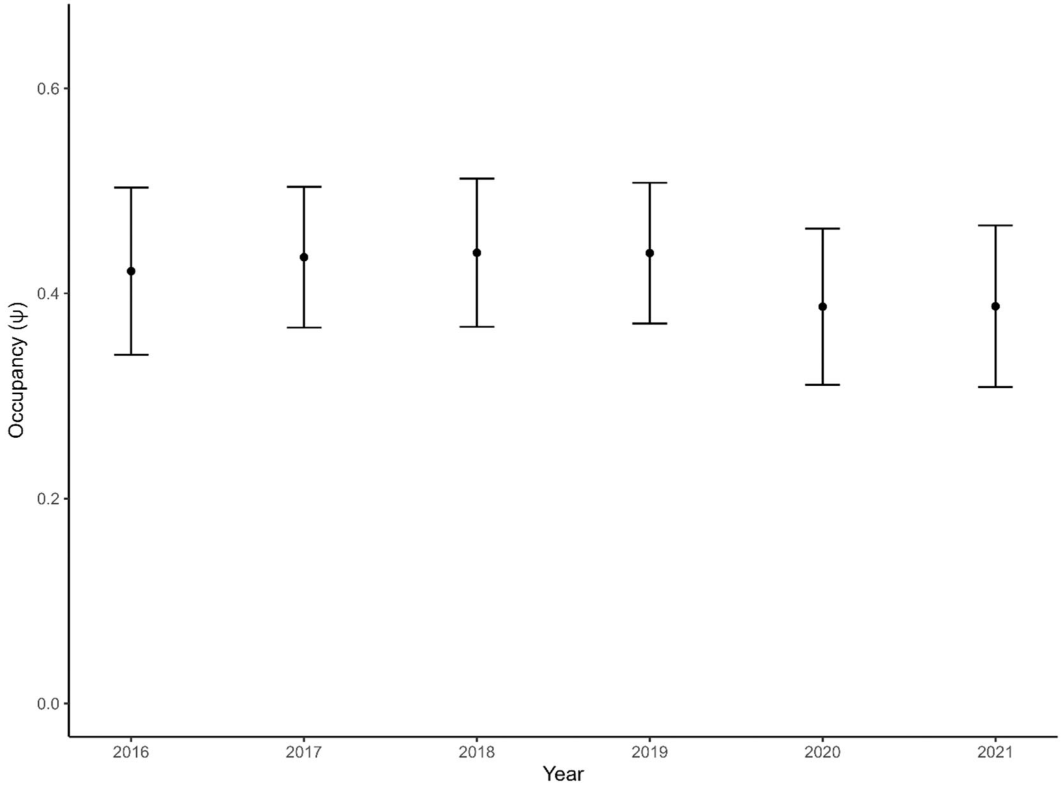

FIGURE 5 Statewide occupancy estimates (±95% CI) for gray wolves from the best supported dynamic occupancy model using motion-sensitive camera images collected each summer in Idaho, USA, 2016–2021.

We also observed several counterintuitive associations with wolf detection probability. Detection probability was negatively related to ungulate image frequency in contrast to our hypothesis that more ungulate images would reflect areas rich in prey, and thus used by wolves more frequently. The converse, however, might be true if ungulates avoided areas commonly used by wolves. We also observed negative relationships between detection probability and the amount of the survey cell that was predicted rendezvous site habitat and road density within the survey cell. These relationships might reflect concentrated use (i.e., near camera locations) of rendezvous site habitat and roads when they were scarce within a cell but dispersed use when a large amount of rendezvous site habitat and numerous roads were present. Although motion-sensitive cameras are effective in eliminating certain factors that commonly influence detection probability (i.e., time of day, observer, and day of year), our model indicated annual variation in detection probability. Because cameras were set up in the same locations each year, annual variation in detection may have been related to changes in local wolf abundance or habitat use (e.g., wolves using a different rendezvous site within the cell).

