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Received: 23 August 2024 | Revised: 30 June 2025 | Accepted: 4 August 2025

DOI: 10.1002/jwmg.70088

THE JOURNAL OF WILDLIFE MANAGEMENT

THE WILDLIFE SOCIETY

RESEARCH ARTICLE

Detection of deer at remote camera sites in relation to snow conditions

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Funding information

Northwest Climate Adaptation Science Center, Grant/Award Number: G19AC00284

Abstract

In the rain-snow transition zone of the Pacific Northwest, climate change is expected to alter the incidence of rain-on-snow and freeze-thaw events, which will change snow density and hardness dynamics. In winter, the ability of economically and ecologically important wildlife species, such as deer (*Odocoileus* spp.), to efficiently move through the landscape and access forage is mediated by snow conditions. Therefore, snow properties such as density and hardness can directly affect how energetically costly it is for these animals to survive. However, little is known about whether and how ungulates use habitats based on snow density and hardness. We deployed a stratified network of remote camera stations in complex forested terrain in Latah County, Idaho, USA, to remotely measure snow depth and detect deer. We also collected snow density and hardness measurements throughout the winter. We used these data to determine the degree to which the probability of deer presence at cameras could be explained by snow conditions and air temperature. Snow depth and density had negative relationships with the probability of deer presence, while ram resistance (a proxy for snow hardness) had a marginal positive effect. We were able to estimate snow conditions important to deer in winter 2020–2021 primarily using data obtained from cameras. This provides an important proof-of-concept that can be applied at different sites and climate conditions to gain a deeper understanding of how deer are affected by snowpack properties. These methods can be used by managers to determine how ungulates are affected by snow depth, density, and hardness collectively and subsequently inform ungulate management in a changing climate.

KEYWORDS

Odocoileus, snow density, snow depth, snow hardness, white-tailed deer, winter severity index

White-tailed deer (*Odocoileus virginianus*; hereafter deer) are of high management interest in the western United States. Deer are ecologically important because of their browsing effects on vegetation communities and density and because they are a source of food for carnivore and scavenger communities (Rooney and Waller 2003). Further, deer are important socially and economically for humans as valued recreational commodities and food resources (Hewitt 2015). When managing this key resource, managers focus on understanding deer demography and population growth in winter when survival rates are lower compared to other seasons, as deer face a higher risk of starvation and predation during winter (Kautz et al. 2020). The health of deer populations after winter is often ascertained using empirical winter severity indices. While the specifics of winter severity indices for use in deer management have changed over time, they typically involve some measure of air temperature and snowpack properties. For example, an early approach used a composite index of climate stress and snow hazard that was estimated using a compaction gauge (Verme 1968). A more recent winter severity index developed by DelGiudice et al. (2002) scores each day based on whether the temperature was <−17.7°C (0 °F) or snow depth was >38 cm, with each day receiving up to 2 points. The winter severity index is the sum of each day's score (DelGiudice et al. 2002). Predictions made using these winter severity indices can then subsequently inform management actions such as the number of tags to allocate to hunters in the following hunting season (Dawe and Boutin 2012).

However, not all snow affects wildlife movement and behavior in the same way. Snowpack depth, density (the mass of water in a snowpack relative to its total depth), and hardness (resistance to penetration; Fierz et al. 2009) collectively determine how much energy deer have to expend when moving through snowy areas (Bunnell et al. 1990). Deep and dense (and therefore heavy) snow creates substantial drag on the legs of deer, forcing them to lift their legs higher to avoid wading through unfavorable snowpack conditions (Parker et al. 1984, Bunnell et al. 1990). If the snow is dense or hard enough, deer may be able to walk on top of the snowpack rather than sink into it, allowing them to move efficiently even where snow is deep (Parker et al. 1984). Thus, the snow's properties can influence the energetic cost of movement.

Ungulates, particularly juveniles, need access to high-quality summer and fall forage to build up necessary fat reserves to compensate for the lack of available forage in the winter (Hurley et al. 2014). Even in mild winters, deer may be in a constant energy deficit (Parker et al. 1999) because grasses and forbs are frequently covered by layers of snow and ice that limit their availability. Other sources of forage such as shrubs, conifer limbs, lichens, and some invasive plant species such as spotted knapweed (*Centaurea stoebe*) may be available as forage above snow cover without much effort (Wright and Kelsey 1997, Christenson et al. 2014). Deer have even been known to take advantage of hard and compacted snow to reach arboreal forage (Massé and Côté 2012). However, when snow is very dense and hard, cratering (i.e., digging holes in snow) for buried grasses and forbs may not be possible, or it may be energetically inefficient (i.e., deer expend more energy reaching the resource than they gain from consuming it; Skogland 1978, Christianson and Creel 2007, Gilbert et al. 2017), leading to declining body condition.

Poor snow conditions that lead to depletion of winter fat reserves in deer can negatively affect vital rates of deer populations (Mech et al. 2001, DelGiudice et al. 2002, Kautz et al. 2020). Deer are at the highest risk of dying of malnutrition or predation in severe winters when limited access to forage depletes their fat stores before the onset of snowmelt (Parker et al. 1999, Mech et al. 2001, Kautz et al. 2020). Deer produce higher foot-loading (mass per surface area of the foot) than wolves (*Canis lupus*) and coyotes (*C. latrans*) because deer have relatively smaller feet than canids, which causes deer to sink deeper into snow than these predators. Thus, deer have more difficulty moving through snow while being pursued, which increases their risk of predation (Telfer and Kelsall 1984, Nelson and Mech 1986, Horne et al. 2019, Olson et al. 2021). Juvenile ungulates, particularly smaller and younger individuals, have the highest winter mortality rate of any age class, and juvenile recruitment strongly influences population dynamics (Lukacs et al. 2018, Horne et al. 2019). Furthermore, females in poor body condition after a harsh winter may give birth later the following year, give birth to smaller offspring, or not breed at all (Horne et al. 2019). Thus, the effects of a severe winter on a population may not become apparent until years later when recruitment or reproductive rates are low (Horne et al. 2019).

