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Reconstructing historical snow depth surfaces to evaluate changes in critical demographic rates and habitat components of snow-dependent and snow-restricted species

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Summary

1. Climate change models consistently predict snow depth declines across the Northern Hemisphere. Snow depth has been linked to the demography of numerous species, and snow depth reduction is expected to affect the demography of some northern species. As many demographic studies depend on long-term population data that extend back beyond available sources of spatially continuous snow depth data, reliable hindcasting of snow depth surface maps is needed.

2. We developed a two-stage regression modelling approach to reconstructing historic snow depths using an existing and readily available spatiotemporal data set of daily meteorological variables across a large, heterogeneous landscape in North America from 1982 to 2003. The final model accounted for ecoregional differences and predicted snow depth as a function of elevation and total snowfall accumulation.

3. Model validations showed that the estimated snow depths were spatially and temporally accurate.

4. We demonstrate how to apply this model with ArcGIS to hindcast monthly and yearly sequences of high-resolution, spatially continuous surfaces of historic snow depths. We also illustrate the utility of the modelled snow depth surfaces for informing predictions of how changes in snow depth may influence the demography and habitats of snow-dependent and snow-restricted species by assessing the spatiotemporal stochasticity of snow conditions that potentially benefit wolverine *Gulo gulo* and the winter ranges, net energy costs and population growth of mule deer *Odocoileus hemionus*.

5. This model can be used to hindcast snow depth surfaces across similar regions; our simple two-stage modelling approach can be applied to other regions where equivalent climate data are available. The resulting spatiotemporal snow depth surfaces estimated from this model can be linked to existing long-term wildlife population data sets to investigate the extent to which snow depth declines may regulate or limit populations.

Key-words: climate change, demography, *Gulo gulo*, hindcasting, mule deer, *Odocoileus hemionus*, population regulation, snow depth, snow model, wolverine

Introduction

Snow depth has decreased across much of the Northern Hemisphere (Mote *et al.* 2005), with the largest reduction in the United States occurring in March–April in the northern and western states, including Idaho. According to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2007), North America should continue to warm. The northern portion of the continent is expected to experience enhanced warming in winter (Mote *et al.* 2005; IPCC 2007), although these projections are complicated by the likely strengthening of the hydrologic cycle and projected increases in precipitation in higher latitudes (Räisänen 2007).

Projected changes in snow conditions have raised concerns by ecologists because some wildlife species can be impacted by snow depth. For example, snow accumulation can negatively affect the abundance, survival, locomotion and population

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growth of some species (Moen & Evans 1971; Parker, Robbins & Hanley 1984) while improving den site selection, hunting success and dispersal of others (Magoun & Copeland 1998; Mech *et al*. 2001; Balkenhol & Waits 2009). Snow depth can be more important than snow cover for some species because snow depth can influence predation rates, dispersal, energy cost associated with movement and availability and access to forage (Parker, Robbins & Hanley 1984; Huggard 1993; Balkenhol & Waits 2009). Thus, some species may be sensitive to changes in snow depth due to the continued changes in climate.

A variety of modelling approaches are available for estimating changes in snow dynamics. Physical-based snow models (e.g. SNOW-17; Notaro *et al*. 2010) have been successfully applied to downscaled climate variables (i.e. precipitation and temperature) to estimate snow accumulation and ablation and project future streamflow, snowmelt and snow depth conditions (Lettenmaier *et al*. 1999). These models provide various outputs (e.g. snowfall, snow depth, snow-water equivalent, snow cover and rain plus snowmelt), although they require subjective model adjustments and can underestimate snow depth where higher snow accumulations occur (Notaro *et al*. 2010). Likewise, downscaling from regional climate models can capture the basic features of snow accumulation and ablation, but Feng *et al*. (2008) emphasized that these approaches involve model uncertainty and biased forcing that cause discrepancies in predicting snow accumulation. Erxleben, Elder & Davis (2002) compared four spatial interpolation methods of snow cover in the Rocky Mountains of the United States and found that regression tree analysis was more accurate than inverse distance weighting, ordinary kriging, and modified residual kriging and cokriging. Additionally, the fit of binary regression tree models has been shown to improve with inclusion of factors that explain snow distribution patterns (Molotch *et al*. 2003). Alternatively, remote sensing algorithms have been successfully applied to simulate snow depth (National Operational Hydrologic Remote Sensing Center 2004), and high-resolution (≤1-km) snow depth data sets are available for some local watersheds in the United States (e.g. Daly, Smith & Smith 2007). While these data sets cover large regions and are readily available, they are unavailable prior to 2003, which constitutes a large portion of the period from which long-term wildlife population data sets are currently available (e.g. Manning 2010).

As existing long-term wildlife population data sets provide estimates of vital demographic rates that span back for decades (Manning 2010), hindcasting historic snow depth surfaces is a vital step to understanding the effects of projected changes in snow depth on critical demographic rates and habitat components of snow-dependent and snow-restricted species. Our goals were to develop and validate a simple hierarchical regression-based modelling approach to identify the suite of factors that best explain snow depth distribution patterns and to use historical records of those factors to hindcast monthly snow depths across the range of geographic and climate conditions in Idaho for years < 2003. This hierarchical approach models snowfall separately from the snowmelt and compaction processes, evaluates the relative importance of factors based on model likelihoods and produces predictive models for extrapolating model coefficients beyond calibration sites to develop spatial maps of snow depth. We chose this region of the Intermountain West because it contains complex terrain and known long-term wildlife population data sets (Manning 2010). We restricted our analyses to this region because wildlife population data are generally not comparable among states (e.g. Rabe, Rosenstock & deVos 2002). We illustrate the utility of this model to assess the spatiotemporal stochasticity of potential snow conditions that benefit a species dependent on deep snow [wolverine *Gulo gulo* (L., 1758)] and one that is negatively affected by it [mule deer *Odocoileus hemionus* (Rafinesque, 1817)].

