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Research Article

Environmental Influences on Dall's Sheep Survival

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ABSTRACT Understanding how species respond to environmental conditions can assist with conservation strategies and harvest management, especially in arctic and boreal regions that are experiencing rapid climate change. Although climatic influences on species distributions have been studied, broad-scale effects of climate on survival are less well known. We examined the interactive effects of meteorological and remotely sensed environmental variables on survival of Dall's sheep (*Ovis dalli dalli*) lambs and adults by synthesizing radio-telemetry data across their range. We used data from 9 studies of adult sheep and 2 studies of lambs that were conducted between 1997 and 2012 at sites spanning the species' range in Alaska, USA, and northwestern Canada. We obtained environmental variables throughout the range of Dall's sheep, including the normalized difference vegetation index (NDVI) from optical remote sensing, freeze-thaw frequency (FTF) from passive microwave remote sensing, and gridded climate variables such as snow water equivalent, temperature, and precipitation. We used Cox proportional hazard regression to investigate the effects of environmental variables recorded during summer, winter, and the previous winter on annual survival rates of Dall's sheep lambs and adults. Summer NDVI was the most influential environmental factor affecting lamb survival, with improved lamb survival occurring in years with a high maximum NDVI. Also, lamb predation by coyotes (*Canis latrans*) and golden eagles (*Aquila chrysaetos*) decreased substantially with increasing NDVI. The previous winter FTF had the strongest effect on adult survival, with decreased survival occurring after winters with high FTF. In addition, these remotely sensed environmental factors interacted with meteorological factors to affect survival, such that effects of winter temperature depended on summer NDVI and winter FTF. Warm winters increased lamb survival only when preceded by summers with high NDVI, and warm winters increased adult survival only when winter FTF was low. Thus, potential benefits of climate warming may be counteracted if wintertime freeze-thaw events markedly increase. Correlations among environmental variables across sites were low, and regional climate cycles such as the Pacific Decadal Oscillation (PDO) had weak effects, indicating substantial local variability in climatic conditions experienced by Dall's sheep across their range. These findings can help managers anticipate how Dall's sheep populations will respond to changes in local environmental conditions. Our results also highlight the utility of multiple remotely sensed environmental conditions for ungulate management, especially passive microwave products that provide valuable information on winter icing events.

KEY WORDS Alaska, Dall's sheep, environmental variables, NDVI, *Ovis dalli dalli*, survival, temperature.

Climatic conditions such as temperature and precipitation can affect the dynamics of animal populations on a local and a regional scale (Hallett et al. 2004). The effect of climate on wildlife populations is primarily mediated by climate-induced changes in demographic rates (e.g., survival), which are particularly relevant in the context of recent and predicted changes in climate (Leopold 1933, Robinson et al. 2007). Climate conditions can affect populations directly via metabolic effects of weather conditions, and indirectly through effects on habitat (Mysterud and Østbye 2006). For

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example, survival of Soay sheep (*Ovis aries*) was affected by winter weather directly through variation in energetic costs or disease, and indirectly through moderated vegetation productivity and forage availability (Hallett et al. 2004). Identifying influential climate variables and their effect on demographic rates can help managers anticipate future changes in population dynamics and adjust conservation strategies and sustainable harvest limits.

Demographic rates in ungulate populations are typically influenced by direct and indirect climate effects (Gaillard et al. 2000, Davis et al. 2016). For example, survival and reproduction of elk (*Cervus canadensis*) may be related to winter precipitation and temperature (Coulson et al. 2000), survival of Soay sheep may be negatively related to spring precipitation (Catchpole et al. 2000), and moose (*Alces alces*) survival may be inversely correlated with temperatures in January (Lenarz et al. 2009). Importance of climate variables can also vary geographically; for instance, snowpack conditions may only be relevant in areas where snow is a dominant landscape feature (Garrott et al. 2003, van de Kerk et al. 2018). Climate variables may interact with other factors to affect population dynamics. For example, increased insect harassment in warmer weather can reduce body condition of caribou (*Rangifer tarandus*) calves (Weladji et al. 2006).