Climate change is expected to generally decrease snow depths and increase winter temperatures (Intergovernmental Panel on Climate Change 2023), so existing winter severity indices based only on these 2 factors will indicate that winters are becoming more favorable for ungulates. Conversely, climate change is also changing the frequency of rain-on-snow (Knowles et al. 2006, Musselman et al. 2018) and freeze-thaw events (Masoero et al. 2020). These climate changes will likely alter snow density and hardness dynamics, which may negatively affect ungulate survival through increased energy expenditure during movement, decreased access to forage, and increased predation risk, all of which may counteract some of the benefits gained through warmer temperatures and lower snow depths. While much attention has been given to how deer use habitats based on snow depth, considerably less has been given to how they use habitats based on snow density and hardness, which are less commonly observed. Thus, it is critical to explore whether existing winter severity indices may become less effective management tools as climate change alters snow conditions in ungulate winter range. Determining if and how deer use habitats based on the snow density and hardness may be the first step in modifying winter severity indices to a changing climate.

The objective of this study was to determine relationships between managed wildlife species (i.e., white-tailed deer) and dynamic environmental variables affected by a changing climate (i.e., snow conditions). We deployed a stratified network of remote camera stations in complex forested terrain to measure snow depth, collect temperature information, and detect deer. We paired these observations with snow density and hardness measurements at camera sites to determine if the probability of deer presence was affected by snow and temperature conditions. We hypothesized there would be a combination of snow properties and temperature predictors that best explained the probability of deer presence at camera sites. We predicted that snow depth and snow density would be negatively related to detection probability, while snow hardness and air temperature would be positively related. A second objective was to determine whether we could use only data from cameras and data that could be reasonably collected in the field to detect these patterns of habitat use. While physically based models such as SnowModel (Liston and Elder 2006) are available that can estimate distributed snow data at fine spatial and temporal scales, we sought to determine whether snow properties derived from more empirical methods (i.e., cameras and measurements at camera sites) would be sufficient to detect patterns of deer use.

STUDY AREA

The study area for this project was Moscow Mountain in Latah County, Idaho (Figure 1). We chose this field site because it has a wide variety of topography, canopy, and climate conditions that produce considerable spatiotemporal variations in snowpack properties (Strickfaden et al. 2023*a*). Moscow Mountain spans approximately 800–1,500 m above sea level (a.s.l.). Tree species on Moscow Mountain include ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and fir (*Abies* sp.; Falkowski et al. 2009). A network of 61 trails covering 106 km allowed for reasonable access over winter to collect measurements and check equipment.

The Moscow Mountain Snow Telemetry (SNOTEL) station (SNOTEL 989; 1,430 m a.s.l.) receives 1,060 mm of precipitation annually on average, with a range of 706–1,440 mm between water years 2001–2021 (1 October 2000–1 October 2021). The mean peak snow-water equivalent (SWE) for Moscow Mountain from water years

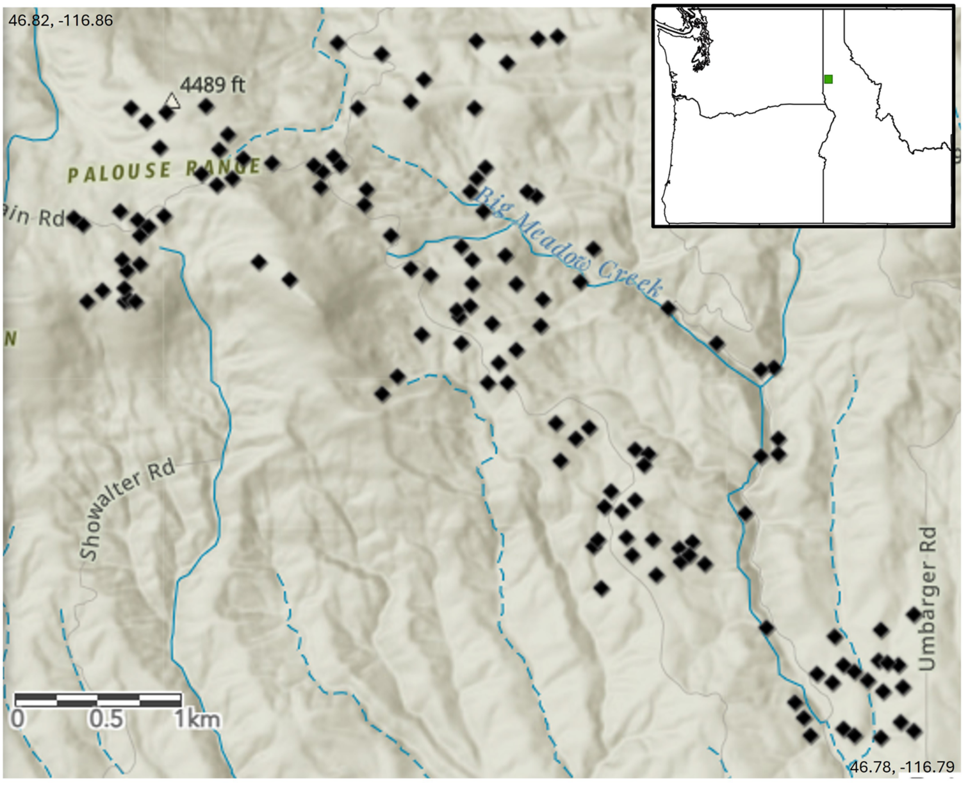

FIGURE 1 Camera locations on Moscow Mountain in Latah County, Idaho, USA, in winter 2020–2021, where we recorded deer presence, snow characteristics, and air temperature.

