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LETTER

Range-wide variation in the effect of spring snow phenology on Dall sheep population dynamics

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Abstract

Understanding the underlying mechanisms of species distributions and range limits is critical to predicting species responses to climate change. The relationship between climate factors and population performance is often assumed to be constant across species' ranges, but factors that limit the persistence and abundance of species may vary spatially. We examined the consistency of climate effects on population performance across the global range of Dall sheep (*Ovis dalli dalli)* in northwestern North America. Using a linear mixed modeling approach, we evaluated the effects of temperature, precipitation, and snow cover on rates of lamb recruitment, which is a key measure of population performance. We used snow cover products derived from NASA's moderate resolution imaging spectroradiometer (MODIS) imagery and gridded climate data as predictors. Lamb recruitment rates were estimated using range-wide aerial survey data from 2000–2015. These consisted of 127 833 records of sheep sightings from 1570 surveys conducted in 24 mountain units over an area of 634 271 km^2. MODIS-derived spring snow cover had stronger effects on lamb recruitment than did temperature or precipitation. Lamb recruitment increased with higher spring snowline elevations, earlier snow disappearance dates, and fewer snow-covered days per year, while the strength of these effects increased strongly with latitude. Simple population models indicate that, based on elasticity estimates, population growth would be reduced by 2% in years with late snow disappearance dates at intermediate northern latitudes, and by 5% at high latitudes. These results suggest that northern Dall sheep populations are more sensitive to changing snow conditions than their southern counterparts. In addition, variable relationships between climatic factors and population performance should be accounted for when modeling species distributions and projecting climate-induced range shifts.

Introduction

Understanding the environmental factors that limit species persistence at range edges is critical to predicting responses to climate change (Sexton *et al* 2009). Most species distribution models predict that ranges will shift with changing climate in a consistent way along all boundaries (Guisan and Thuiller 2005). That is to say, even though environmental conditions vary spatially, the relationship between a given environmental condition and population growth is assumed to be consistent across the species range. However,

a wide range of mechanisms could result in variable relationships between environmental conditions and population performance throughout species ranges, such as influences of interspecific competition, local adaptation, and complex interactions between biotic and abiotic factors (Parmesan *et al* 2005). Knowing whether the relationships between climate factors and population performance are spatially consistent or variable is critical for improving predictions of climate-induced range shifts.

Numerous species worldwide are shifting their geographical distributions to higher latitudes and

elevations in response to climate change (Chen *et al* 2011, Elsen and Tingley 2015). Chen *et al* (2011) found that the distances moved by species are greatest in areas showing the highest levels of warming, with average latitudinal range shifts that have tracked temperature shifts. However, they also concluded that individual species vary greatly in their rates of change, suggesting that the range shift of each species depends on multiple internal species traits and external drivers of change (Chen *et al* 2011).

One climate variable that is changing rapidly is snow. In wildlife population studies, the impacts of changing Arctic snowpacks are not well understood. Snow is a dominant environmental driver that shapes habitat and natural communities in northern ecosystems (Mysterud *et al* 1997, Telfer and Kelsall 1984). Of the many environmental changes occurring in these regions, alterations to snow conditions may have the strongest impact on wildlife populations (Jones *et al* 2001). While warming could lead to earlier snowmelt, expected increases in precipitation in some areas may contribute to deeper snowpack and counteract this effect (IPCC 2013, Manning and Garton 2012). Greater snow accumulation can negatively affect survival and reproductive success of some species by directly reducing forage availability or increasing vulnerability to predation (Collins and Smith 1991, Telfer and Kelsall 1984, Post and Stenseth 1998). Alternatively, the fitness of other species could be improved due to snow cover improving den site conditions, hunting success and dispersal (Magoun and Copeland 1998, Mech *et al* 2001, Balkenhol 2009).

Snowpack conditions are driven by interactions between precipitation and temperature with significant modification caused by solar radiation, vegetation cover, and wind (Pomeroy and Brun 2001, Tews *et al* 2007, Liston *et al* 2002, Pomeroy *et al* 2006). Snow cover has significantly declined in the Arctic in the past 50 years (Brown *et al* 2010). Annual or monthly time series of temperature and precipitation, used in many climate-change studies (e.g. Araújo *et al* 2005, McKenney *et al* 2007), may be inadequate to accurately depict snow cover and assess climate change impacts on high-latitude species (Brodie and Post 2010). Snow cover exhibits tremendous spatial and temporal variability, making satellite-based remote sensing the most feasible approach for comprehensive snow monitoring in remote and inaccessible regions. Remote sensing provides information on snow cover extent because the unique spectral properties of snow make it readily distinguishable from other land cover types (Dozier *et al* 2009). Using remote sensing data to hindcast historic snow extent is a vital step in understanding northern species' responses to projected climate change (Manning and Garton 2012).

Dall sheep (*Ovis dalli dalli*) inhabit northern alpine ecosystems, which may be especially sensitive to environmental change because they occur at both high elevations and high latitudes (figure 1). The Arctic is warming at twice the rate of lower latitudes; temperatures are predicted to rise by 3 °C–6 °C by 2080 (Callaghan *et al* 2004, Olsen *et al* 2011). Average temperature increases and associated changes are likely amplified in northern ecosystems due to strong temperature inversions associated with elevational increases in cold regions. Lack of knowledge about the impacts of climate variability and climate change in alpine ecosystems represents a critical gap in our understanding of how northern ecosystems and their inhabitants are being affected by global change (Putkonen and Roe 2003).

As large herbivores that reside in northern mountain ranges year-round, Dall sheep have strong impacts on alpine plant communities and are important prey for a variety of predators (Hoefs and Cowan 1979). In addition, Dall sheep provide valued subsistence harvest opportunities for residents and draw tourists and trophy hunters from around the world (Watson 1986). Dall sheep likely function as bellwethers of alpine ecosystem health, and signs are pointing towards increasing ailment. Rangewide, Dall sheep populations have declined by 21% since 1990, with sharp declines in parts of their range leading to emergency harvest closures (Koizumi *et al* 2011, Alaska Department of Fish and Game 2014). These declines may be indicators of broad-scale changes occurring throughout alpine areas in northern regions. Indeed, other alpine species are declining as well, including pikas (*Ochotona collaris*) and marmots (*Marmota caligata*) (Lanier *et al* 2015). Although survival of adult Dall sheep appears to be relatively stable over time and space, large fluctuations in lamb production and survival rates (i.e. recruitment rates) are common (Arthur and Prugh 2010, Wilmshurst *et al* 2006). For example, not a single lamb was observed during surveys in a region of the Brooks Range after the exceptionally late spring of 2013 (Rattenbury *et al* 2016). While such extreme years are suspected to cause sheep population declines (Loehr *et al* 2010, Alaska Department of Fish and Game 2011), no quantitative analyses have examined why some populations appear to be resilient while others appear to be vulnerable.

We examined the relationship between environmental conditions and Dall sheep population performance using 16 years of sheep survey data, remotely-sensed snow cover, and gridded climate data. Snow cover may affect Dall sheep recruitment rates in two main ways. First, the birthing (i.e. 'lambing') period generally coincides with spring green-up; if snow cover persists into the lambing period, ewes might not have sufficient reserves to lactate and lambs may starve (Rachlow and Bowyer 1994). Second, snow cover could impede movement and increase vulnerability to predation, a major source of lamb mortality (Arthur and Prugh 2010). Therefore, we hypothesized that recruitment would be negatively affected by delays in snowmelt. We estimated daily snow extent throughout the global range of Dall sheep using moderate

Figure 1. A herd of Dall sheep ewes and lambs are dwarfed by the mountainous landscape in Wrangell St. Elias National Park, Alaska, March 2017. Dall sheep occur in the mountain ranges of northwestern North America, which are generally covered in snow from September through April. Photo credit: Laura Prugh.

resolution imaging spectroradiometer (MODIS) satellite remote sensing imagery that has been collected daily since 2000. Additionally, we synthesized all available Dall sheep survey data from 2000–2015 throughout their global distribution. We paired the remote sensing data with the sheep survey data to analyze the relationship between spring snow cover and recruitment. We also compared the effect of snow with the effects of temperature and precipitation, two covariates widely used when studying range shifts.