Materials and methods

STUDY AREA

Our study area was Idaho, USA (218 261 km^2), which represents the majority of the eastern portion of the Interior Columbia River Basin. Snow depth in this area affects the abundance, distribution and fitness of numerous vertebrate species (Christensen *et al*. 1995). Numerous mountain ranges, deep drainages and high desert flats create a wide climatic gradient extending from 216 to 3859 m elevation. This area contains a diversity of vegetation communities (Pfister *et al*. 1977; Hironaka, Fosberg & Winward 1983) and the largest intact wilderness areas in the contiguous United States. Annual precipitation varies from < 25 to > 228 cm, with the majority falling as snow in the northern mountains. Average monthly temperature varies from −9·4 to 32·8°C, with generally higher temperatures in the southeast where humidity is lowest. Further details on the region's environment can be found in Quigley, Haynes & Hann (1996).

Precipitation and average annual temperatures have increased as much as 20% in areas of southern Idaho over the past 100 years, whereas some northern areas have experienced a > 10% decline in precipitation (Karl *et al*. 1996; US Climate Change Science Program 2000). These changes have undoubtedly affected snow depths across this region. Population and occurrence data collected over the past two decades by the Idaho Department of Fish and Game (IDFG) are available for some species across this region and are suitable for evaluating relationships between snow depth, species occurrence and demography.

DATA AND METHOD

We developed a two-stage, hierarchical linear regression modelling approach to estimate snow depth that accounts for snowfall, compaction and melt, which can influence local snow depths (Packer 1962; Jost *et al*. 2007). Our modelling approach was based on developing spatiotemporal data sets of snow depth from an existing land surface grid containing accurate daily meteorological variables that were previously corrected for geographic conditions such as slope, aspect and elevation (Thornton, Running & White 1997). Linear regression models are well suited for spatial prediction such as this because they can include categorical and continuous predictor variables and produce estimates of model parameters that can be used for prediction with observed data from sites beyond those used for model development (Neter, Wasserman & Kutner 1989).

First, we determined model parameters and rates (coefficients) to estimate snowfall readings at snowpack telemetry (SNOTEL) sites from the meteorological data associated with the land surface grid and used these coefficients to convert the grid to estimated snowfall on a monthly basis each year. Second, we estimated snow depth from snowfall by determining parameters and rates associated with compaction and melt processes, extrapolated the snow depth rates across the grid and developed an annual sequence of monthly snow depths.

Meteorological variables

To develop a spatiotemporal data set of snow depths, we first compiled daily estimates of precipitation (cm), maximum temperature (°C) and minimum temperature (°C) from the DAYMET U.S. Data Center http://www.daymet.org with a horizontal grid spacing of 30 arc sec (*ca.* 1 km) across the study area (Thornton, Running & White 1997). Data from DAYMET are well suited for generating snow depth surface maps because it generates a daily sequence of meteorological variables across a 1-km resolution gridded surface based on local conditions including elevation, slope, aspect and latitude and has been shown to be spatially and temporally accurate (Thornton, Running & White 1997). We converted these data to feature class files with ArcGIS 9.2 (ESRI, Redlands, CA, USA) and used these for analysis. The availability of this accurate and validated grid of interpolated daily meteorological variables adjusted for slope, aspect and elevation (Thornton, Running & White 1997) makes these data uniquely suited for reconstructing snowfall and snow depth in each of the 218 261 1 × 1-km grid cells across the study area.

Estimation of snowfall

We used measures of precipitation calculated from the DAYMET U.S. Data Center's daily meteorological variables to estimate observed monthly snowfall at SNOTEL sites ($n = 16$ from a population of 79 sites) across Idaho from 1982 to 2003. SNOTEL data were extracted from the available digital layers within the Western U.S. Climate Historical Summaries http://www.wrcc.dri.edu/summary/climsmid.html. This system of sites was designed to collect snowpack and related climate data in the western United States in places where previous Natural Resource Conservation Service historic snow data correlated well with streamflow volumes (Schaefer & Johnson 1992) and has successfully been used to characterize spatiotemporal features of snowpack (Mizukami *et al.* 2008). The 16 sites we used contained weather data recorded in ≥60% ($n \geq 15$) of the 25 years, and nine of these were the subset of the 440 U.S. sites in Idaho considered homogeneous and of the highest quality by the plurality of seven expert judges in the study by Kunkel *et al.* (2009).

In each grid cell, we separated the DAYMET precipitation totals into snowfall and rainfall components according to air temperature close to the ground (Hamlet *et al.* 2005). Because snowfall is influenced by temperature and relative humidity, the majority of precipitation in nearby regions generally falls as snow at daily mean temperatures between 0 and 4°C (Daly, Smith & Smith 2007). Thus, we calculated four measures of daily precipitation based on these two temperature endpoints. These four measures characterized precipitation throughout the day as snowfall when (i) daily maximum temperature was <4°C, (ii) minimum temperature was <0°C, (iii) mean temperature was <4°C and (iv) mean temperatures was <0°C. We summed each daily measure separately on a monthly basis in each cell to calculate four measures of precipitation for December, January and February of each water year (October 1–September 30), http://amsglossary.allenpress.com/glossary/search?id=water-year1, and used each to reconstruct snowfall. We chose this period because it generally corresponds with the greatest monthly snow accumulations and reduces variability in snow depth attributed to excessive snowmelt outside this period (Croft 1944).