2001–2021 was 529 mm with a range of 150–902 mm, while the peak SWE in water year 2021 was 594 mm. The mean December–February temperature on Moscow Mountain from water years 2001–2021 was −1.9°C with a range of −4.1–0.3°C, while the mean December–February temperature in water year 2021 was −2.0°C (Natural Resources Conservation Service 2025). These factors together indicate that Moscow Mountain saw average temperatures but more precipitation than average in winter 2021. A few rain-on-snow events followed by freezing periods were observed on Moscow Mountain, primarily in February and March 2021. Moscow Mountain is undergoing dramatic alteration to the snow regime driven by climatic change (Klos et al. 2014; Musselman et al. 2017, 2018; Marshall et al. 2019).

METHODS

Camera site deployments

We deployed 134 camera stations from October 2020–May 2021. We used Reconyx® Hyperfire™ and Hyperfire II cameras (Reconyx, Holmen, WI, USA). We programmed cameras to record one image each hour of the day, including nighttime hours, so each camera recorded at least 24 images every day throughout its deployment. We also programmed the cameras to take motion-triggered images to capture wildlife detections. We set cameras to the highest sensitivity with 3 images taken per trigger and a 1-second delay between images.

We stratified camera sites by elevation, aspect, and canopy cover to sample a variety of snow conditions. Elevation was divided into 5 bins, aspect into 4 bins, and canopy cover into 3 bins for a total of 60 unique combinations of site conditions. Given the number of cameras available to us, this allowed us to place 2 or 3 cameras in each unique combination of site conditions. When cameras were still needed to satisfy a set of conditions, technicians would navigate to areas with the needed elevation and aspect and then find a suitable camera site with the appropriate canopy cover using a densiometer.

On the deployment date, we recorded the height and direction of the camera and the latitude, longitude, elevation, and canopy cover. We mounted and locked cameras onto trees at a height of 2–3 m to prevent snow from blocking the cameras. We maintained cameras every 2–4 weeks throughout the season, coincident with snow density and hardness measurements, to change batteries, ensure proper function, and remove obstructing vegetation. We retrieved each camera after all snow cover had melted at that camera site (April–May 2021).

During camera deployment, we took reference images for superimposing a virtual snow stake (VSS) onto images to measure snow depth (Strickfaden et al. 2023*b*). We placed a reference snow stake with 2- and 10-cm gradations at 5 m, 10 m, and 15 m (when possible) within the viewshed of the camera, and we allowed the camera to take motion-triggered images. We took an additional set of reference images on camera retrieval to account for potential changes in the camera's viewshed during its deployment. We then superimposed VSSs onto images using functions in the edger package (Strickfaden et al. 2023*b*). The VSS approach ensures that deer detections are not biased because physical snow stakes can 1) encourage deer to enter the camera site when they otherwise may not have to investigate the snow stake, or 2) discourage deer from entering the camera site to avoid the snow stake (Strickfaden et al. 2023*b*).

We placed an external LogTag ® TRIX 8 (LogTag, Auckland, New Zealand) temperature recorder at each camera station. We programmed the LogTags to record temperatures at 45-minute intervals. The LogTags were housed inside plastic protective coverings and radiation shields. Each radiation shield was made from 15 cm of polyvinyl chloride (PVC) pipe covered in aluminum foil tape to reflect shortwave radiation and reduce longwave radiation loading. We drilled holes into the radiation shields to allow for increased air flow (Terando et al. 2017). We suspended the LogTag in its housing at the same height as the camera in a sheltered area to minimize the potential impacts of direct shortwave radiation.

After retrieval of each camera, we recorded snow presence, snow depth, and detections of wildlife in each image. We measured snow depth using VSSs present in images. All camera sites had VSSs at 5 m and 10 m from the camera, and some additionally had a VSS at 15 m. If snow depth was >150 cm (the height of the VSS), we recorded it as >150 cm. We identified wildlife to species or genus or marked them as unknown if they could not be confidently identified. We processed images manually using Timelapse2 software (Greenberg 2020).

Snow density and hardness sampling

We measured snow density and hardness at camera sites throughout the winter beginning in December 2020. We took 3 measurements each of snow density and hardness every 3–4 weeks as logistics allowed. We took density and hardness samples near the camera sites in snow visually similar to the snow in the camera viewshed to prevent snow conditions in the camera viewshed from being disturbed beyond normal camera deployment. We measured depth-integrated snow density rather than detailed density profiles to efficiently collect key data to accomplish the project objectives with minimal disturbance of local snow conditions.