We investigated whether the effects of climatic factors on Dall sheep recruitment were constant throughout their range. If the relationship between climate and population performance varies geographically, we would expect the relationship between recruitment and climate variables to vary with factors such as latitude or distance to the range center. Based on the estimated relationships between recruitment, snow cover, temperature, and precipitation, we assessed the effects that changes in climate might have

on Dall sheep population dynamics in different parts of their range. The results of these analyses provide insight about the underlying mechanisms of range limits, thus improving our ability to predict how ranges may shift in response to continued climate change.

Methods

Study area and species

Dall sheep are endemic to northern alpine ecosystems in Alaska and northwestern Canada. This species is a rare example of a North American large mammal that occupies nearly all of its native range and maintains close to historic numbers (Worley *et al* 2004); its current distribution has been relatively unaffected by anthropogenic influences such as habitat alteration or excessive hunting. There is significant genetic variation among eight subpopulations, and these populations have limited dispersal between mountain ranges (Worley
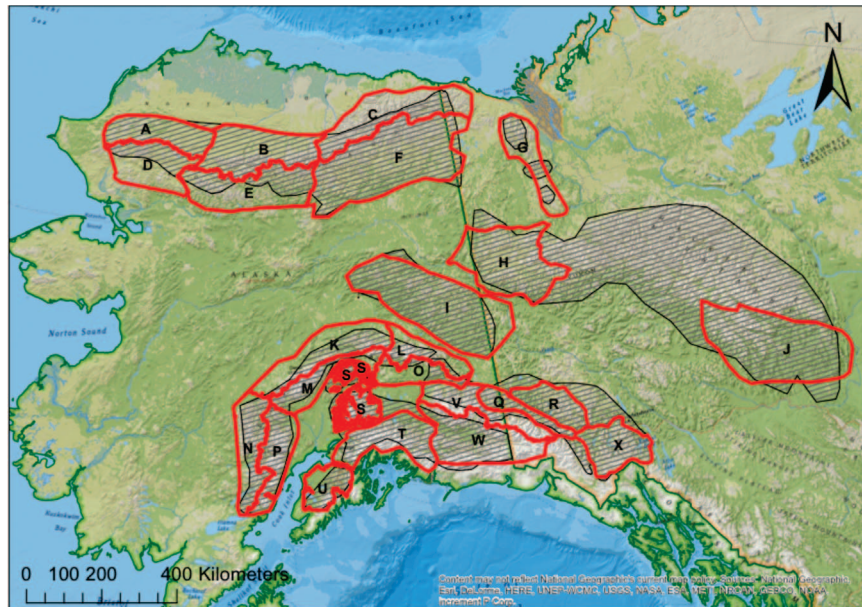
Figure 2. The study domain in Alaska and northwestern Canada, depicting survey units (red outlines) across the global range of Dall sheep (shaded grey areas). We divided the Dall sheep range into 24 mountain units: A = Western Brooks North Slope, B = Central Brooks North Slope, C = Eastern Brooks North Slope, D = Western Brooks South Slope, E = Central Brooks South Slope, F = Eastern Brooks South Slope, G = Richardson Mountains, H = Ogilvie Mountains, I = Tanana Uplands, J = Mackenzie Mountains, K = Central Alaska Range North Slope, L = Eastern Alaska Range North Slope, M = Central Alaska Range South Slope, N = Western Alaska Range North Slope, O = Eastern Alaska Range South Slope, P = Western Alaska Range South Slope, Q = Kluane Mountains, R = Ruby Range, S = Talkeetna Mountains, T = Chugach Mountains, U = Kenai Mountains, V = North Wrangell Mountains, W = South Wrangell Mountains, X = Coast Mountains. Background map source: National Geographic. Map image is the intellectual property of Esri and is used herein under license. Copyright © 2017 Esri and its licensors. All rights reserved.

et al 2004, Sim *et al* 2016, Roffler *et al* 2014). Dall sheep require open, rugged terrain to forage efficiently and to provide for detection and evasion of predators, which include golden eagles (*Aquila chrysaetos*), wolves (*Canis lupus*), and coyotes (*Canis latrans*) (Nette *et al* 1984). They require year-round access to forage and generally occupy areas between 900 m and 2100 m in elevation (Alaska Department of Fish and Game 2014).

Sheep survey data used in this study originated from 14 major mountain ranges, encompassing the global distribution of Dall sheep (figure 2). The Alaska Range (figures 2(*k*)–(*p*)) and Wrangell Mountains (figures 2(*v*)–(*w*)) experience a south-to-north gradient from a maritime to a continental climate under the influence of the Pacific Ocean, whereas both the Alaska Range and Brooks Range (figures 2(*a*)–(*f*)) experience this gradient from west-to-east (Verbyla 2008, Haugen and Brown 1980). Therefore, we divided the Wrangell Mountains into two units (north and south), while the Alaska and Brooks Ranges were each divided into 6 units, resulting in a total of 24 mountain units (figure 2).

Survey data

We obtained sheep survey data collected during 2000–2015 throughout Alaska and Canada from Alaska Department of Fish and Game, National Park Service, Parks Canada, Environment Yukon and Government of Northwest Territories (appendix 1 available at stacks.iop.org/ERL/13/075008/mmedia). Sheep count

and composition data originated from state and federal monitoring surveys, and consisted of 127 833 records of sheep sightings from 1570 surveys conducted over a 634 271 km² area. Surveys were mostly performed during summer (appendix 2), and were conducted using either a fixed wing aircraft or helicopter. Sheep were counted from the air using either distance sampling, stratified random sampling, or minimum count methods (Schmidt *et al* 2012).

Raw sheep counts were not comparable across surveys due to differences in survey methods, locations, and areas. Therefore, we used the ratio of lambs per 'ewe-like' sheep as an indicator of recruitment. Such age ratios are an imperfect estimate of recruitment because they are affected by adult survival as well as lamb survival. However, the survival of adult ungulates is generally so stable that the vast majority (96%) of variation in the ratio is caused by temporal variation in juvenile survival (Harris *et al* 2008). Like other mountain sheep, Dall sheep segregate into groups of adult males (rams) and nursery groups comprised of adult females (ewes), lambs, young rams with small horns, and yearlings of both sexes. Because yearlings, young rams, and ewes are difficult to distinguish during aerial surveys, biologists typically group nursery sheep into lambs and 'ewe-like' sheep, and record the number of sheep in each of these categories. Lamb-to-'ewe-like' ratios are commonly used as indices of sheep recruitment (e.g. Wehausen *et al* 1987, Goldstein *et al* 2005). For simplicity, we will refer to these ratios as lamb-to-

Table 1. Description of covariates expected to have an effect on lamb-to-ewe ratios that were included in the analyses.