The effects of climate variables on survival can be difficult to untangle because of interactions with predation. Simultaneously considering the direct effects of climate, climate-related changes in food resources, and predation may facilitate the development of mechanistic survival models that can be used in ungulate management in the face of climate change (Davis et al. 2016). Climate factors may influence observed declines in Dall's sheep (*Ovis dalli dalli*) populations (Loehr et al. 2010, Alaska Department of Fish and Game 2011). Dall's sheep are endemic to alpine ecosystems in northwestern North America, and they may be especially sensitive to environmental change because they occur at high elevations and high latitudes. The Arctic is warming at twice the rate of lower latitudes; temperatures are predicted to rise by 3–6°C by 2080 (Callaghan et al. 2004, Olsen et al. 2011). As large herbivores that reside in mountain ranges year-round, Dall's sheep have strong effects on alpine plant communities and are important prey for a variety of predators (Hoefs and Cowan 1979). In addition, Dall's sheep provide valued hunting opportunities for residents and draw tourists and sport hunters from around the world (Watson 1986). Therefore, knowledge of factors that affect Dall's sheep population dynamics is needed to understand the ecological processes they facilitate and mitigate influences associated with climate-induced changes (Garrott et al. 2009).

Historically, strong fluctuations have been observed in Dall's sheep populations (Lambert Koizumi et al. 2011, Alaska Department of Fish and Game 2014). In the central Alaska Range, Arthur (2003) reported that observed lamb survival rates of 12–36%, combined with mean adult female survival rates of 86%, were not sufficient to sustain population numbers. Analyses of life-history characteristics of long-lived large herbivores like Dall's sheep indicate that population growth is most sensitive to changes in adult female survival and least sensitive to juvenile survival (Garrott et al. 2003). Additionally, many studies demonstrate the reverse pattern in temporal variation, with adult female survival being remarkably constant and juvenile survival being highly variable (Eberhardt 1977, Gaillard et al. 2000). Overall, Dall's sheep appear to follow those general trends, with high mortality during the first year of life and relatively low mortality of adults (Murphy and Whitten 1976, Nichols 1978, Arthur and Prugh 2010). Scotton (1997) noted that the extreme variability observed in lamb-to-female ratios of Dall's sheep was greater than variability in calf-to-female ratios in northern caribou and moose populations, which may indicate that Dall's sheep experience greater sensitivity to external influences such as temperature, precipitation, and vegetation productivity.

Although meteorological variables such as temperature and precipitation are included in survival analyses more often, satellite remote sensing products also allow examination of variables such as productivity of vegetation (as indicated by the normalized difference vegetation index [NDVI]) and frequency of freeze-thaw events. The link between NDVI and vegetation productivity is based on the amount of near-infrared and red light that is reflected by vegetation to be captured by the satellite sensor, and this relationship has been well documented (Pettorelli et al. 2005*a*). The index is positively correlated with ungulate demographics, such as caribou body mass and calf survival in Norway (Pettorelli et al. 2005*b*) and red deer (*Cervus elaphus*) recruitment in Norway and France (Loe et al. 2005). Although NDVI has been widely used by wildlife biologists, products derived from passive microwave sensors like freeze-thaw events are rarely used. Freeze-thaw cycles can directly affect ungulate populations by causing the formation of ice crusts blocking access to forage (Gunn et al. 1989, Kohler and Aanes 2009, Stien et al. 2010). These ice crusts have reportedly caused major die-offs of muskoxen (*Ovibos moschatus*) and reindeer (Gunn et al. 1989, Putkonen and Roe 2003).

Our objective was to evaluate effects of climate and vegetation productivity on survival and cause-specific mortality of Dall's sheep throughout the species' range in northwestern North America. We examined the effects of meteorological climate variables that are likely to affect ungulate demographics locally, such as precipitation and temperature. Because harsh winter weather has been demonstrated to have a negative effect on ungulate survival, we expected a positive effect of temperature and a negative effect of precipitation (Loison and Langvatn 1998, Cook et al. 2004). Additionally, we included satellite remote sensing products in our analyses that we also expected to affect Dall's sheep survival, such as productivity of vegetation and frequency of freeze-thaw events (Putkonen and Roe 2003, Loe et al. 2005). We also included regional climate patterns such as the Pacific Decadal Oscillation (PDO) and the Arctic Oscillation (AO). These have been shown to influence survival of several ungulates in Alaska, USA, and Canada (Hik and Carey 2000, Loehr et al. 2010, Joly et al. 2011), so we expected them to affect Dall's sheep survival as well. Finally, we examined the timing of mortalities throughout the year, and hypothesized that environmental conditions during periods of peak mortality would have the strongest effects on annual survival rates.