Snow density

For snow depths >100 cm, we measured snow density using a federal snow sampler (Kinar and Pomeroy 2015). Because federal samplers perform poorly in shallow snow, we measured snow density in snow depths <100 cm using homemade samplers made of 7.6-cm-diameter (3-inch) PVC pipe (Hanson 2015). We inserted the sampler into the snow to remove a snow core. We retained the core if the depth of snow in the sampler was at least 90% of the actual snow depth and the base of the snowpack had been reached, as evidenced by litter or a soil plug at the base of the core. After we removed the soil plug, we weighed the core to determine its snow-water equivalent (SWE). We converted the SWE measured with the samplers into a density measurement by dividing the SWE by the snow depth. Starting mostly in late February, air pockets would form in the snow, which could make it difficult to take snow density samples that were at least 90% of the total snow depth because the snow could collapse in the sampler. If a snow core of adequate quality could not be obtained after several minutes of effort, we did not measure density on that sampling occasion. We were able to collect acceptable density samples on 549 of the 596 sampling occasions because air pockets were present in the snow during 47 sampling occasions.

We interpolated snow density values measured in the field to derive estimates in the days between measurements at camera sites. On the first day of snowfall, or on the day of camera deployment if the camera was deployed while snow was already present, we set the snow density to 80 kg/m^3 because this was the lowest snow density value recorded in field measurements. On the last day with snow cover, we set the snow density to 600 kg/m^3, the physical upper limit of snow density (Sturm et al. 2010). We then linearly interpolated these physical limits and the density values measured in the field to estimate the snow density on all camera deployment days. We used this approach because snowpacks gradually and steadily densify over time following a generally linear trend (Jonas et al. 2009) because of compaction, melt refreezing, and metamorphic processes driven by temperature and vapor gradients that reduce grain sizes (Bormann et al. 2013). While these snow density estimates include assumptions of minimum and maximum values and linear evolution, they should provide realistic relative values for statistical analysis.

Snow hardness

We measured snow hardness using a ram penetrometer or ramsonde (Snowmetrics, Fort Collins, CO, USA). A ramsonde provides an approximation of the amount of force needed to penetrate through layers of snow (ram resistance). The ram resistance serves as a proxy for snow hardness. True hardness of snow cannot be measured with a ramsonde because of its physical properties (K. Elder, U.S. Forest Service Hydrologist and owner of SnowMetrics [Fort Collins, CO], personal communication). We followed the procedure described by the American Avalanche Association (2016) to collect ram resistance samples on 596 sampling occasions. We were able to collect ram resistance samples on more occasions than snow density because the quality of measurements was not negatively affected by air pockets in the snow.

Our methods required estimates of ram resistance in all images to determine deer presence sensitivity to snow hardness. Yet our measurements were intermittent, and therefore we often did not have measurements at the same time as images. Moreover, physically based models and equations for estimating snow hardness are rare or non-existent as snow hardness is not well characterized in the snow hydrology literature (Rutter et al. 2009). We therefore developed a method to use the collected snow density and ram resistance measurements to back-estimate liquid water content (LWC) from an established empirical equation and then to subsequently use this estimated LWC value to estimate ram resistance (Takeuchi et al. 2007). Liquid water content is the amount of water in a snowpack that is in a liquid state. The LWC in a snowpack influences its resistance to penetration because 1) liquid water is the result of loss of the ice bonds that provide strength to a snowpack, and 2) liquid water lubricates snow grains within the snowpack, which allows the grains to slip past each other. After densification following initial deposition, higher LWC indicates softer snowpacks that provide less resistance, while lower LWC indicates harder snowpacks.

Takeuchi et al. (2007) derived an empirical equation relating snowpack strength (a measure of resistance to pushing and pulling force) to the snow's LWC and density. Whereas LWC is the percent of the snow's total water volume made up of liquid water, density includes both liquid and frozen water. The following is the equation from Takeuchi et al. (2007; hereafter the Takeuchi equation), as translated by Ito et al. (2012):

$$H = 1.31 \times 10^{-8} \times \rho^4 \times e^{-0.18 \times LWC}, \tag{1}$$

where H is the snow strength (kPa) and ρ is the snow density (kg/m^3). This equation can then be rearranged to solve for LWC.

$$LWC = \ln\left(\frac{H}{1.31 \times 10^{-8} \times \rho^4}\right)/-0.18 \tag{2}$$

Given a density sample and hardness profile for a camera site, this equation allows for the estimation of LWC during each snow property sampling occasion.

Ito et al. (2012) measured density and hardness along fixed depth intervals into a snowpack, but we measured depth-integrated density and ram resistance, so we instead calculated the LWC index for the entire snowpack. While these estimated LWC values may not perfectly reflect true LWC (including possible negative values), they provide a useful index for the subsequent estimate of snow hardness from camera images. Additionally, both Takeuchi et al. (2007) and Ito et al. (2012) used a push-pull gauge to measure snow strength, which measures the maximum pressure needed to break through the snow. We recognize that our ramsonde-derived hardness metric and push-pull gauge-derived strength metrics (Takeuchi et al. 2007, Ito et al. 2012) are different measurements for which there is no accepted conversion, but they are acceptable analogs for the objectives of this investigation.

Because the Takeuchi equation estimates snow strength in kPa, we converted the ram resistance of each snow layer into an approximation in kPa by dividing the ram resistance by 1,000 and then dividing again by the surface area of the conical head of the ramsonde, which is approximately 0.00281 m^2. We determined the maximum ram resistance value recorded in each snow hardness sample to most closely match their methods. We then took the mean of the 3 maximum ram resistance values from each sampling occasion to account for spatial variability in snow hardness. Finally, we used the mean of the maximum ram resistances and the snow density value to solve for LWC using the rearranged Takeuchi equation.