To account for differences in humidity and other climatic variables that may influence the precipitation phase among regions, we used level II delineations of ecological regions in North America (CEC 1997) to stratify the study area into two ecoregions (Western Cordillera and Cold Deserts), each containing eight SNOTEL sites. Although snow accumulation can be strongly correlated with elevation (Jost *et al.* 2007), we did not include elevation in our snowfall models because the DAYMET weather data already accounted for this and other and topographic features.

We used coordinates from each SNOTEL site to extract the 4 monthly measures of precipitation calculated from the DAYMET data and joined these data with the SNOTEL summaries of monthly snowfall. We used all possible combinations of additive and multiplicative effects of ecoregion on each temperature threshold to construct 12 multiple linear regression models (Table 1). Each model estimated the minimum amount (intercept) and accumulation (slope) of snowfall as a function of a monthly measure of precipitation. Models were ranked using the small sample variant of Akaike's Information Criterion (AIC_c; Burnham & Anderson 2002). We considered the highest-ranked model to contain the best snowfall estimates and corresponding measure of precipitation and assessed fit and structure of the best model with residual plots.

Estimation of snow depth

Estimating snow depth required correcting snowfall for compaction and melt. We used records of observed snow depth ($n = 395$) compiled in December, January and February during ≥1 water year between 1996 and 2003 at 68 Snow Course sites defined by and available from digital layers within the Natural Resources Conservation Service National Water and Climate Center Snow Course Survey data http://www.wcc.nrcs.usda.gov/. We chose these sites from the 83 total available in Idaho because only these contained data for the three winter months during ≥1 years of the study period. At each site, we estimated snowfall accumulations by summing our reconstructed monthly snowfall levels from the preceding months during a given water year, starting on December 1.

We split the data set of snow depth records into calibration ($n = 35$) and validation samples (temporal: $n = 275$; spatial: $n = 85$; Table S1). We chose the sample of 35 calibration records because they represented the largest subset of records that were available during a single month and year (January 1998), which was necessary to maximize sample size while avoiding pitfalls associated with using temporally correlated climate data (Araújo *et al.* 2005). These calibration records were from 35 separate Snow Course sites and encompassed a broad range of snow depths (0–185 cm, $\bar{x} = 67$ cm) elevations, slopes and aspects (NE-facing = 7 sites, SE-facing = 10, NW-facing = 11 and SW-facing = 7) comparable to those in Idaho (Table S1).

We constructed a candidate set of 25 linear regression models that accounted for snow compaction and melt by estimating the minimum amount and accumulation of snow depth as a function of snowfall; twelve models also included a natural log (ln) term to further account for snow compaction as a curvilinear function of total snowfall (i.e. increased compaction with greater snowfall; Table 2). We included elevation, aspect and/or slope in some models because it can strongly influence the relationship between snowfall, melt and snow depth (Packer 1962; Jost *et al.* 2007). Aspect was transformed as the

Table 1. Linear regression models developed to predict monthly snowfall from daily DAYMET precipitation and temperature data in the Idaho portion of the Interior Columbia River Basin from 1982 to 2003

Model	No. of parameters	ΔAIC_c	Adjusted r^2
Precipitation* at mean temp† $<0°C \times$ ecoregion‡	4	0	0·58
Precipitation at mean temp $<0°C$ + ecoregion	3	20·8	0·57
Precipitation at max temp $<4°C \times$ ecoregion	4	64·2	0·54
Precipitation at max temp $<4°C$ + ecoregion	3	70·5	0·54
Precipitation at mean temp $<0°C$	2	79·2	0·53
Precipitation at max temp $<4°C$	2	103·5	0·52
Precipitation at min temp $<0°C \times$ ecoregion	4	131·7	0·50
Precipitation at min temp $<0°C$ + ecoregion	3	151·5	0·49
Precipitation at mean temp $<4°C \times$ ecoregion	4	185·2	0·47
Precipitation at min temp $<0°C$	2	187·7	0·46
Precipitation at mean temp $<4°C$ + ecoregion	3	196·2	0·46
Precipitation at mean temp $<4°C$	2	227·1	0·44

Sample size = 1137 monthly totals at 16 SNOTEL sites from December to February, 1982–2003. ΔAIC is the difference from the model with the lowest Akaike Information Criterion value. We chose the top-ranked model as the best.
*Daily accumulation per month (cm).
†Daily average temperature.
‡Western Cordillera (coded in model as 0) and Cold Deserts (1) (CEC 1997).

Table 2. Linear regression models developed to predict monthly snow depth in December, January and February from snowfall in the Idaho portion of the Interior Columbia River Basin from 1982 to 2003

Model	No. of Parameters	ΔAIC_c	Adjusted r^2
Total snowfall* + elevation†	3	0	0·70
ln(total snowfall) + elevation	3	0·2	0·69
ln(total snowfall) + elevation + aspect‡	4	1·0	0·69
Total snowfall + elevation + aspect	4	1·6	0·68
Total snowfall + elevation + ecoregion§	4	1·8	0·68
Total snowfall + elevation + slope	4	2·0	0·68
ln(total snowfall) + elevation + slope	4	2·0	0·68
ln(total snowfall) + elevation + ecoregion	4	2·2	0·68
ln(total snowfall) + elevation + aspect + slope	5	2·9	0·68
ln(total snowfall) + elevation + ecoregion + aspect	5	2·9	0·67
Total snowfall + elevation + ecoregion + aspect	5	3·0	0·67
Total snowfall + elevation + aspect + slope	5	3·5	0·67
Total snowfall + elevation + ecoregion + slope	5	3·8	0·67
ln(total snowfall) + elevation + ecoregion + slope	5	4·0	0·67
ln(total snowfall) × elevation × ecoregion	6	4·1	0·67
ln(total snowfall) + elevation + ecoregion + aspect + slope	6	4·7	0·67
Total snowfall × elevation × ecoregion	6	4·9	0·67
Total snowfall + elevation + ecoregion + aspect + slope	6	5·0	0·66
Total snowfall	2	13·1	0·53
Total snowfall + ecoregion	3	14·7	0·53
ln(total snowfall) × ecoregion	4	15·3	0·53
ln(total snowfall)	2	15·3	0·50
ln(total snowfall) + ecoregion	3	16·2	0·50
Total snowfall × ecoregion	4	16·4	0·51
Elevation	2	29·5	0·25