Although statewide wolf occupancy did not change appreciably during our study, this does not indicate that wolf density and abundance were also stationary (Stauffer et al. 2021). We considered a survey cell used if a camera captured a single image or thousands of images of wolves during each 2-week sampling interval; thus, fewer animals could lead to the same probability of occupancy. Researchers of individual packs in Idaho reported declines in recruitment, group size, and density since harvest began (Ausband et al. 2015, 2017; Bassing et al. 2020). A synthesis of 38 wolf studies by Adams et al. (2008) indicated that human-caused mortality rates >29% may be additive for wolf populations. Considering the estimated harvest rates for the 2019–2020 (38%) and 2020–2021 (31%) hunting seasons (i.e., numerator = total human-caused mortality documented by IDFG for 1 year following each summer abundance estimate, denominator = summer, camera-based abundance estimate; Thompson et al. 2022), it is possible that harvest reduced wolf abundance or limited wolf

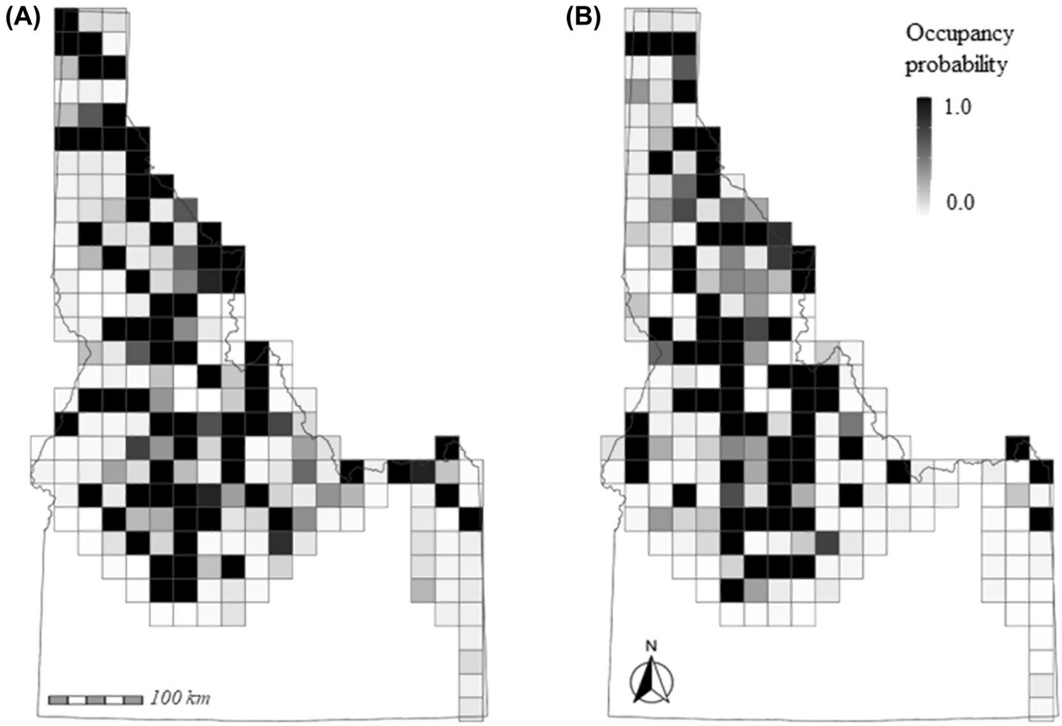

FIGURE 6 A) 2016 and B) 2021 cell-specific predicted probability of occupancy of wolves from the best supported dynamic occupancy model using motion-sensitive camera images collected each summer in Idaho, USA, 2016–2021.

TABLE 4 Model selection results for single-season occupancy models using motion-sensitive camera images to examine the effects of cumulative wolf harvest on wolf occupancy in Idaho, USA, summer 2021. We ranked models using Akaike's Information Criterion adjusted for small sample size (AIC_c). Base model included forest cover, amount of rendezvous site habitat, elevation, slope, livestock images. Wolf harvest^2 indicates the inclusion of a quadratic relationship.

Model	Parameters	AIC	ΔAIC_c	Model weight
Base + wolf harvest^2	11	729.88	0.00	0.53
Base + wolf harvest	10	730.18	0.29	0.99
Base	9	739.11	9.23	0.01

population growth in Idaho during this study. Although recent abundance estimates, albeit somewhat limited in their precision, do not indicate a significant decrease in wolf population size (Thompson et al. 2022).