We evaluated a suite of generalized linear models (GLMs) to predict the estimated LWC values on each sampling occasion using data collected at the camera sites to develop a model that could be used to estimate LWC values on days between sampling occasions. We tested different combinations of variables including interpolated snow density, the air temperature at the time of the sample, the 48-hour mean air temperature before the sampling occasion, the total number of daily freeze-thaw cycles that occurred before the sampling occasion, and whether it was precipitating during a sampling occasion. We defined a freeze-thaw cycle as a 24-hour interval in which both above-freezing and below-freezing temperatures were recorded. All temperature values used were recorded by the LogTags rather than by the cameras because cameras tend to record biased temperatures because of the delay in heat transfer from the exterior of the camera into the body of the camera where temperature is measured (Strickfaden 2020). We calculated Pearson's correlation values (Pearson 1895) between these predictors and found that the 2 air temperature metrics, 48-hour mean air temperature and immediate air temperature, have a correlation value of 0.68 (Figure S1). This was the only pair of correlated predictors used in these models; all other pairs had correlation values between −0.27 and 0.52. Because we only used this model to estimate ram resistance values and do not attempt to make any inferences about this model itself, the inclusion of moderately correlated predictors in this model is justified to provide the best fit possible to our study area and year.

We tested combinations of these variables and their interactions, and we selected the top model based on Akaike's Information Criterion scores (AIC; Akaike 1973) and coefficient of determination (R^2) values (Table S1). Given the highly complex thermal processes involved in snow melt and refreezing (Pomeroy and Brun 2001), we used many interactions in our suite of models. We did not necessarily seek to build an LWC model that would be applicable in other study areas and years but one that provided the best fit and predictions for our data. We applied the top GLM for LWC to the camera data and used the model to predict ram resistance values throughout the camera's deployment (Table S1). If a predicted ram resistance value exceeded a reasonable upper limit of 3,000 kPa for snow hardness (Höller and Fromm 2010), we set that ram resistance value to 3,000 kPa. We only used the LWC values to estimate snow hardness and did not use them for the ultimate deer presence model.

Deer presence models

Once we estimated snow density and hardness, we used logistic regression analysis with a mixed model structure to examine associations between snow and temperature conditions and white-tailed deer presence at cameras. We grouped data by day for each camera. Snow depth, snow density, ram resistance, and air temperature from the LogTag were recorded as daily means. We scaled predictors before model fitting to make the estimates more comparable by dividing each variable by its standard deviation. We determined Pearson's correlation values (Pearson 1895) between predictors before model building, and all correlation values ranged between −0.35 and 0.31, suggesting no major issues with correlation between predictors (Figure S2). Furthermore, snow depth, density, and hardness are necessarily related to each other; building models that contained combined metrics would go against our attempt to disentangle the effects of snow depth, density, and hardness on deer presence. We tested interactions between snow depth and density, depth and hardness, and density and hardness to account for different ways that snow may influence deer presence, but we did not include a 3-way interaction for ease of interpretation. We also tested an interaction between snow depth and temperature because snow depth and temperature are typical covariates in winter severity indices for ungulates (DelGiudice et al. 2002, Dawe and Boutin 2012). We recorded daily deer presence as a 1 if a deer was detected at any time on that day or as a 0 if no deer were detected on that day. Every model included a random effect for camera site.

We tested combinations of these predictors and interactions using the lme4 package (Bates et al. 2015) in the R programming language (R Core Team 2022), and we selected the most supported model using AIC scores (Akaike 1973). We assessed the classification accuracy of the models using area under curve (AUC; Hosmer and Lemeshow 2000) analysis with the pROC package (Robin et al. 2011). We used DeLong's test for ROC curves to determine significant differences between AUC scores (DeLong et al. 1988). We used analysis of variance (ANOVA) to assess the significance of the random effect.

RESULTS

We captured approximately 852,000 images across 23,165 camera days. These included 1,819 white-tailed deer detections in 15,529 images distributed across 857 camera days. We also detected mule deer (*Odocoileus hemionus*) in 1,022 images, but we excluded these from analysis because of potential differences in habitat use between white-tailed deer and mule deer. We included 24 images of 6 individuals in the *Odocoileus* genus that could not be identified to species. The mean snow depth, snow density, and maximum ram resistance were 49.9 cm (SD = 44.7), 247.9 kg/m^3 (SD = 130.3), and 68.1 kPa (SD = 87.9), respectively. Though snow depth could only be measured to 150 cm from images, we recorded snow depths of up to 203 cm during snow density and hardness sampling.

Snow hardness estimation

The top GLM (R^2 = 0.60) for LWC contained interactions between snow depth, snow density, air temperature at the time of the sample, the 48-hour mean temperature, and the total number of daily freeze-thaw cycles. Though the highly complex interactions make it difficult to determine the relative influence of each of these variables on predicted maximum ram resistance, this is acceptable because this model is consistent with how snow hardness is understood (Pomeroy and Brun 2001). The depth and density of a snowpack affect how long it will take that snowpack to warm or cool with changes in the energy balance, which also necessitates the inclusion of both the immediate air temperature and the average air temperature over the last couple of days. The total number of freeze-thaw cycles then indirectly accounts for the potential formation of hard layers within the snowpack.

The maximum ram resistance calculated with the predicted LWC values matched reasonably well with the measured maximum ram resistance at lower maximum ram resistance values (<100 kPa) but matched poorly at higher maximum ram resistance values (>100 kPa; Figure 2). This model has a greater tendency to underestimate ram resistance. While there were larger errors in the predictions at higher ram resistance values, only 25% of all measured ram resistance values were >100 kPa.

Probability of deer presence

There were 3 competing logistic regressions describing daily probability of deer presence at cameras (Table 1). All 3 competing models contained snow depth, snow density, and an interaction between depth and density, suggesting that these covariates had the strongest effect on the probability of deer presence. Two of the top models also contained ram resistance, and one contained air temperature, though temperature was not a significant parameter in this model ($P = 0.854$).