STUDY AREA

Dall's sheep are distributed across mountain ranges in Alaska and the Canadian Yukon and Northwest Territories. Dall's sheep require year-round access to forage and therefore prefer areas with light snowfall and strong winds to expose forage in winter (Nichols and Bunnell 1999). They typically forage in open grass and sedge meadows, but access to foraging grounds is limited by their dependence on nearby rugged cliffs and rocks as escape terrain from predators (Nette et al. 1984, Nichols and Bunnell 1999). They generally occupy areas between 900 m and 2,100 m in elevation, and vegetation in their range includes sedges (*Carex* spp.), rushes (*Juncus* spp.), bunchgrasses (*Festuca* spp.), bluegrasses (*Poa* spp.), dwarf willows (*Salix* spp.), huckleberry (*Vaccinium* spp.), mountain avens (*Dryas* spp.), crowberry (*Empetrum* spp.), and a variety of lichens and mosses (Nichols and Bunnell 1999, Alaska Department of Fish and Game 2014). In winter, Dall's sheep often move to lower elevations, where they may also encounter dense stands of dwarf birch (*Betula* spp.), alder (*Alnus* spp), and mountain hemlock (*Tsuga mertensiana*; Valdez and Krausman 1999).

Our data were collected during 1997–2012 in areas of the Alaska Range, Brooks Range, White Mountains, Yukon-Tanana Uplands, and Richardson Mountains where Dall's sheep were radio-collared (Fig. 1). Study sites were between 60° to 68° latitude and −137° to −155° longitude, and mean elevation was 1,008 m (range = 775–1,348 m). Sites were on average 1,464 km^2 in size (range = 566–2,960 km^2), and all sites together covered an area of 13,172 km^2. Climate conditions varied widely among study sites, but winters (Sep–Apr) were typically cold and dry in the northern and interior mountains, with little snow and temperatures rarely reaching above freezing, whereas the maritime climate in the south resulted in higher temperatures and deeper snow (Nichols and Bunnell 1999). Summers (May–Aug) were generally warm and dry in the northern and interior mountains, and cool and moist in the south (Nichols and Bunnell 1999).

In general across the study domain, Dall's sheep was the numerically dominant ungulate in alpine areas, whereas moose and caribou were dominant at lower elevations. A diverse suite of predators was present in most areas, including wolves (*Canis lupus*), grizzly bears (*Ursus arctos horribilis*), black bears (*Ursus americanus*), wolverines (*Gulo gulo*), coyotes (*Canis latrans*), and golden eagles (*Aquila chrysaetos*). Land ownership was predominantly federal, and hunting or other forms of recreation were the dominant land uses. Study areas and site-specific climate conditions during each study were previously described in more detail for each individual study (Table S1, available online in Supporting Information).

METHODS

Sheep Data

We used global positioning system and very high frequency telemetry data from 9 studies of Dall's sheep. All studies collected data on adult sheep, and 2 also collected data on lambs. Studies ranged in duration from 1–10 years and