Sample size = 35 Snow Course stations in January 1998. ΔAIC is the difference from the model with the lowest Akaike Information Criterion value. We chose the top-ranked model as the best.
*Daily accumulation per month (cm).
†Averaged from digital elevation model (m).
‡Transformed as $\sin[A + (90 - A_{max})] + 1$, where A is observed aspect and A_{max} is the direction of most importance (Beers, Dress, & Wensel 1966); here, $A_{max} = 180$ to represent the direction of maximum importance for reducing snow depth through snowmelt attributed to solar radiation.
§Western Cordillera (coded in model as 0) and Cold Deserts (1) (CEC 1997).

$\sin[A + (90 - A_{max})] + 1$, where A was the observed aspect and A_{max} was the direction of most importance (Beers, Dress & Wensel 1966). Here, we considered $A_{max} = 180$ as the direction of maximum importance for reduction in snow depth through snowmelt attributed to solar radiation. As the mountains of the Western Cordillera region generally receive higher snow density and colder late-winter temperatures than the Cold Deserts region, we also included ecoregion as a factor to account for potential regional differences in melt and compaction processes. Models were ranked using AIC_c; we also compared bias and precision among competing models.

Although drifting snows can influence snow depths in the southern mountains (Winstral & Marks 2002), data on local snow drift conditions were unavailable at these spatiotemporal resolutions and thus were not included in the predictor data sets used to calibrate our models. However, the observed snow depth records included in our models did account for the effects of drift on snow depth. We used residual plots to assess fit and structure of our best snow depth model and used the model coefficients to reconstruct land surface maps of accumulated snow depths in December, January and February across the Idaho region each year.

Model validation and uncertainty

We conducted spatial and temporal validations with separate data sets (Table S1) to assess the accuracy of the single or set of competing ($\Delta AIC_c < 2{\cdot}0$) best-ranked snow depth model(s) (Araújo *et al.* 2005). Each validation entailed fitting a trend line [predicted = β (observed)] to monthly snow depths for December, January and February to illustrate the degree to which observed and predicted depths approximated a 1 × 1 correspondence. For each accuracy assessment, we assessed bias with the slope and relative precision with the correlation coefficient (r) and calculated the root mean square error (RMSE) for predicted values. We also used envelope uncertainty maps (EUM) to investigate the extent to which calibration sites captured the range of environmental conditions across our study region (Platts *et al.* 2008). All statistical analyses were performed in Program R (R Development Core Team 2010).

Application to a snow-dependent species: wolverine Gulo gulo

We demonstrated the utility of using spatiotemporal data sets of snow depth to predict the area and inter-annual persistence of snow conditions that could potentially benefit a snow-dependent species such as the wolverine each year from 1982 to 2003. The wolverine is a large solitary mustelid that is morphologically adapted to survive and forage in snow (Haglund 1966; Tefler & Kelsall 1984). This species is dependent on deep, persistent snow for reproduction because females establish reproductive den sites and rear young where snow depths are ≥1 m in March (Magoun & Copeland 1998). In the absence of spatiotemporal snow depth data sets, models of wolverine distribution and investigations of habitat relationships over the past decade have focused on snow cover as a key habitat component (Magoun & Copeland 1998; Aubry, McKelvey & Copeland 2007; Copeland *et al.* 2010).

We predicted the inter-annual area and persistence of snow conditions that potentially benefit wolverines based on grid cells with snow depths ≥1 m on February 28 (Magoun & Copeland 1998). We calculated persistence as the per cent of the 22 years where depth was > 1 m on February 28. We also used historical wolverine locations to examine how well our snow depth model predicted the distribution of snow conditions that potentially benefit wolverines and to evaluate the relationship between wolverine sightings and snow persistence. For comparison, we built an analogous model based on the number of snow cover days. Wolverine locations were from the Idaho Conservation Data Center (IDFG, Boise, ID) and based on observation, photography or collection of specimens from 1982 to 2003. We developed a map of the number of snow cover days (grid cells with ≥1 days having ≥1 cm of snow cover) by February 28 of each year and compared the number of locations encompassed by each distribution map.

Application to a snow-restricted species: mule deer Odocoileus hemionus

We used long-term population data from mule deer to demonstrate how spatiotemporal snow depth data sets from our model may be combined with long-term population data to estimate relationships between snow depth and critical demographic rates. The mule deer is a migratory ruminant adapted to a variety of habitats in most life zones across western North America (Walmo 1981). The presence and depth of snow can influence the ability of ungulates to travel, migrate and avoid predation (Parker, Robbins & Hanley 1984; Huggard 1993). Severe winter weather can depress deer survival and population size, and snow depths > 51 cm increase energy costs, reduce food supplies and reduce survival (Leopold *et al.* 1951; Gilbert, Wallmo & Gill 1970). In areas like Idaho where snow accumulates, deer migrate to traditional wintering areas (Nicholson, Bowyer & Kie 1997). However, analyses on the effects of habitat on population demography largely exclude snow depth because of an absence of reliable snow depth data (e.g. Bishop, Unsworth & Garton 2005).