Covariate	Mean (±SD)	Description
SDD	day 138 (±11.4)	The average snow disappearance date
SLE	795 m (±488.0)	The snowline elevation on May 15
SCD	216 days (±33.1)	The annual number of snow covered days
Temperature	−4.0 °C (±3.1)	The annual average monthly temperature
MayTemp	3.3 °C (±3.0)	The average May temperature
Precipitation	126 mm (±98.3)	The total annual precipitation
WinterPrecip	29 mm (±32.0)	The total winter (October–April) precipitation
Elevation	1078 m (±369.6)	The average elevation
Latitude	63° (±2.9)	The latitude of the center point of each mountain unit
Longitude	−146° (±5.9)	The longitude of the center point of each mountain unit
Distance	460 km (±178.6)	The distance from the center point of each mountain unit to the range center
Year	2008 (±4.7)	The year

ewe ratios. Although these ratios are lower than true lamb-to-ewe ratios due to inclusion of yearlings and young rams in the ewe category, they are still useful as indices of recruitment. Since lamb mortality would cause the number of lambs to decline over time after the birth peak, we hypothesized that the timing of surveys may have an effect on the lamb-to-ewe ratio. However, nearly all surveys took place at least a month after the birth peak, in which the majority of lamb mortality occurs (Arthur and Prugh 2010). Our analyses showed no effect survey timing on lamb-to-ewe ratios (appendix 2). Because the size of the surveyed area was not reported for the majority of the surveys (66%), we were not able to estimate sheep density for all our data to investigate density dependence. However, an analysis based on a subset of the data showed no effect of sheep density on recruitment rates (appendix 2).

Covariates

We estimated daily snow cover extent from April 1 until July 31 as described in detail by Verbyla *et al* (2017). Briefly, we used the MODIS snow covered-area and grain size (MODSCAG) product to estimate the fraction of each 500 m pixel that was covered by snow (Painter *et al* 2009). If this fraction was >0.15, we classified a pixel as snow covered on that day (Rittger *et al* 2013, Raleigh *et al* 2013). We then estimated the annual first date without snow cover for each pixel, and calculated the annual snow disappearance date for each mountain unit by averaging over all the pixels within the unit (SDD). We also computed the mean SDD for each 100 m elevation zone and used linear regression (all R^2 values >0.95) to estimate the snowline elevation for each mountain unit as a function of the day of the year. The regression equations were then used to estimate the annual snowline elevation on May 15 (hereafter, SLE), since lambing typically occurs mid-May (Rachlow and Bowyer 1991).

We used a satellite derived snow cover metric to evaluate the effect of snow cover duration (SCD) on Dall sheep. Using 500 m MODIS daily snow cover data (MOD10A1 v6), we calculated the number of days each year, from August 1 until July 31, during which snow cover was observed in each pixel. We then computed the mean of all pixel-level snow duration values

within each mountain unit. We accounted for cloud effects by counting cloudy pixels as snow-covered if days before and after were snow-covered (Crumley *et al* 2018).

In addition to the three snow cover variables (SDD, SLE, and SCD), we identified several other covariates that we expected to have an effect on lamb-to-ewe ratios (table 1). For each mountain unit, we estimated the distance to the center of the Dall sheep range, mean latitude, mean longitude, and mean elevation from the Global Multi-resolution Terrain Elevation Data 2010 produced by the United States Geological Survey. We used monthly gridded climate products from the Scenarios Network for Alaska + Arctic Planning (SNAP) to estimate average annual temperature, average May temperature, total annual precipitation, and total winter (October–April) precipitation.

Data analysis

Because snow variables are affected by weather conditions, we first used linear models to examine how much variation in each of the three snow variables was explained by our temperature and precipitation variables. Then, we calculated annual average lamb-to-ewe ratios and covariates for each mountain unit for 2000–2015. To account for the different number of surveys aggregated per data point, we used the number of surveys per mountain unit for each year as weighting factor in our models. First, we used linear mixed models with a random effect of mountain unit weighted by the number of surveys to assess how lamb-to-ewe ratios were affected by of each of the three snow covariates, (1) SDD, (2) SLE, and (3) SCD. We then included the other covariates as additive fixed effects or two-way interactions and used a model selection approach to identify the covariates that best predicted recruitment. We also included models with either (a) latitude, (b) longitude, or (c) distance to the range center. We inspected model residuals to ensure there was no autocorrelation or violations of the model assumptions of homogeneity, normality, and independence. We did not include SDD, SLE, and SCD in the same models because they were largely based on the same remote sensing products. Additionally, we created a correlation matrix with all the covariates and did not include any covariates that were correlated at a level of 0.7

or greater together in the same model (Tabachnick and Fidell 2013). We restricted the number of parameters per model to four to avoid overparameterization. We ranked the models based on the akaike information criterion (AIC) calculated based on the maximum likelihood, and obtained estimates by refitting the models using restricted maximum likelihood (Bolker *et al* 2009). All analyses were performed using R v. 3.3.1 (R Development Core Team 2016) and R package lme4 (Bates *et al* 2012).

Population dynamics

To assess the effect that a predicted increase in climate extremes may have on Dall sheep population dynamics and range shifts, we used elasticity values for Dall sheep population vital rates (e.g. lamb survival, adult fecundity) reported by Prugh and Arthur (2015). The elasticity value of a population vital rate indicates how a relative change in vital rate is expected to affect the population growth rate, λ (Caswell 2001). The reported elasticities were based on a matrix population model parameterized with vital rates from a Dall sheep population in the Central Alaska Range North unit. Estimates of elasticities are relatively robust to changes in vital rates (Caswell 2001), so we assumed the reported values were representative of Dall sheep populations rangewide. In other words, recruitment and survival rates may vary among populations, but the relative importance of each vital rate should not vary because the life history strategy of Dall sheep does not vary geographically. We used our highest ranked linear mixed model to predict lamb-to-ewe ratios under either average spring snow conditions or extreme spring snow conditions. We then assumed that relative differences in lamb-to-ewe ratios correlated directly with relative differences in lamb survival, and we used the elasticity value of lamb survival from Prugh and Arthur (2015), which was 0.094, to calculate the effect of spring snow conditions on λ via impacts on recruitment.

Results

Temperature and precipitation did have an effect on the snow variables, but did not explain all the variation. At best, MayTemp explained 12% of the variation in SLE, and the additive effects of MayTemp and WinterPrecip explained 52% and 64% of the variation in SDD and SCD, respectively (appendix 3). The average lamb-to-ewe-like (hereafter, 'lamb-to-ewe', see Methods) ratio was 0.31 (SD 0.11). Mean annual temperature and latitude were negatively correlated ($r = -0.76$), and seasonal temperature and precipitation estimates were positively correlated with corresponding annual estimates, but correlations among all other covariates were < 0.7 (appendix 4). Overall, there was substantial spatial variability in snow cover that did not show a latitudinal gradient (appendix 5). Lamb-to-ewe ratios

Table 2. Results from the top generalized linear mixed model of climatic factors affecting Dall sheep lamb-ewe ratios, refitted with standardized variables. Intercept and coefficient estimates with their associated standard errors and *p*-values are shown for the fixed effects, and the standard deviation of the random effect is shown.