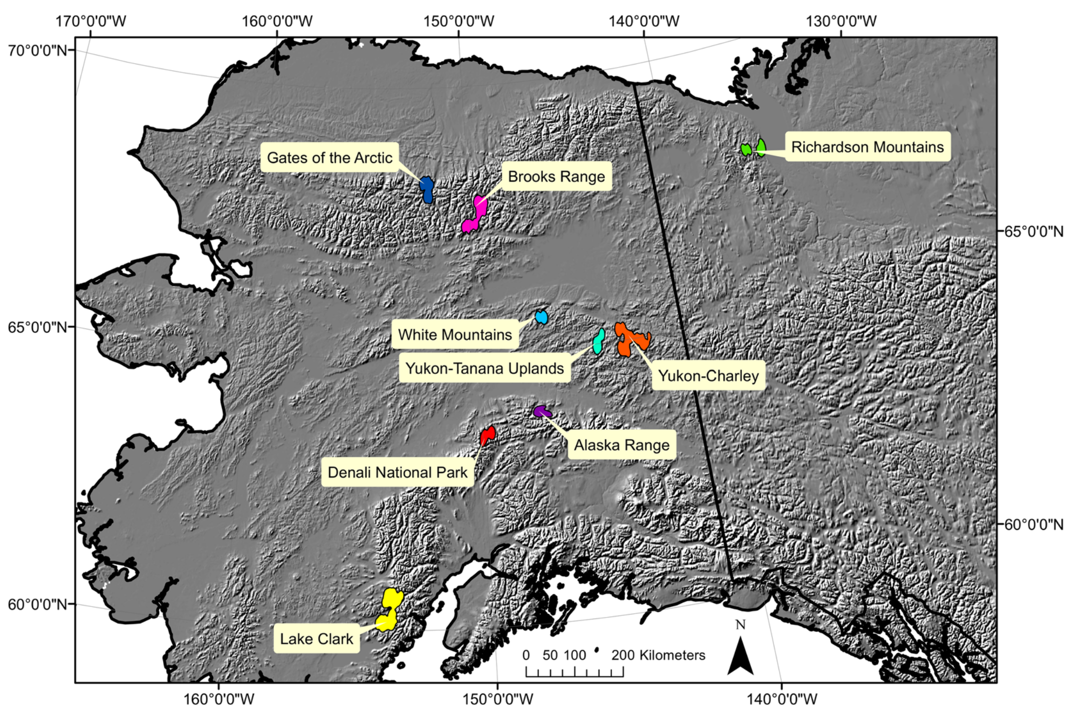

Figure 1. The location of Dall's sheep study sites in Alaska, USA, and northwestern Canada, 1997–2012.

Table 1. Number of male and female lambs and adult Dall's sheep, years of study by site, the agency that provided the data, and a citation for additional details. ADFG = Alaska Department of Fish and Game, NP = National Park, NPS = National Park Service, GRRB = Gwich'in Renewable Resources Board, USFWS = United States Fish and Wildlife Service, BLM = Bureau of Land Management.

			Lambs		Adults				
Site	Agency	Years	Female	Male	Female	Male	$\bar{x}$ elevation (m)	Size (km^2)	Citation
Alaska Range	ADFG	1999–2008	54	64	32	0	1,344	640	Arthur and Prugh (2010)
Brooks Range	ADFG	2009–2012	32	37	28	0	986	1,917	Arthur (2013)
Denali NP	NPS	2007			10	6	1,239	807	Philips et al. (2010)
Gates of the Arctic NP	NPS	1998–2002			19	6	1,094	1,178	Lawler (2004)
Lake Clark NP	NPS	2006–2008			25	14	841	2,960	Mangipane (2011)
Richardson Mountains	GRRB	2004–2008			0	8	673	946	Lambert Koizumi and Derocher (2010)
White Mountains	USFWS, BLM, ADFG	2004–2008			40	13	842	566	Bertram et al. (2018)
Yukon-Tanana Uplands	NPS	1999–2003			77	0	1,060	1,546	Lawler et al. (2005)
Yukon-Charley	NPS	1997–2000			20	3	996	2,611	Burch and Lawler (2001)