To first demonstrate that our modelled snow depths could be reliably applied to historic deer data, we assessed the prediction that mule deer density in winter ranges would decline with snow depth (Gilbert, Wallmo & Gill 1970; Nicholson, Bowyer & Kie 1997) and compared the relative importance of our modelled snow depths against an alternative metric, snow cover. We used aerial sightability survey data collected from winter ranges in IDFG Game Management Unit (GMU) 14 (1488 km^2) south of Lewiston, Idaho, in December of 1992 and 1999 to assess and compare the influence of snow depth and average number of snow cover days per month (days with snow depth ≥1 cm) on deer density (Appendix S1). Additionally, we used aerial deer survey data from 1988 to 2003 in GMU 72 (1085 km^2) in southeast Idaho to illustrate the utility of using spatiotemporal snow depth data to evaluate critical demographic rates; we predicted annual population growth as a function of snow depth (Appendix S1). Lastly, to reveal how our modelled snow depth data may help elucidate spatiotemporal patterns in the quality of critical habitat components, we predicted the relative increase in net energy cost for deer to travel in snow depths present in winter ranges each year across Idaho from 1982 to 2003. We applied the estimated snow depth in grid cells on February 28 each year to the empirical energy cost model of Parker, Robbins & Hanley (1984) to calculate net energy costs in each km^2.

Results

The highest-ranked snowfall model predicted monthly snowfall as the total of daily precipitation when the minimum temperature was < 0°C, with an interactive effect between precipitation and ecoregion (Total monthly snowfall in the ith cell = 8·4 × total monthly of daily precipitation when average daily temperature was $< 0°C_i - 6{\cdot}7 \times \text{ecoregion}_i - 2{\cdot}9 \times$ interaction of these variables + 20·1; $F_{3,133} = 230{\cdot}7$, $P < 0{\cdot}001$; Table 1). This model estimated a greater minimum amount and accumulation of snowfall in the Western Cordillera ecoregion compared with the Cold Deserts. Residual plots suggested the model fit the data well, and there was fairly good correspondence between predicted and observed snowfall levels (slope = 0·95, r = 0·79, RMSE = 71·6).

Five competing highest-ranked models ($\Delta AIC_c < 2·0$) explained variability in snow depth as a function of total snowfall and elevation, with added effects of either aspect or ecoregion (Table 2). The two highest-ranked models included only total snow depth and elevation, with the second-ranked model adjusting total snowfall as a natural log to account for increased compaction at greater snowfall levels. The addition of ecoregion or aspect to these two models did not improve model fit (i.e. based on ΔAIC_c, aspect or ecoregion was in either the third-, fourth-, fifth- and eighth-ranked models). Our validations of the two highest-ranked models indicated that the model including the ln of total snowfall produced biased estimates across time and space (time: slope = 0·75, r = 0·81; space: slope = 0·83, r = 0·71), whereas those from the model without the ln term (Snow depth in the ith cell = 0·7 × total snowfall$_i$ (cm) + 0·04 × elevation$_i$ (m) − 41·4; $F_{2,32}$ = 38·4, P < 0·001) were unbiased (Fig. 1). Residual plots further suggested the model without the ln term fit the data well; we considered the simpler model without the ln term as the best and used it to develop a monthly sequence of snow depth surfaces each year. This model was rarely forced to extrapolate far beyond the parameter spaced used to develop the calibration envelope, with envelope uncertainty being highest only at the extreme low (219–721 m) and high (2720–3843 m) elevations (Fig. S1a). Although slope was not in our best model, a non-weighted proportional distance map of this variable showed that the calibration sites encompassed slopes that adequately extrapolated across the majority of the study region (proportional distance of grid cells from the calibration envelope < 0·1; Fig. S1b).