The model with the lowest AIC score contained snow depth, snow density, an interaction between depth and density, and ram resistance (Table 2). In this model, there was strong evidence for snow density and the depth-density interaction term ($P < 0.001$ for both), weak evidence for ram resistance ($P = 0.085$), and no evidence for snow depth ($P = 0.249$; Figure 3). The mean daily probability of deer presence when there was no snow was 0.138 (95% CI = 0.112–0.167). For each 10-cm increase in snow depth alone, the probability of detecting a deer decreased by 8% (95% CI = 0.799–1.062; Figure 4). For each 50-kg/m^3 increase in snow density alone, the

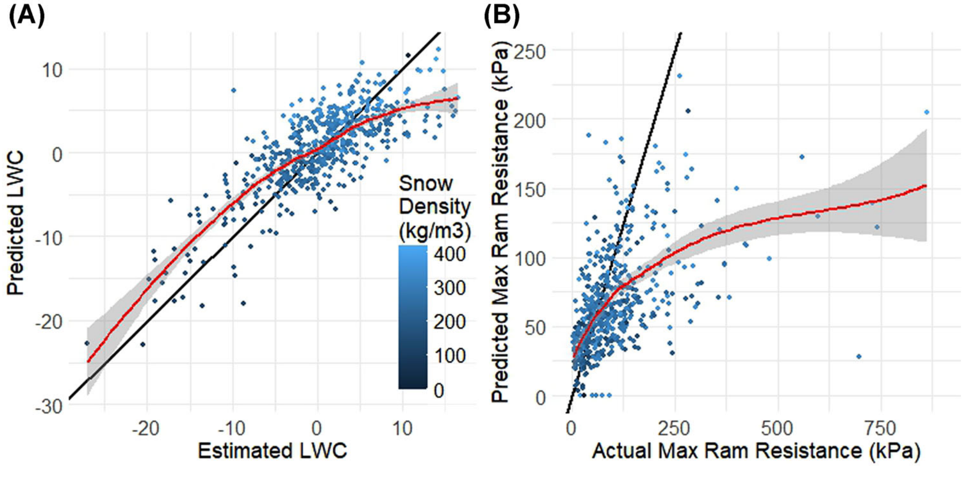

FIGURE 2 A) Estimated liquid water content (LWC) versus predicted LWC from a generalized linear model, as estimated using an inversed version of the snow hardness equation by Takeuchi et al. (2007), and B) actual ram resistance from field measurements versus predicted maximum ram resistance using the predicted LWC values. The black line is a 1:1 line indicating perfect prediction, while the red line is the best-fit line with a locally weighted regression smoother.

TABLE 1 Top models for probability of deer presence on Moscow Mountain in Latah County, Idaho, USA, in winter 2020–2021 according to Akaike's Information Criterion (AIC). Models include snow characteristics (depth, density, and resistance) and air temperature (air temp). Also shown are area under curve (AUC) values. Only models with weight (w_i) > 0.01 are shown.

Model	Intercept	df	Log likelihood	AIC	ΔAIC	w_i	AUC
Depth × density + resistance	−1.98	6	−2,802.57	5,617.14	0.00	0.42	0.8939
Depth × density	−1.98	5	−2,803.90	5,617.80	0.66	0.30	0.8940
Depth × density + resistance + air temp	−1.99	7	−2,802.55	5,619.11	1.97	0.16	0.8940
Depth × density + air temp	−1.97	6	−2,803.87	5,619.75	2.61	0.11	0.8939

TABLE 2 Model coefficients and 95% confidence intervals (CI) for the most supported logistic regression model (snow depth × snow density + ram resistance) of probability of deer presence on Moscow Mountain in Latah County, Idaho, USA, in winter 2020–2021. We determined the P-value for the random effect from analysis of variance on a model containing the same coefficients but no random effect.

Variable	Estimate	Low 95% CI	High 95% CI	SE	Z	P
Intercept	−1.982	−2.188	−1.789	0.100	−19.775	<0.001
Depth	−0.367	−1.004	0.267	0.318	−1.152	0.249
Density	−0.236	−0.303	−0.172	0.033	−7.188	<0.001
Resistance	0.059	−0.013	0.123	0.034	1.723	0.085
Depth:density	−1.334	−1.730	−0.952	0.195	−6.852	<0.001
Random	0.743			0.862		<0.001

probability of detecting a deer decreased by 9% (95% CI = 0.890–0.936). The interaction between snow depth and snow density indicates a steeper decrease in detection probability at high values of depth or density and a less steep decrease in detection probability at low values. Finally, for each 50-kPa increase in ram resistance, the probability of detecting a deer increased by 3% (95% CI = 0.993–1.073). The ANOVA test on the top model with and without the random effect found that adding the random effect reduced the AIC score ($P < 0.001$).

The AUCs of the 3 competing models were all approximately 0.894, indicating high predictive power. There was strong evidence that the AUC scores of these models differed from a status quo model containing only snow depth and mean temperature (AUC = 0.881; $P < 0.001$). This indicates the top models all were better at predicting whether a deer was detected on a particular day than the status quo model, though the practical effect was small (roughly 0.013 AUC points higher).