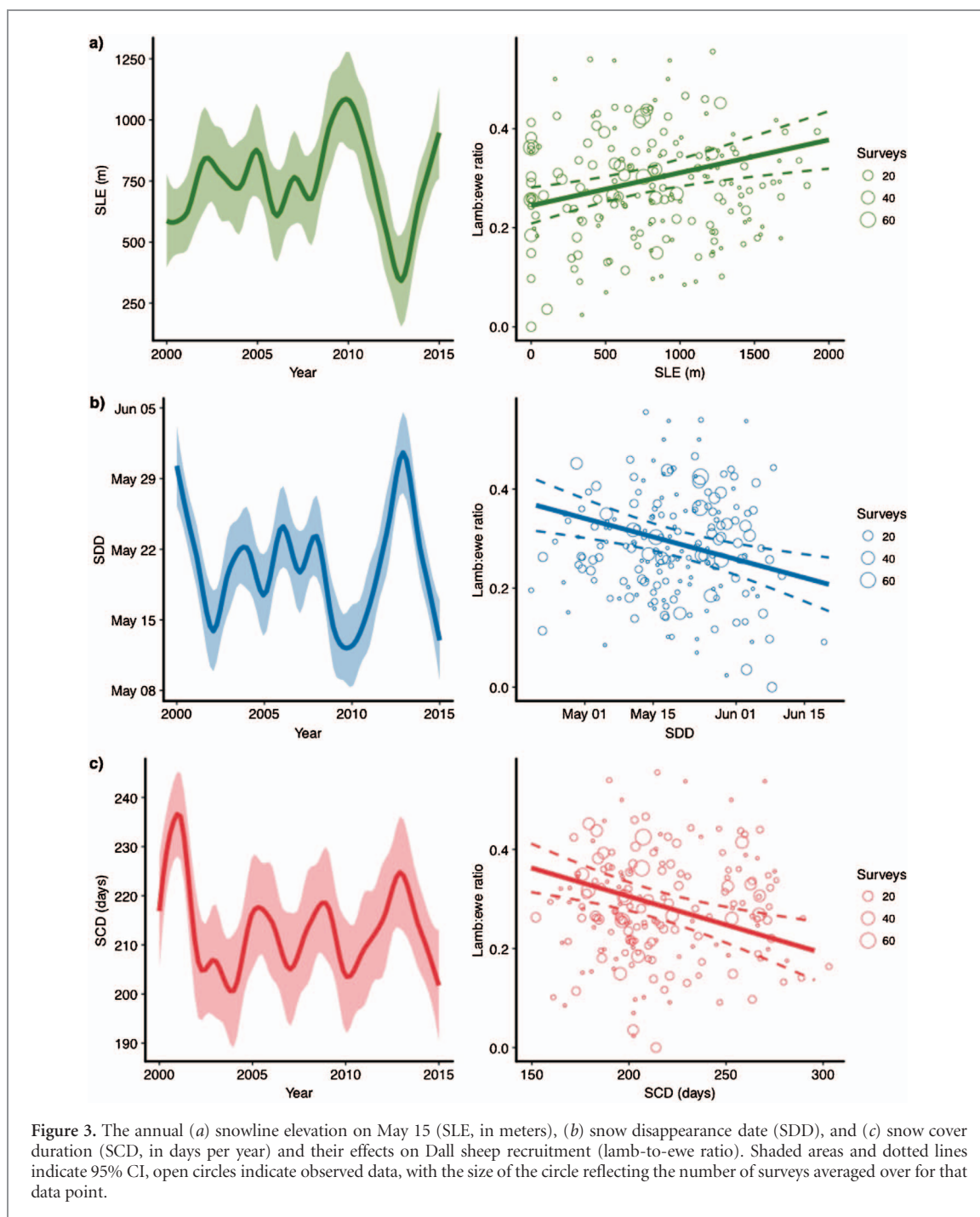| Covariate	Estimate	*p*-value
Intercept	0.187 (SE 0.111)	0.001
SDD	−0.309 (SE 0.081)	0.008
Latitude	0.329 (SE 0.110)	<0.001
SDD:latitude	−0.325 (SE 0.079)	<0.001
random (MountainUnit)	SD = 0.034	

increased with higher SLE (figure 3(*a*), slope: 0.066, 95% CI: 0.026–0.106) and decreased with later SDD (figure 3(*b*), slope: −0.003, 95% CI: −0.004 to −0.001) as well as longer SCD (figure 3(*c*), slope: −0.418, 95% CI: −0.651 to −0.185).

The best-supported model had an AIC model weight of 0.35 and included an interactive effect of SDD and latitude (appendix 6). This model indicated that lamb-to-ewe ratios decreased strongly with later SDD at higher latitudes, decreased less strongly with later SDD at intermediate latitudes, and was not affected by changes in SDD at lower latitudes (table 2, figure 4). SDD was negatively correlated with mean May temperature ($r = -0.7$), but models that included *MayTemp* received almost no model support (appendix 2). Interestingly, SDD was not correlated with either mean annual precipitation ($r = 0.1$) or mean winter precipitation ($r = 0.2$) and showed a different spatial pattern (figure 5, appendix 4).

Because the elasticity values reported by Prugh and Arthur (2015) were based on vital rates from a population in Central Alaska Range North, we used the highest ranked model to predict lamb-to-ewe ratios in this mountain unit. The average SDD in this unit was May 8, corresponding to a predicted lamb-to-ewe ratio of 0.350. Extreme conditions were observed in 2013, when the SDD in this unit was May 28 (the latest observed), corresponding with a predicted lamb-to-ewe ratio of 0.278. Assuming that the predicted 21% decline in lamb-to-ewe ratios translates to a 21% decline in lamb survival, this 20-day delay in SDD yields a decline of 2% in the population growth rate, λ ($\{[0.278–0.35]/0.350\}^{*}0.094$). Alternatively, in the most northern mountain unit (Eastern Brooks Range North) a similar 20-day delay in SDD would yield a decline of 5% in λ ($\{[0.131–0.309]/0.309\}^{*}0.094$) compared to average conditions (SDD: may 26).

Discussion

There is compelling evidence that changes in climate are affecting the distribution and viability of species across a wide range of taxonomic groups worldwide, which underlines the importance of understanding and anticipating the response of species to future climate change (Bellard *et al* 2012, Humphries *et al* 2004). We studied the effect of the timing and duration

Figure 3. The annual (*a*) snowline elevation on May 15 (SLE, in meters), (*b*) snow disappearance date (SDD), and (*c*) snow cover duration (SCD, in days per year) and their effects on Dall sheep recruitment (lamb-to-ewe ratio). Shaded areas and dotted lines indicate 95% CI, open circles indicate observed data, with the size of the circle reflecting the number of surveys averaged over for that data point.

of snow cover and other climate variables on recruitment of Dall sheep throughout their range. We found that (1) all three snow variables were substantially better predictors of Dall sheep recruitment than temperature and precipitation, (2) spring snow cover negatively affected Dall sheep recruitment, (3) snow disappearance date (SDD) was the best predictor for recruitment, and (4) the effect of SDD on recruitment amplified with latitude. The variable relationship between snow cover and population performance was highlighted by our models indicating that a 20-day delay in the SDD would have no effect on the growth rates of southern populations and induce substantial declines in growth rates of northern populations. Our

results thus demonstrate that the effect of climate variables on wildlife is not always uniform throughout a species' range; an assumption that is often made in species distribution models.