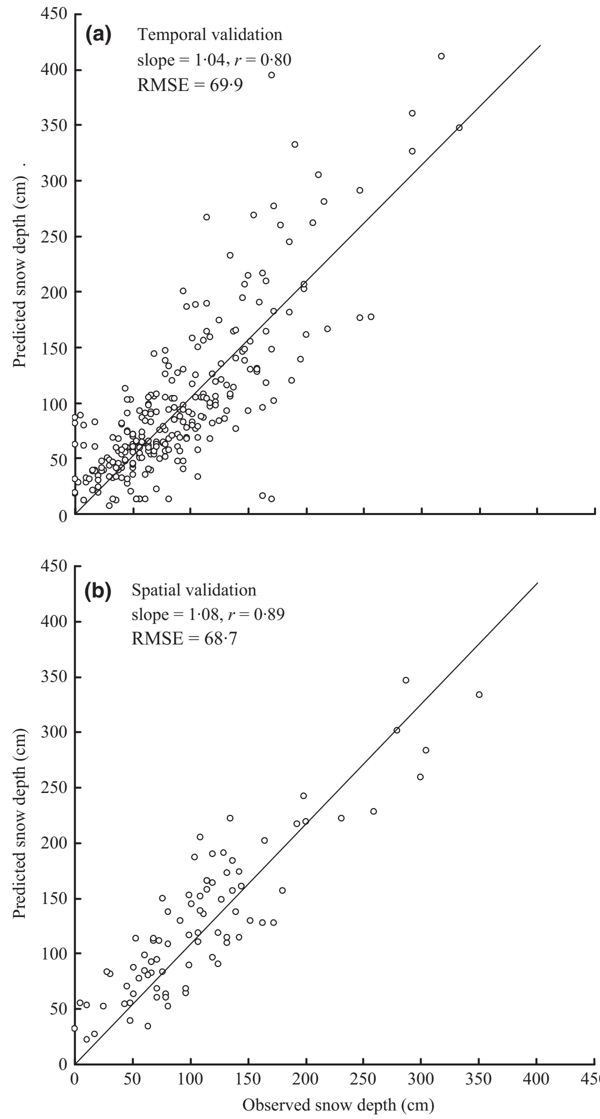

Fig. 1. Accuracy assessment of snow depth model performance across time (a) and space (b). The slope of the trend-line illustrates the degree to which observed and predicted snow depths approximated a 1 × 1 correspondence. A slope near 1 indicated the predictions were unbiased (i.e. did not over- or under-predict snow depth). The correlation coefficient (r) represented the relative precision of the model. Predictive models with $r \geq 0·8$ were considered precise. The spatial validation was based on observed and predicted snow depths from 1996 to 2003 at the 33 snow course stations not used in model calibration (n = 85 temporal records from 33 stations; Table S1). The temporal validation was completed on temporal records of snow depth from 1996 and 1998–2003 (excluding January 1998) at the same 35 Snow Course stations used for model calibration (n = 275 temporal records from 35 stations; Table S1). The Snow Course stations used in the spatial validation were also located across a broad range of elevations, slopes, and aspects (Table S1). Sample sizes between both assessments were unequal due to monthly and annual availability of data at stations.

Predicting winter habitat of wolverine Gulo gulo *1982–2003*

Our snow depth model predicted 101 377 km^2 distributed across the Idaho region where snow depth was > 1 m on February 28 for ≥1 years (Fig. 2, Table S2). This area encompassed 83% (n = 36) of the wolverine locations during this period compared with 98% (n = 42) encompassed by the distribution of cells based on the number of snow cover days. The model revealed that the area supporting potentially beneficial snow depths varied annually from 21 847 to 98 512 km^2 ($\bar{X}$ = 55 539, SD = 21 183), with the greatest reductions occurring in 1987, 1991, 1992 and 2001 (Fig. S2). It also showed that the persistence of potentially beneficial snow depths varied spatially ($\bar{X}$ = 0·55, SD = 0·33).

Predicting effects of snow depth on mule deer Odocoileus hemionus *1982–2003*

Snow depth was a better predictor of deer density than number of snow cover days (ΔAIC_c = 9·9). Snow depth estimates in GMU 14 were negatively related to mule deer density as predicted (Density = −0·15 × snow depth (cm) + 9·1; adjusted r^2 = 0·46, $F_{1,45}$ = 38·16, P < 0·001). Density ranged from 0 to 18 deer per km^2; the linear regression model predicted density at < 1·5 deer per km at the 51-cm critical depth and 0 at a depth of 61 cm.

With an additive affect of snow depth (*population growth* = 1·22 − 0·00008 × N − 0·020 × snow depth; adjusted

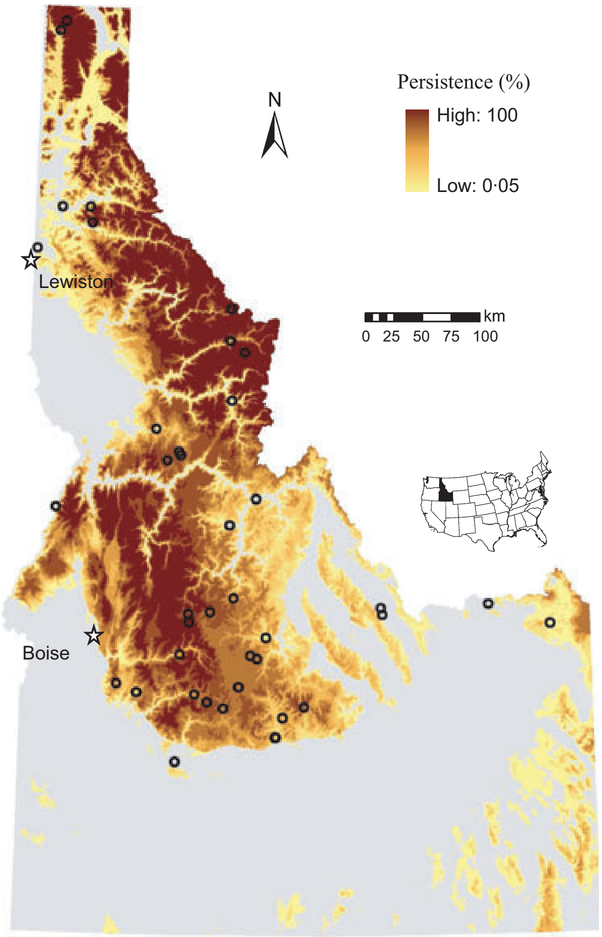

Fig. 2. Inter-annual persistence of areas containing snow conditions that potentially benefit wolverines *Gulo gulo* (snow depth ≥1 m) on February 28 across Idaho, USA from 1982 to 2003. Grey areas are where persistence = 0. Hollow circles are winter locations (December–March; n = 43) of wolverines obtained from Idaho Department of Fish and Game's Idaho Conservation Data Center. Because information on breeding status was largely unavailable, this dataset likely included locations across the winter range beyond that associated with den sites. This model does not differentiate among vegetation types that wolverines are generally associated with (e.g., subalpine, coniferous forest, talus slopes; Edelmann & Copeland 1999; Aubry, McKelvey, & Copeland 2007; Copeland *et al.* 2007) because our focus was not to develop a habitat map, but rather elucidate the benefits of using a snow depth model to evaluate broad-scale changes in this habitat component across space and time.

r^2 = 0·21, $F_{2,\ 12}$ = 1·63, P = 0·2), the population growth model revealed a negative relationship between snow depth and population growth (Fig. S3). By accounting for snow depth, we predicted that the population was at equilibrium density (*population growth* = 0) across a range of abundances and snow depths (Fig. S3). We were also able to show that when the population was at its lowest pre-harvest abundance (N = 1973), equilibrium density was predicted to occur when snow depth = 54·3 cm. At the highest population size (N = 7594), equilibrium density was predicted when snow depth = 32·7 cm.