DISCUSSION

We used data readily available from cameras to determine that snow density on its own and the interaction between depth and density had a strong negative effect on the probability of deer presence, while maximum ram resistance (the proxy for snow hardness) had a marginal positive effect on probability of deer presence. All of these findings together indicate that snow depth alone may not be a reliable predictor of deer presence in winter. Temperature did not meaningfully affect deer presence during the one winter of our study. Although low

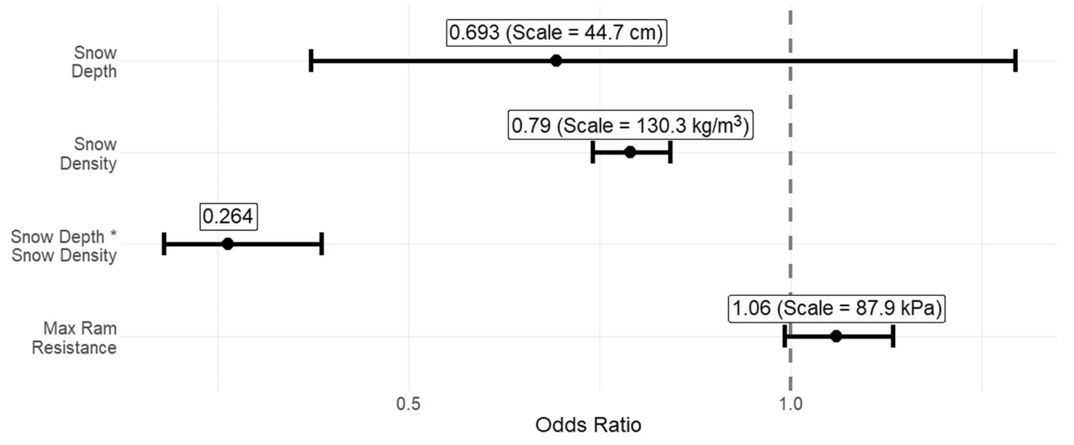

FIGURE 3 Mean estimates and 95% confidence intervals for odds ratios of scaled variables in the top model of probability of deer presence on Moscow Mountain in Latah County, Idaho, USA, in winter 2020–2021. When variables are scaled, the scalar is provided in the text box above each error bar along with the mean estimate. The dashed line shows where no change in odds occurs.

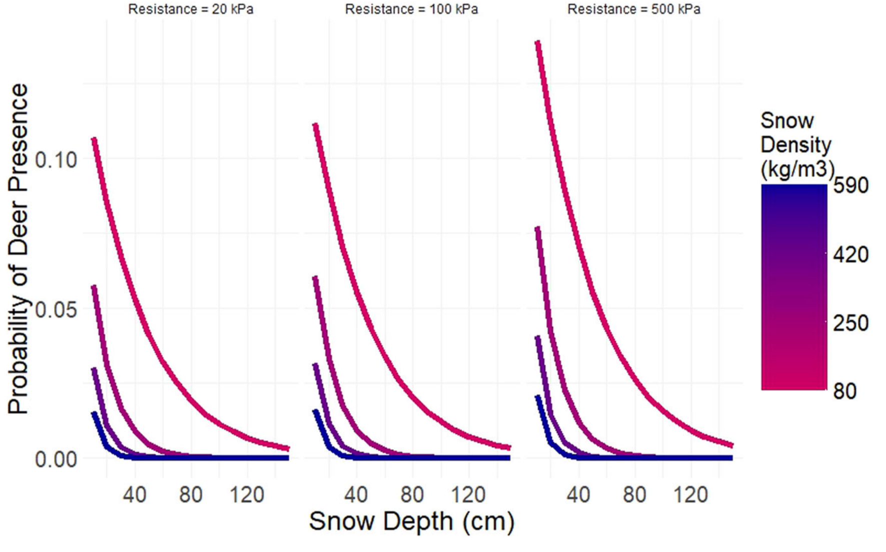

FIGURE 4 Predicted probabilities of deer presence on Moscow Mountain in Latah County, Idaho, USA, in winter 2020–2021. Sub-plots are different levels of maximum ram resistance in kilopascals.

temperatures can influence deer movements (Courbin et al. 2017), environmental conditions such as snow also can have marked impacts on deer and other ungulates. For example, Parker et al. (1999) observed that walking through snow and cratering for forage requires 4.7 times more energy expenditure in black-tailed deer (*O. hemionus sitkensis*) than maintaining homeothermy in cold temperatures. Mech et al. (2001) observed that an early freezing rain event cut off access to forage for elk (*Cervus canadensis*), increasing elk susceptibility to predation throughout the winter. Snow depths of 38 cm are often thought to represent an upper limit of snow depth beyond which deer will no longer use areas (DelGiudice et al. 2002). We detected 112 deer in snow depths >38 cm. While we do not dispute that snow depth affects deer movements and habitat use (Courbin et al. 2017, Gilbert et al. 2017, Anton et al. 2022), our findings show that snow density and hardness can also influence deer presence in winter.

There was considerable variability in probability of deer presence among camera sites, which was captured by the random effect for camera in the models. This random effect could have captured factors such as home ranges of individual deer or deer groups, distribution of forage resources, availability of thermal cover, risk of predation, and differences in false negatives (i.e., missed detections of deer) across camera sites for which we did not explicitly account. Additionally, we recorded several instances of deer walking through existing tracks made by other deer in camera images; the random effect could be capturing preferential use of areas with existing tracks that made movement less energetically expensive. The random effect (and its variance) in our model, nevertheless, was still smaller than the interaction between snow depth and density on deer presence. Thus, after accounting for the inherent variation among cameras, the site's snow depth, density, and hardness demonstrated meaningful effects on probability of deer presence.