As our findings highlight, populations of the same species occurring in distinct environments can experience opposing responses to the same climate variable (Grotan *et al* 2009). The abundant center hypothesis predicts that habitat quality becomes marginal at range edges, often leading to lower population performance (Caughley *et al* 1988, Talley 2007, Sexton *et al* 2009). However, we did not find an effect of the distance to the range center on Dall sheep recruitment. We instead found that recruitment was more sensitive
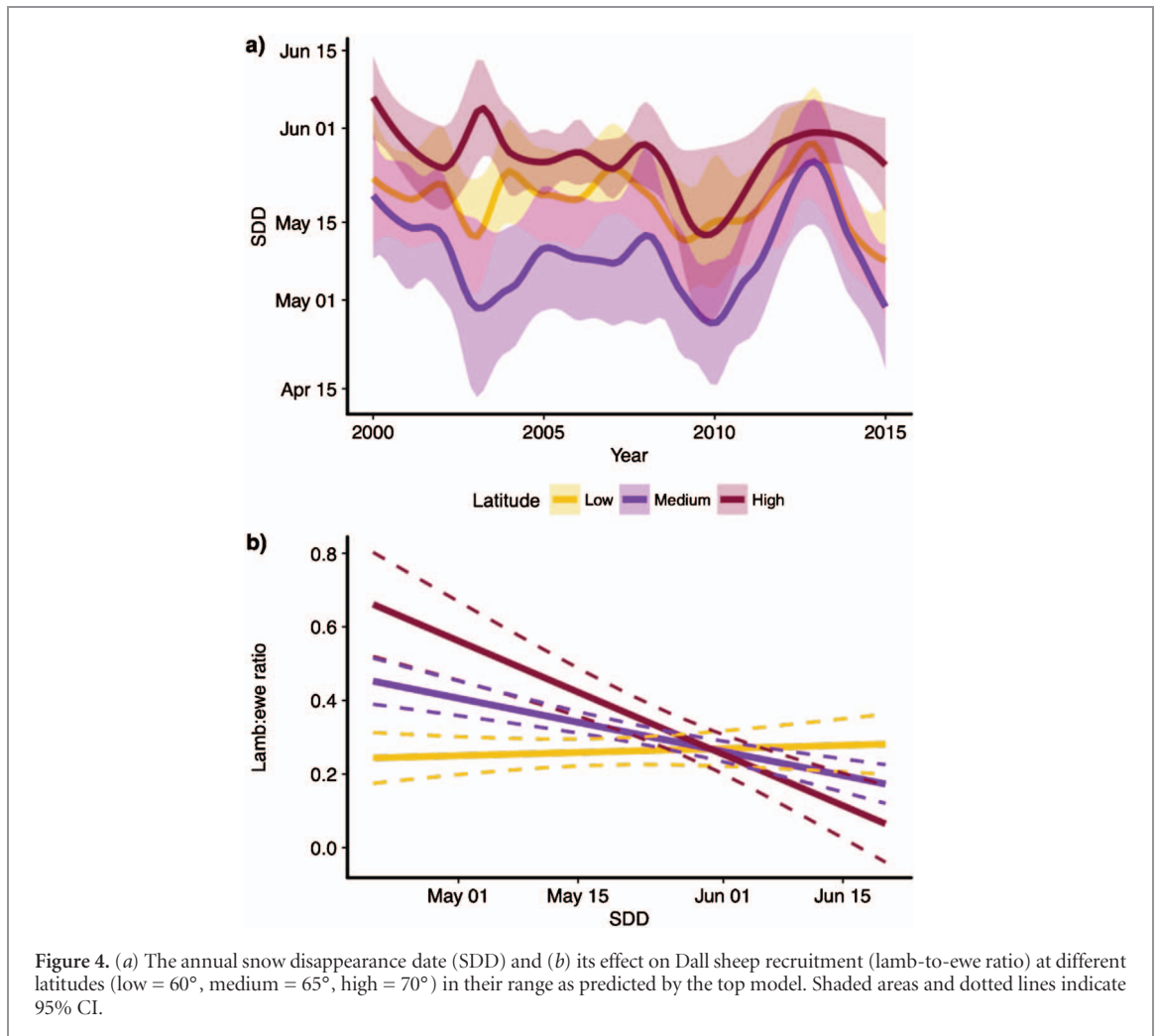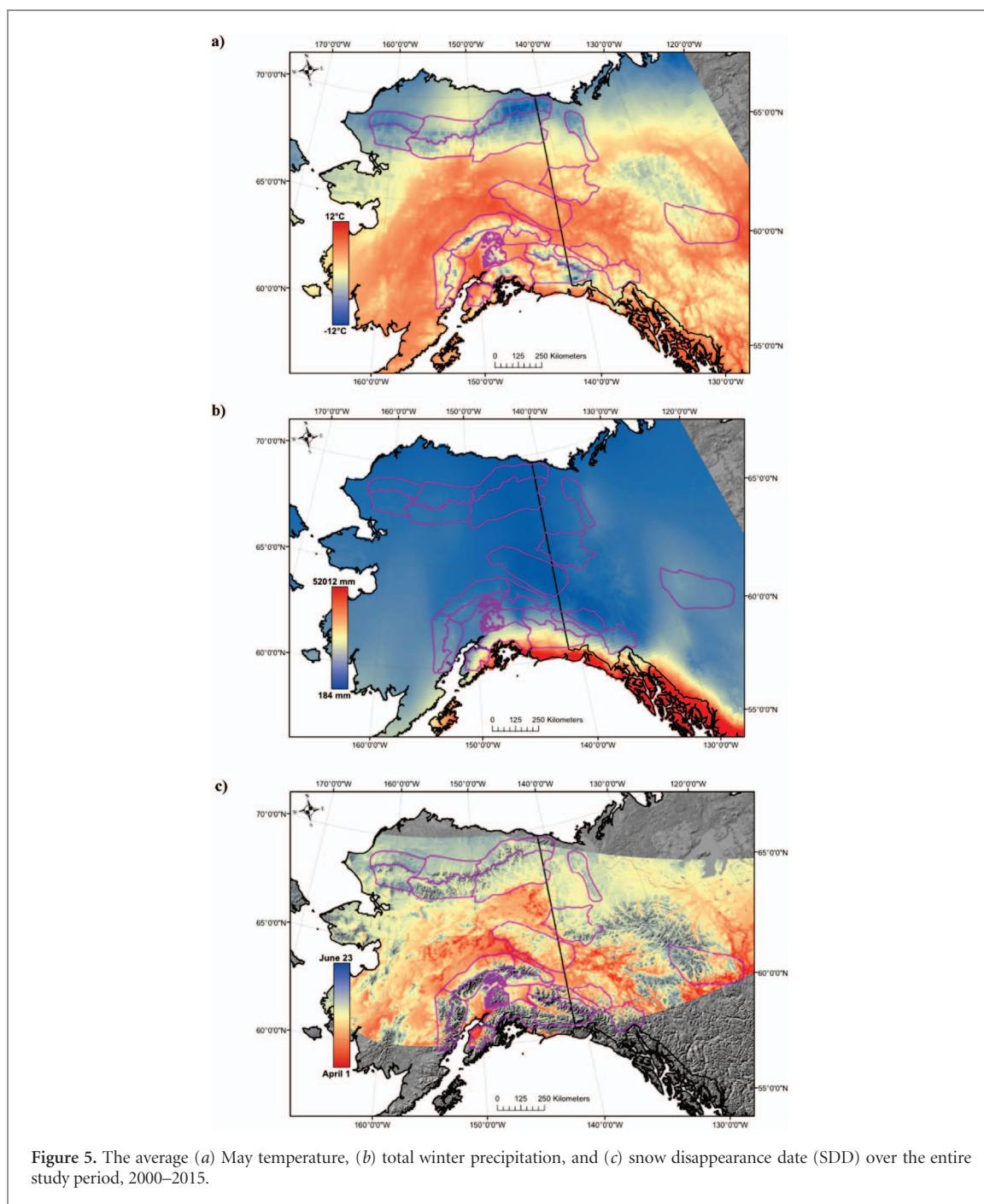
Figure 4. (*a*) The annual snow disappearance date (SDD) and (*b*) its effect on Dall sheep recruitment (lamb-to-ewe ratio) at different latitudes (low = 60°, medium = 65°, high = 70°) in their range as predicted by the top model. Shaded areas and dotted lines indicate 95% CI.

to SDD at higher latitudes than at lower latitudes. SDD might have a stronger effect at high latitudes simply because the snow there generally melts later. However, we found that a wide range of SDDs occurred independent of latitude (figure 4(*a*)). Other possibilities for a stronger effect at high latitudes are shorter growing seasons and decreased amounts of forage, and higher energetic costs due to lower temperatures (Sand *et al* 1995). Although both latitude and SDD were correlated with temperature metrics, models that included temperature received far less support than models that included latitude and SDD. Thus, the latitudinal gradient in sensitivity to snow cover cannot be explained by temperature alone. The lack of an effect of SDD on recruitment at low latitudes indicates that snow cover is not the limiting factor for Dall sheep persistence at their southern range edge. Dall sheep in the south may instead be limited by factors such as interspecific competition, supporting the theory that some range edges may be physically stressful while others may be biologically stressful (Guisan and Thuiller 2005, Brown *et al* 1996).