By using our snow depth model, we also discovered that snow depth on February 28 required mule deer to expend 85·6–197·4% more energy over the past 22 years than expected for travel on bare ground ($\bar{X}$ = 128·9%, SD = 28·9), with apparent multi-year cycles in the time series of energy expenditure (Fig. S4).

Discussion

Spatiotemporal data sets of historical snow depths are needed to assess the extent to which snow depth limits populations and improve predictions on how foreseeable changes in snow depth because of climate change will impact wildlife. We developed and validated a simple two-stage model that reliably reconstructs monthly snow depths in December, January and February of each year from 1982 to 2003 across a large region of complex terrain where known long-term wildlife population data sets exist. A data set of daily meteorological variables that is readily available for the western United States. Thornton, Running & White (1997) was used to first reconstruct snowfall at a 1-km^2-resolution, and broad differences among ecoregions were handled as multiplicative effects. Snowmelt and compaction were accounted for by modelling snow depth separately as a function of snowfall and elevation.

The long-term time sequence of historic snow depth surfaces that can be reconstructed by our model can be used to assess historic patterns in changes of suitable habitats and reliably linked to wildlife population data sets, as demonstrated with wolverine and mule deer. Although the small sample of wolverine locations prevented us from assessing how well wolverine locations matched snow depths annually, our simple predictive model of snow conditions that potentially benefit wolverines identified broad fluctuations in availability of this habitat component based on snow depths > 1 m. This wolverine model excluded 14% of the wolverine locations that were encompassed by a map derived from the number of snow cover days, which possibly reflect differences in how these two snow metrics may account for dispersal records. As snow depth is important for the reproduction, dispersal and distribution of wolverines (Magoun & Copeland 1998; Balkenhol & Waits 2009), our snow depth model can help direct further investigations into the relationships of this increasingly limited resource and its role as a limiting factor on the demography, distribution and dispersal of this species (Aubry, McKelvey & Copeland 2007). Additionally, the estimated inter-annual persistence and annual availability of potentially suitable winter habitat can be coupled with genetic data to identify the importance of these environmental variables as predictors of population connectivity and viability (Balkenhol & Waits 2009; Schwartz *et al.* 2009).

Snow depth and weather variables have been implicated in the dynamics of deer populations (Gilbert, Wallmo & Gill 1970), yet these factors are rarely incorporated directly in analyses or modelled projections of population dynamics (see Edwards 1956; Peek, Dennis & Hershey 2002 for exceptions). As we demonstrated with the population growth model, joining long-term snow depth and population data can reveal the snow depth that coincides with equilibrium density of a local population. This is a necessary step in estimating the direct or interactive role of snow depth with density-dependent intrinsic factors (Grenfell *et al*. 1998; Turchin 2003), and projecting the impacts of future predicted snow depth declines on population dynamics. Another aspect of predicted climate change impacts that may alter the demography of populations involves possible shifts in the period of precipitation and snowmelt during winter (Mote *et al*. 2005), an aspect we did not investigate.

The North American Mule Deer Conservation Plan identified research objectives that included the compilation, review and analysis of available data on trends of climatic conditions within mule deer ranges, with a focus on long-term weather data (i.e. snow) to develop maps of critical areas (Mule Deer Working Group 2004). The historical snow depths and predicted energy expenditures estimated from our model can be combined with long-term data on local mule deer populations across much of the Western Cordillera and Cold Deserts ecoregions to achieve these objectives and help elucidate the importance of snow depth relative to other factors known to affect the dynamics of northern ungulate populations (e.g. predation, density dependence, habitat loss and harvest).

Our external validations showed that our reconstructed snow depths were strongly correlated with observed snow depth (space $r = 0{\cdot}89$; time $r = 0{\cdot}80$) at Snow Course validation sites. We attribute the residual variation primarily to slope, aspect and land cover, which can further explain variability in snow within watersheds (Packer 1962; Daly, Smith & Smith 2007; Koeniger *et al*. 2008). Snowmelt may be more pronounced in low-elevation south aspects, which could contribute additional stochastic variation and decreased accuracy for snow depths estimated from our model in those areas. However, some of our models included slope and aspect, and our best model did not include these variables probably because snow accumulation across large extents is explained mostly by elevation (Jost *et al*. 2007). Another potential source of error may originate from inaccuracies in the gridded meteorological DAYMET data, which can overestimate the number of cells with precipitation on days when precipitation falls across a large region and underestimate the number of dry cells when precipitation is spatially scattered (Thornton, Running & White 1997). However, Thornton, Running & White (1997) demonstrated high overall success rates at predicting daily precipitation and temperature, and we assume that these sources of error balanced out over our large study area and 1-month temporal scale. We also acknowledge that land cover may be important for predicting snow depth, although we did not include land cover in our models because it was not static across the study area over the 22-year period, and no annual land cover data were available. However, even without land cover in our model, our validations showed that our best model provided reliable estimates of snow depth.