Climate-based predictors of deer presence can be estimated or derived from camera data, making our methods relatively easy for other researchers to replicate. We derived snow depth from hourly images taken by the cameras. Similarly, air temperature measurements from cameras that are not in direct sunlight are accurate to within 2°C of true air temperature about 66% of the time (Strickfaden 2020). We supplemented camera temperatures with temperature data from data loggers; other studies that provide data loggers for each camera site may benefit from the more accurate temperature estimates. Finally, while *in situ* snow sampling is preferred and would likely provide more accurate results, models for the estimation of snow density based on day of year (Pistocchi 2016) and meteorological data (Meløysund et al. 2007, Jonas et al. 2009) are available without the need for *in situ* samples as were used in this study.

Snow hardness is highly complex and can change dramatically over the course of a day depending on meteorological conditions, which makes it difficult to estimate empirically. Ito et al. (2012) built their empirical snow hardness equation using data collected in a highly controlled laboratory experiment over the course of only 2 days. The snowpack in our study experienced complex combinations of processes that would not be present in a short laboratory experiment, including dry and wet snow metamorphism (the changing of the shape of snow grains due to age and weather), compaction, canopy unloading (snow falling from the tree canopy), and wind scouring over a long period. These processes contributed to higher ram resistance values than would be expected at a given snow density, which caused the inverted Takeuchi equation to sometimes return negative LWC values. We also expect that estimates of LWC affected by these natural processes led to instances of underestimation of snow hardness at higher values of ram resistance. Despite this, fewer than 1% of our snow hardness estimates were outside of the physically possible values for snow hardness (0–3,000 kPa; Höller and Fromm 2010). Thus, we find that this empirical model performed reasonably well for our single winter of snow observations, particularly when maximum ram resistance was <100 kPa. However, our procedure using sequential equations could have propagated errors in our snow hardness estimates. Testing snow hardness during additional winters at other locations would be helpful to evaluate the robustness of our predictions. The method could also be further improved by collecting snowpack LWC measurements synchronously with hardness measurements.

A single estimate of maximum ram resistance may not provide a complete picture of deer habitat use over winter, which could somewhat explain the marginal effect of hardness found in this study. Deer may respond differently to hard crusts at the surface, middle, or bottom of a snowpack because of differences in how these layers affect movement and foraging (Bunnell et al. 1990). A more thorough examination of how snow hardness affects deer would require an evaluation using complex multi-layer, physically based numerical models (e.g., SNTHERM; Corona et al. 2015), possibly complemented by detailed snow pit observations, to produce a more detailed representation of variability in the snowpack stratigraphy. Such an approach would require detailed climate and snow property data, which were beyond the scope and objectives of the current investigation but may prove more useful to managers. To be more broadly applicable, we sought to use relatively simple data from remote camera stations; therefore, the snowpack density and hardness approach was reasonable for our objectives.

A final important caveat of this work is that the climate at the study location is characterized by a continental-maritime climate regime that is intermediate between the generally warmer and wetter conditions of the more maritime-influenced mountain ranges and colder and drier conditions that are typical for the more inland mountain ranges. In this climate regime, snow deposition frequently occurs close to the freezing point, and midwinter temperature oscillations around 0°C and rain-on-snow events are relatively common (though the region lacks extreme chinook events). As a result, wet-snow metamorphism and refreezing of liquid water within the snowpack can produce relatively dense and strong layers in the snowpack. This is in contrast to colder continental and high elevation snowpacks that may contain very weak depth hoar layers with similar densities to stronger superjacent layers. Therefore, the use of snow density as an analog of ecologically relevant snow properties is likely limited to this and other similar snow regimes.

MANAGEMENT IMPLICATIONS

Deer are often managed post-winter using winter severity indices including only snow depth and temperature, yet we show the importance of snow density and hardness for deer occurrence. Using data readily available from cameras and existing data streams, we modeled snow conditions relevant to deer in a way that can be replicated to provide managers with a more informed assessment of winter severity on deer. This research provides insight into how changing snow and climate conditions might affect deer in regions undergoing a transition from snow- to rain-dominated precipitation regimes. Collaborative efforts deployed to monitor snow conditions can yield valuable datasets that can be applied to entire systems beyond just a single-species focus (Reinking et al. 2022). Further investigation of the methods used here, tested in other areas and other years with different climate conditions could provide finer detail for species management.

ACKNOWLEDGMENTS

This research was funded by the United States Geological Survey Northwest Climate Adaptation Science Center, through funds to the Idaho Cooperative Fish and Wildlife Research Unit and through Cooperative Agreement G19AC00284. Cameras were provided by Idaho Department of Fish and Game. We thank the United States Fish and Wildlife Service, Coeur d'Alene Tribe, Idaho Department of Lands, Bennett Lumber Products Inc., City of Troy, University of Idaho, a private landowner, Star Campos Garcia, Clayton Christiensen, Ryan Martin, and Kat Petersen. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to report.

ETHICS STATEMENT

We did not capture or handle animals as part of this study. We used noninvasive sampling (i.e., cameras) for data collection, and our study plan was reviewed by Idaho Department of Fish and Game and U.S. Geological Survey and adhered to the Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study can be found at https://doi.org/10.21429/bma6-xn17 as well as on the ScienceBase website at https://www.sciencebase.gov/catalog/item/63f7ab26d34e4f7eda4565e7.

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Associate Editor: Tana Verzuh.

SUPPORTING INFORMATION

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How to cite this article: Vega, K. S., A. M. Marshall, L. K. Svancara, D. E. Ausband, and T. E. Link. 2025. Detection of deer at remote camera sites in relation to snow conditions. Journal of Wildlife Management e70088. https://doi.org/10.1002/jwmg.70088