Later SDDs could negatively affect Dall sheep recruitment via several mechanisms. Later snowmelt in spring could indicate that ewes have been exposed to prolonged cold winter conditions, increasing energy

expense and reducing body condition, resulting in lower lamb survival in spring (Telfer and Kelsall 1984, Rachlow and Bowyer 1991). If prolonged exposure to winter conditions caused the negative effect of later springs on recruitment, SCD should have a stronger effect on recruitment than the other snow cover metrics, but our analysis showed that SDD was a better predictor for recruitment. This finding suggests that spring snow cover in particular is more important than the total number of days of snow cover throughout the year. SDD may also have a negative effect on recruitment because deep snow limits the mobility of lambs, making them vulnerable to starvation and predation (Boan 2014). Snow conditions during spring may be more important than conditions during the rest of the winter through their effect on vegetation: later SDDs could alter forage quality and availability, so that sheep may not reap the maximum benefits of spring green-up. For example, Bunnell (1980) found lambs born in early May experienced a higher mortality rate likely due to reduced availability and quality of forage for ewes. Additionally, Rachlow and Bowyer (1998) found ewes selected more for escape terrain during a mild spring when forage was plentiful relative to a late spring when forage availability and quality was lower and ewes foraged less efficiently. Analysis of

Figure 5. The average (*a*) May temperature, (*b*) total winter precipitation, and (*c*) snow disappearance date (SDD) over the entire study period, 2000–2015.

northern hemisphere NDVI over the last two decades are consistent with expanding growing seasons resulting from earlier snow melt (Myneni *et al* 1997, Jia *et al* 2003).

Our results indicated that Dall sheep populations on the northern range edge have the strongest response to spring snow cover. Therefore, we would expect these populations to disproportionately benefit from climate warming. The Arctic has experienced significant warming in the past three decades, with warming expected to continue through the 21st century (Serreze *et al* 2000, Overland *et al* 2004). In particular, northern Alaska has experienced warming by 0.58 °C–1.08 °C per decade during recent years (Serreze *et al* 2000), which has decreased snow cover duration and

extent (Dye 2002, Stone *et al* 2002, Euskirchen *et al* 2006, Euskirchen *et al* 2007, Chapron *et al* 2003, Brown *et al* 2010) and lengthened the growing season (Smith *et al* 2004). Surveys have shown, however, stronger declining trends in northern than in southern populations. For example, biologists have observed a 50% decline of the population in Central Brooks Range in recent years (Rattenbury *et al* 2016). Thus, Dall sheep may be affected by increased climate variability more than by changes in mean climate conditions. The timing of snowmelt has become more variable (Hinzman *et al* 2005), and the projected increase in winter storm frequency may negatively impact wildlife populations (Boyce *et al* 2006, IPCC 2013, Kunkel *et al* 2013, Schwartz and Schmidlin 2002). Increasing

winter temperatures have also resulted in more frequent rain-on-snow and thaw-refreeze events, resulting in impenetrable ice layers that restrict access to winter forage (Wilson *et al* 2013). Additionally, our time series, while fairly short, did not show any temporal trends in the three snow variables, and at least one study found that snow accumulation in the Alaska Range had in fact doubled since 1840 (Winski *et al* 2017).

The expected increase in the frequency and magnitude of climate extremes may have stronger impacts on ecosystem functioning than gradually shifting mean conditions, and these changes could have detrimental effects on wildlife populations (Boyce *et al* 2006, Nippert *et al* 2006, Hansen *et al* 2013, IPCC 2013). Whereas populations may be resilient to occasional extreme weather conditions, they may not be able to persist if these conditions become more frequent. In particularly harsh years, there are sometimes no surviving lambs at all, which occurred in Central Brooks Range in 2013 (Rattenbury *et al* 2016). Even in the best years however, ewes rarely have more than one lamb, so population recovery is slow (Hoefs 1978). Therefore, the benefits of warming may not outweigh the adverse effects of harsh years occurring at a higher frequency. For the Porcupine caribou (*Rangifer tarandus granti*) herd in the Yukon Territory, the positive effects of summer warming, including increased amounts of green forage and improved calf survival, were counteracted by the adverse effects of winter warming, which included difficulty foraging due to ice layers formed by temperatures rising above freezing for a portion of the day (Hinzman *et al* 2005). Hinzman *et al* (2005) concluded that such contrasting effects might be expected for other Arctic species.

Increasing evidence indicates that, in response to climate change, species throughout the world are shifting their geographical distributions, with meta-analyses finding shifts to higher latitudes and elevations in three-quarters of species (Chen *et al* 2011, Elsen and Tingley 2015). Predictions regarding range shifts are commonly made based on climate envelope models, which use the current distribution of a species to infer its environmental requirements and predict the extent and location of a potential species' distribution under predicted climate scenarios (Hijmans and Graham 2006, Shoo *et al* 2005). These models have been criticized because they only consider climate variables and do not include effects of biotic variables such as competition for resources (Pearson and Dawson 2003, Araújo and Luoto 2007). Additionally, climate envelope models, as well as species distribution models in general, rarely include interactive effects between predictor variables. Including interactions increases the number of model parameters and can complicate interpretations (Rushton *et al* 2004, Guisan and Thuiller 2005). However, our results suggest that the effect of a climate variable can vary dramatically within a species range. Assuming a uniform effect throughout the range could lead to underestimations

of climate change impacts in parts of the range, and overestimations in other parts.

Our results indicate that snow cover was a much stronger predictor for Dall sheep recruitment than more commonly used precipitation and temperature variables, underlining the importance of explicitly including snow cover as a climate variable. Therefore, our study highlights the need for remote sensing data as well as meteorological data, since snow cover is not a simple function of temperature and precipitation (Brodie and Post 2010). We used MODIS satellite imagery, which provides daily, global 500 m resolution products available starting in 2000. Alternatively, snow cover products can be derived from Landsat imagery, which is available starting in 1972 at a 30 m, 8-day resolution (Macander *et al* 2015). While Landsat-derived snow cover provides finer resolution and a longer time series than MODIS snow cover, the temporal accuracy of quantifying snow cover dates is lower. Regardless of the source, we strongly recommend incorporating remotely sensed snow cover in studies examining the responses of northern species to climate change.

Conclusion

Predicting and managing species range shifts in response to climate variability and change relies on understanding the environmental factors that limit species persistence at their range edges. Although climate variables such as temperature and precipitation are often used in species distribution models, our analyses showed that snow cover, a variable rarely considered, is a better predictor of Dall sheep recruitment. We expect this to be the case for many species that occur in snow dominated landscapes. Our findings indicate that the potential benefit of warming on northern Dall sheep populations may be counteracted by the strong negative effects of years with extremely late springs, which are expected to occur more frequently in the future. Although the Dall sheep range has remained relatively stable up to now, our results indicate that their populations are sensitive to spring snow conditions, which are expected to change. The interaction of spring snow conditions with latitude demonstrates that the importance of different environmental factors can vary across range edges, and that the effect of climatic factors can vary throughout a species' range. This concept can aid in the understanding of spatiotemporal variation in population sizes and metapopulation dynamics. Additionally, it is generally believed that declining species contract their range, so that conservation should focus on the core. However, we showed that for Dall sheep, populations at the southern range edge could be the most resilient. Examining how other population vital rates, such as adult survival and reproduction, are affected by different climate variables would be a valuable next step.