MANAGEMENT IMPLICATIONS

Public interest in large carnivores is high and wildlife managers need reliable and cost-effective population monitoring techniques. Our study suggests that motion-sensitive cameras can be used to produce useful metrics for managers to assess spatial and temporal changes in wolf occupancy at large spatial scales. Our analyses indicated that although harvest may have influenced wolf occupancy at local scales, wolves were still widely distributed throughout Idaho.

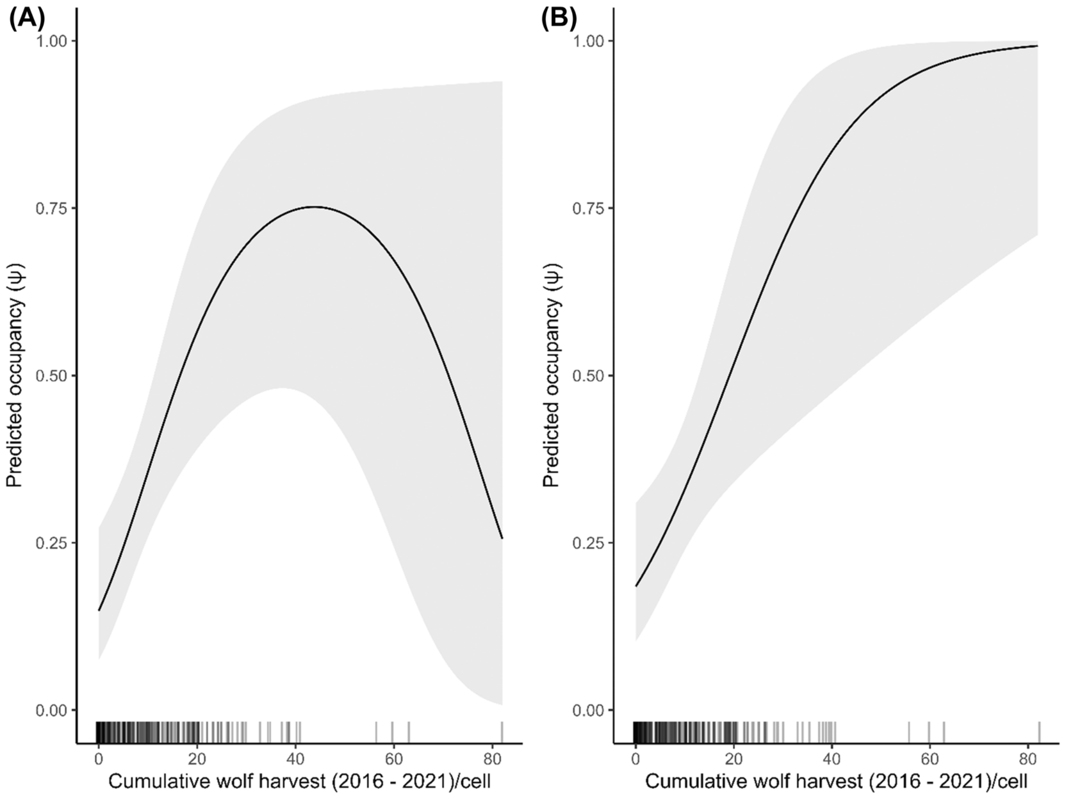

FIGURE 7 Partial effects of cumulative (2016–2021) gray wolf harvest on occupancy (ψ_{2021}) estimated from the best supported single-season occupancy models using motion-sensitive camera images collected in Idaho, USA, summer 2021. A) Model containing a quadratic relationship to cumulative wolf harvest, and B) model including a linear relationship to cumulative wolf harvest. Shaded areas represent 95% confidence intervals and tick marks indicate cell-specific cumulative wolf harvest.

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CONFLICT OF INTEREST STATEMENT

The authors report no conflict of interest.

ETHICS STATEMENT

Our study used noninvasive techniques (i.e., cameras) and adhered to ethics of animal welfare during sampling (American Society of Mammologists 2016).

DATA AVAILABILITY STATEMENT

Data used in analyses can be found at Zenodo (10.5281/zenodo.7897945).

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