Although independent, our sample of validation sites was obtained from the same type of snow records used to develop our models. As these sites were preferentially installed to forecast water supplies where relatively large amounts of snow accumulate, models calibrated from SNOTEL and Snow Course sites may overestimate snow depth at other locations across the landscape. Additionally, potential sources of measurement error can affect snow depth measurements in SNOTEL data (Julander & Bricco 2006), which likely introduced stochastic variation in our model. However, despite these issues, these point data currently represent the only source of historical long-term snowfall and snow depth records. Notwithstanding the geographic bias in the sampling distribution, the data we used to calibrate and validate our snow depth model were derived from sites located across a broad range of elevations, slopes and aspects representative of those across much of Idaho, and the non-weighted proportional distance map of slope showed that calibration sites encompassed slopes that adequately extrapolated across the majority of Idaho. Moreover, our EUM revealed that our model was rarely forced to extrapolate far beyond the parameter space used for calibration, indicating that it can be extrapolated across most of Idaho with high confidence. Given our validations and EUM, we believe our model can be used to estimate snow depth in the Western Cordillera and Cold Deserts ecoregions. Nonetheless, we caution against applying our model to the Pacific Northwest portions of these ecoregions because we did not account for the effects of maritime climate along the coastal region.

As climate change continues, changes in snow depth across the Northern Hemisphere will likely have a large impact on the demography and distribution of many species (Inouye *et al*. 2000). To increase our understanding of how changes in snow depth will impact the dynamics of populations and inform conservation strategies, it is important to gain insight into the extent to which snow depth limits populations. The two-stage modelling approach presented here provides a simple method of obtaining reliable time-series data on historical snow depths that can be linked to long-term population data. This approach can be applied to other regions where spatiotemporal data sets of meteorological variables and snow recording sites exist. The resulting time series of continuous snow depth surfaces enables researchers to develop spatiotemporal data sets of snow depth relevant to historic data sets for multiple populations. Such data can be used to gain insight into the elative importance of snow depth as a limiting factor on populations by incorporating the time-series data as environmental covariates in population growth models (e.g. Dennis, Kemp & Taper 1998), as well as models of occupancy and distribution.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Environmental coverage of predictor variables: (a) envelope uncertainty map (EUM) for extrapolating the best snow depth model beyond the parameter space used in model calibration and (b) non-weighted proportional distance map from slopes associated with the calibration sites used in model development across Idaho, USA, 1982–2003. The EUM is a contribution-weighted average of distance maps associated with each model parameter. This method estimates prediction uncertainty by calculating the proportional distance of each grid cell across a study region from the calibration envelope with respect to each covariate in a model, and uses the average of these distance maps, weighted according to the relative contribution of covariates in the model (drop in explained deviance with covariate removed; Platts *et al.* 2008). Dormann (2007) recommends that model predictions should not be extrapolated beyond 1/10th of the parameter range; therefore, caution is advised for regions where the EUM $> 0{\cdot}1$ since this indicates that ≥1 predictors was extrapolated beyond the 1/10th-level (Platts *et al.* 2008).

Fig. S2. Annual estimates of total area containing snow conditions that potentially benefit wolverine *Gulo gulo* winter habitat area (snow depths ≥1 m on February 28) in Idaho, USA from 1982 to 2003.

Fig. S3. Population growth of mule deer in Idaho Department of Fish and Game Game Management Unit 72 from 1982 to 2003 predicted by a Ricker model (Ricker 1954) with an additive affect of snow depth. Population size was estimated from aerial sightability surveys (Unsworth *et al.* 1994) and corrected for harvest; harvest data were obtained from IDFG reports available at https://research.idfg.idaho.gov/wildlife/Wildlife%20Technical%20Reports/Forms/Show%20All%20Reports.aspx. Instantaneous rates vary from $-\infty$ to ∞, with 0·0 representing a stable population, and the maximum value ($r_{\max}$) occurring when a population increases at the maximum possible rate. Graph depicts the ranges of population size and snow depth present during the study.

Fig. S4. Estimated energy costs for mule deer *Odocoileus hemionus* on February 28 of year in the Idaho, USA from 1982 to 2003. Energy costs (%) are relative to traveling on bare ground based on Parker, Robbins & Hanley (1984) energy cost model ($Y = [0{\cdot}71 + 2{\cdot}6 \times (\rho - 0{\cdot}2)] \times \mathrm{RSD} \times e^{[0{\cdot}019 + 0{\cdot}016 \times (\rho - 0{\cdot}2)] \times \mathrm{RSD})}$, where Y = relative increase in energy costs for travel in snow (%), ρ = snow density (g cm^{-3}), and RSD = relative sinking depth [(sinking depth brisket per height) × 100]. We used mean snow density (0·35 g cm^{-3}) for ρ (Parker, Robbins & Hanley 1984) because snow densities were unavailable. Sinking depth is a function of snow depth, density, and hardness (Parker, Robbins & Hanley 1984), and the depth an ungulate sinks into snow is the most appropriate measure of 'effective' snow depth (Parker, Robbins & Hanley 1984). However, no such values are published for mule deer in the Columbia River Basin. Following Parker, Robbins & Hanley (1984), who found that deer sank to the ground during controlled experiments in Oregon and Wyoming (i.e., sinking depth equaled snow depth), we assumed that sinking depth was equal to snow depth (e.g., Turner, Wallace & Brenkert 1994), and used mean brisket height of mule deer (58 cm; Parker, Robbins & Hanley 1984) to compute *RSD* in the corresponding 1-km^2 cell. The relative increase in net cost of locomotion therefore increased exponentially as a function of relative sinking depth. Vertical bars are ±SD.

Table S1. Topographic conditions and data summary associated with Snow Course stations used for snow depth model calibration and validation for winter months in years < 2003 in the Idaho portion of the Interior Columbia River Basin. Numbers in parentheses are averages.

Table S2. Frequency of wolverine *Gulo gulo* locations ($n = 43$) and available area according to inter-annual persistence of potential suitable wolverine winter habitat on February 28 across Idaho, USA from 1982 to 2003.

Appendix S1. Supplemental analyses of mule deer density datasets.

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