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References

Alaska Department of Fish and Game 2011 *Dall Sheep Management Report of Survey-Inventory Activities 1 July 2007–30 June 2010, Project 6.0* ed P Harper (Juneau, AK: Alaska Department of Fish and Game)

Alaska Department of Fish and Game 2014 Trends in Alaska sheep populations, hunting, and harvests *Division of Wildlife Conservation, Wildlife Management Report ADFG/DWC/WMR-2014-3* (Juneau, AK: Alaska Department of Fish and Game)

Araújo M B *et al* 2005 Validation of species-climate impact models under climate change *Glob. Change Biol.* **11** 1504–13

Araújo M B and Luoto M 2007 The importance of biotic interactions for modelling species distributions under climate change *Glob. Ecol. Biogeogr.* **16** 743–53

Arthur S M and Prugh L R 2010 Predator-mediated indirect effects of snowshoe hares on Dall's sheep in Alaska *J. Wildlife Manage.* **74** 1709–21

Balkenhol N 2009 Evaluating and improving analytical approaches in landscape genetics through simulations and wildlife case studies *PhD Dissertation* (Moscow, ID: University of Idaho)

Bates D, Maechler M and Bolker B 2012 lme4: Linear mixed-effects models using S4 classes Version 0.999999-0 (http://cran.r-project.org/package=lme4)

Bellard C *et al* 2012 Impacts of climate change on the future of biodiversity *Ecol. Lett.* **15** 365–77

Boan B V 2014 Dall sheep demographics: a peek at the intrinsic and extrinsic effects *MSc Thesis* (Reno, NV: University of Nevada)

Bolker B M *et al* 2009 Generalized linear mixed models: a practical guide for ecology and evolution *Trends Ecol. Evol.* **24** 127–35

Boyce M S *et al* 2006 Demography in an increasingly variable world *Trends Ecol. Evol.* **21** 141–8

Brodie J F and Post E 2010 Nonlinear responses of wolverine populations to declining winter snowpack *Popul. Ecol.* **52** 279–87

Brown J H, Stevens G C and Kaufman D M 1996 The geographic range: size, shape, boundaries, and internal structure *Annu. Rev. Ecol. Syst.* **27** 597–623

Brown R, Derksen C and Wang L 2010 A multi-data set analysis of variability and change in Arctic spring snow cover extent, 1967–2008 *J. Geophys. Res.* **115** D16111

Bunnell F L 1980 Factors controlling lambing period of Dall's sheep *Can. J. Zool.* **58** 1027–31

Callaghan T V *et al* 2004 Synthesis of effects in four Arctic subregions *AMBIO* **33** 469–473

Caswell H 2001 *Matrix Population Models: Construction, Analysis, and Interpretation* 2nd edn (Sunderland, MA: Sinauer Associates Inc.)

Caughley G *et al* 1988 The edge of the range *J. Anim. Ecol.* **57** 771

Chapron G *et al* 2003 Which future for the French Pyrenean brown bear *(Ursus arctos)* population? An approach using stage-structured deterministic and stochastic models *C. R. Biol.* **236** S174–82

Chen I-C *et al* 2011 Rapid range shifts of species associated with high levels of climate warming *Science* **333** 1024–6

Collins W B and Smith T S 1991 Effects of wind-hardened snow on foraging by reindeer (*Rangifer tarandus*) *Arctic* **44** 217–22

Crumley R L, Nolin A W, Sproles E A and Mar E G 2018 SnowCloudMetrics: snow information for everyone *Remote Sens.* in preparation

Dozier J *et al* 2009 Interpretation of snow properties from imaging spectrometry *Remote Sens. Environ.* **113** S25–37

Dye D G 2002 Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972–2000 *Hydrol. Process.* **16** 3065–77

Elsen P R and Tingley M W 2015 Global mountain topography and the fate of montane species under climate change *Nat. Clim. Change* **5** 772–6

Euskirchen E S *et al* 2006 Importance of recent shifts in soil thermal dynamics on growing season length, productivity, and carbon sequestration in terrestrial high-latitude ecosystems *Glob. Change Biol.* **12** 731–50

Euskirchen E S, McGuire A D and Chapin F S 2007 Energy feedbacks of northern high-latitude ecosystems to the climate system due to reduced snow cover during 20th century warming *Glob. Change Biol.* **13** 2425–38

Goldstein E J *et al* 2005 Relationships among fecal lungworm loads, fecal glucocorticoic metabolites, and lamb recruitment in free-ranging Rocky Mountain Bighorn sheep *J. Wildlife Dis.* **41** 416–25

Grotan V *et al* 2009 Spatial and temporal variation in the relative contribution of density dependence, climate variation and migration to fluctuations in the size of great tit populations *J. Anim. Ecol.* **78** 447–59

Guisan A and Thuiller W 2005 Predicting species distribution: offering more than simple habitat models *Ecol. Lett.* **8** 993–1009

Hansen B B *et al* 2013 Climate events synchronize the dynamics of a resident vertebrate community in the high Arctic *Science* **339** 313–5

Harris N C, Kauffman M J and Mills L S 2008 Inferences about ungulate population dynamics derived from age ratios *J. Wildlife Manage.* **72** 1143–51

Haugen R K and Brown J 1980 Coastal-inland distributions of summer air temperature and precipitation in northern Alaska *Arctic Alpine Res.* **12** 403

Hijmans R J and Graham C H 2006 The ability of climate envelope models to predict the effect of climate change on species distributions *Glob. Change Biol.* **12** 2272–81

Hinzman L D *et al* 2005 Evidence and Implications of recent climate change in northern Alaska and other Arctic regions *Clim. Change* **72** 251–98

Hoefs M 1978 Twinning in Dall sheep *Can. Field Nat.* **92** 292–3

Hoefs M and Cowan I 1979 Ecological investigation of a population of Dall sheep (*Ovis dalli dalli* Nelson) *Syesis* **12** 1–81

Humphries M M, Umbanhowar J and McCann K S 2004 Bioenergetic prediction of climate change impacts on northern mammals *Integr. Comp. Biol.* **44** 152–62

IPCC 2013 Climate change 2013: the physical science basis *Contribution of Working group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* ed T F Stocker, D Qin, G K Plattner, M Tignor, S K Allen, J Boschung, A Nauels, Y Xia, V Bex and P M Midgley (Cambridge: Cambridge University Press)

Jia G J, Epstein H E and Walker D A 2003 Greening of Arctic Alaska, 1981–2001 *Geophys. Res. Lett.* **30** 1–3

Jones H G *et al* 2001 *Snowecology: An Interdisciplinary Examination of Snow-Covered Ecosystems* (Cambridge: Cambridge University Press)

Koizumi C L *et al* 2011 *Status of Dall's sheep (Ovis dalli dalli) in the Northern Richardson Mountains, Yukon Fish and Wildlife Branch Report TRC-11-01* (Whitehorse, Yukon, Yukon Environment)

Kunkel K *et al* 2013 *Regional climate trends and scenarios for the US national Climate Assessment. Part 4. Climate of the US Great Plains NOAA Technical Report* NESDIS 142-4

Lanier H C *et al* 2015 Comparative phylogeography highlights the double-edged sword of climate change faced by Arctic- and alpine-adapted mammals *PLoS ONE* **10** e0118396

Liston G E *et al* 2002 Modelled changes in Arctic tundra snow, energy and moisture fluxes due to increased shrubs *Glob. Change Biol.* **8** 17–32

Loehr J *et al* 2010 The role of phenotypic plasticity in responses of hunted thinhorn sheep ram horn growth to changing climate conditions *J. Evol. Biol.* **23** 783–90

Macander M J *et al* 2015 Landsat-based snow persistence map for northwest Alaska *Remote Sens. Environ.* **163** 31

Magoun A J and Copeland J P 1998 Characteristics of wolverine reproductive den sites *J. Wildlife Manage.* **62** 1313

Manning J A and Garton E O 2012 Reconstructing historical snow depth surfaces to evaluate changes in critical demographic rates and habitat components of snow-dependent and snow-restricted species *Methods Ecol. Evol.* **3** 71–80

McKenney D W *et al* 2007 Potential impacts of climate change on the distribution of North American trees *BioScience* **57** 939

Mech L D *et al* 2001 Winter severity and wolf predation on a formerly wolf-free elk herd *J. Wildlife Manage.* **65** 998

Myneni R B *et al* 1997 Increased plant growth in the northern high latitudes from 1981–1991 *Nature* **386** 698–702

Mysterud A, Bjornsen B H and Ostbye E 1997 Effects of snow depth on food and habitat selection by roe deer *Capreolus capreolus* along an altitudinal gradient in south-central Norway *Wildlife Biol.* **3** 27–33

Nette T, Burles D and Hoefs M 1984 Observations of golden eagle, *Aquila chrysaetos*, predation on Dall sheep, *Ovis dalli dalli*, lambs *Can. Field Nat.* **98** 252–4

Nippert J B, Knapp A K and Briggs J M 2006 Intra-annual rainfall variability and grassland productivity: can the past predict the future? *Plant Ecol.* **184** 65–74

Olsen M S *et al* 2011 The changing Arctic cryosphere and likely consequences: an overview *AMBIO* **40** 111–8

Overland J E *et al* 2004 Seasonal and regional variation of Pan-Arctic surface air temperature over the instrumental record *J. Clim.* **17** 3263–82

Painter T H *et al* 2009 Retrieval of subpixel snow covered area, grain size, and albedo from MODIS *Remote Sens. Environ.* **113** 868–79

Parmesan C *et al* 2005 Empirical perspectives on species borders: from traditional biogeography to global change *Oikos* **108** 58–75

Pearson R G and Dawson T P 2003 Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* **12** 361–71

Pomeroy J W *et al* 2006 Shrub tundra snowmelt *Hydrol. Process.* **20** 923–41

Pomeroy J W *et al* 2001 Physical properties of snow *Snow Ecology: An Interdisciplinary Examination of Snow-Covered Ecosystems* ed H G Jones (Cambridge: Camridge University Press) pp 45–126

Post E and Stenseth N C 1998 Large-scale climatic fluctuation and population dynamics of moose and white-tailed deer *J. Anim. Ecol.* **67** 537–43

Prugh L R and Arthur S M 2015 Optimal predator management for mountain sheep conservation depends on the strength of mesopredator release *Oikos* **124** 1241–50

Putkonen J and Roe G 2003 Rain-on-snow events impact soil temperatures and affect ungulate survival *Geophys. Res. Lett.* **30** 1188

Rachlow J L and Bowyer R T 1998 Habitat selection by Dall's sheep *(Ovis dalli)*: maternal trade-offs *J. Zool.* **245** 457–65

Rachlow J L and Bowyer R T 1991 Interannual variation in timing and synchrony of parturition in Dall's sheep *J. Mammal.* **72** 487–92

Rachlow J L and Bowyer R T 1994 Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? *J. Mammal.* **75** 328–37

R Development Core Team 2016 R: A language and environment for statistical computing Version 3.3.1 (www.r-project.org/)

Raleigh M S *et al* 2013 Ground-based testing of MODIS fractional snow cover in subalpine meadows and forests of the Sierra Nevada *Remote Sens. Environ.* **128** 44–57

Rattenbury K *et al* 2016 Recent trends in Dall's sheep populations in Alaska's national parks and preserves *Alaska Dall Sheep Working Group Meeting, February 20–21, 2016* (Anchorage, AK: Alaska Dall Sheep Working Group)

Rittger K, Painter T H and Dozier J 2013 Assessment of methods for mapping snow cover from MODIS *Adv. Water Resour.* **51** 367–80

Roffler G H *et al* 2014 Lack of sex-biased dispersal promotes fine-scale genetic structure in alpine ungulates *Conserv. Genet.* **15** 837–51

Rushton S P, Ormerod S J and Kerby G 2004 New paradigms for modelling species distributions? *J. Appl. Ecol.* **41** 193–200

Sand H, Cederlund G and Danell K 1995 Geographical and latitudinal variation in growth patterns and adult body size of Swedish moose *(Alces alces) Oecologia* **102** 433–42

Schmidt J H *et al* 2012 Using distance sampling and hierarchical models to improve estimates of Dall's sheep abundance *J. Wildlife Manage.* **76** 317–27

Schwartz R M and Schmidlin T W 2002 Climatology of blizzards in the conterminous United States, 1959–2000 *J. Clim.* **15** 1765–72

Serreze M C *et al* 2000 Observational evidence of recent change in the northern high-latitude environment. *Clim. Change* **46** 159–207

Sexton J P *et al* 2009 Evolution and ecology of species range limits *Annu. Rev. Ecol. Evol. Syst.* **40** 415–36

Shoo L P, Williams S E and Hero J-M 2005 Potential decoupling of trends in distribution area and population size of species with climate change *Glob. Change Biol.* **11** 1469–76

Sim Z *et al* 2016 Genome-wide set of SNPs reveals evidence for two glacial refugia and admixture from postglacial recolonization in an alpine ungulate *Mol. Ecol.* **25** 3696–705

Smith N V, Saatchi S S and Randerson J T 2004 Trends in high northern latitude soil freeze and thaw cycles from 1988–2002 *J. Geophys. Res.* **109** D12101

Stone R S *et al* 2002 Earlier spring snowmelt in northern Alaska as an indicator of climate change. *J. Geophys. Res. Atmos.* **107** ACL 10-1–13

Tabachnick B G and Fidell L S 2013 *Using Multivariate Statistics* 6th edn (Boston, MA: Pearson)

Talley T S 2007 Which spatial heterogeneity framework? Consequences for conclusions about patchy population distributions *Ecology* **88** 1476–89

Telfer E S and Kelsall J P 1984 Adaptation of some large North American mammals for survival in snow *Ecology* **65** 1828–34

Tews J, Ferguson M A D and Fahrig L 2007 Potential net effects of climate change on high Arctic Peary caribou: lessons from a spatially explicit simulation model *Ecol. Model.* **207** 85–98

Verbyla D *et al* 2017 Remote sensing of 2000–2016 alpine spring snowline elevation in Dall sheep mountain ranges of Alaska and western Canada *Remote Sens.* **9** 1157

Verbyla D 2008 The greening and browning of Alaska based on 1982–2003 satellite data *Glob. Ecol. Biogeogr.* **17** 547–55

Watson S M 1986 Dall sheep hunting in Alaska: what is it worth? *Biennial Symp. Northern Wild Sheep Goat Council* **5** 129–49

Wehausen J D *et al* 1987 Recruitment dynamics in a southern California mountain sheep population *J. Wildlife Manage.* **51** 86

Wilmshurst J F, Greer R and Henry J D 2006 Correlated cycles of snowshoe hares and Dall's sheep lambs *Can. J. Zool.* **84** 736–43

Wilson R R *et al* 2013 Frequency, timing, extent, and size of winter thaw-refreeze events in Alaska 2001–2008 detected by remotely sensed microwave backscatter data *Polar Biol.* **36** 419–26

Winski D *et al* 2017 Industrial-age doubling of snow accumulation in the Alaska Range linked to tropical ocean warming *Sci. Rep.* **7** 17869

Worley K *et al* 2004 Population genetic structure of North American thinhorn sheep *(Ovis dalli)*. *Mol. Ecol.* **13** 2545–56