occurred from 1997–2012 (Table 1; Fig. 1). Although protocols varied by study, researchers captured adult sheep >1 year of age by net-gunning from helicopters (Arthur 2003) and tracked them at intervals ranging from daily to every 2 weeks. Researchers determined sex at capture and estimated age based on the number of horn annuli (Hemming 1969). We hand-captured neonate lambs <3 days old after pursuit with a helicopter, and weighed and sexed each one; older lambs could outrun human pursuers and were not sampled. Researchers captured and handled sheep in compliance with animal handling procedures approved by their respective agencies (protocol numbers DENA-2006-SCI-0002, ADFGACUCA 04-015, and NWTWCC 007-009) that meet or exceed the guidelines for the use of wild mammals in research of the American Society of Mammalogists (Sikes and Gannon 2011). Detailed field methods for each study are available in previous publications (Table 1). When possible, field crews investigated mortalities to determine the likely proximate cause of death based on tracks, hairs, and feces of predators, size and pattern of tooth marks or other injuries, and characteristic carcass use (Arthur and Prugh 2010). Aerial surveys performed by the National Park Service and the Alaska Department of Fish and Game provided some information on sheep densities during studies at 3 of the sites (Alaska Range, Yukon-Tanana Uplands, Yukon-Charley). We calculated density by dividing the minimum counts from these surveys by the survey area. These estimates should thus be considered indices of density because not all landscapes within each survey area were suitable.

Environmental Variables

We defined 2 seasons for developing environmental covariates: summer, consisting of mostly snow-free months May–August, and winter, consisting of mostly snow-covered months September–April. We defined 2 seasons rather than 4 because preliminary analyses indicated that spring and fall covariates were less influential than summer and winter covariates, and 4-season model sets included too many variables given sample size limitations. We developed seasonal covariates for 7 environmental variables: temperature, precipitation, snow water equivalent (SWE), freeze-thaw frequency (FTF), NDVI, PDO, and AO for each of the study sites (Table 2). We defined study sites as the 95% kernel density based on the sheep location data from each study, which we estimated in Program R using the package adehabitatLT (Calenge 2006). We used kernel density estimation (KDE) because sampling intervals varied among studies, and KDE is more robust to differences in sampling frequency compared to other methods (Börger et al. 2006, Mills et al. 2006). We used the 95% isopleth to include the majority of the area used by each study population while excluding outliers and occasional sallies (Powell 2012).

We used monthly gridded climate products from the Scenarios Network for Alaska and Arctic Planning (SNAP; SNAP 2017) to estimate mean temperature and precipitation for each season. The SNAP data consisted of monthly mean temperatures and monthly total precipitation at 1-km spatial resolution. We averaged the monthly values across months for grid cells within each site and season to obtain site-specific, seasonal estimates. Weather variables

Table 2. Environmental variables used as predictors of in our analyses of Dall's sheep survival at 9 locations throughout their range, Alaska, USA, 1997–2012.

Variable	Abbreviation	Statistic	Seasons
Temperature	Temp	$\bar{x}$	Summer, winter
Precipitation	Precip	$\bar{x}$	Summer, winter
Pacific Decadal Oscillation	PDO	$\bar{x}$	Summer, winter
Arctic Oscillation	AO	$\bar{x}$	Summer, winter
Snow water equivalent	SWE	$\bar{x}$	Summer, winter
Freeze-thaw frequency	FTF	Total	Winter, October
Normalized Difference Vegetation Index	NDVI	Max.	Summer

such as temperature and precipitation are affected by regional cyclic patterns in climate such as the PDO and AO. The AO and PDO are indices of differences in oceanic temperatures and sea-level pressure (Thompson and Wallace 1998). We downloaded monthly indices from the National Oceanic and Atmospheric Administration's (NOAA) Earth System Research Laboratory (Jones et al. 1997). Because these indices do not vary spatially, they are the same for all sites at any given time.

We included 2 climate variables of particular relevance for species in northern regions: a snow variable and a freeze-thaw variable. We obtained the snow variable, SWE, from Daymet version 3 (Thornton et al. 2016). The SWE represents the amount of water that would result from melting the snowpack. Daymet is a collection of gridded estimates of daily weather parameters generated by interpolation and extrapolation from daily meteorological observations. It provides gridded estimates of SWE at 1-km spatial resolution and daily temporal resolution, which we averaged by site for each season. We estimated the freeze-thaw variable, FTF, using the Making Earth System Data Records for Use in Research Environments (MEaSUREs) Global Record of Daily Landscape Freeze-Thaw Status, version 3 (Kim et al. 2016). This record provides data on the daily freeze-thaw status of the landscape derived from satellite observations of radiometric brightness temperatures at a 25-km spatial resolution. For our study period, we derived these records from Scanning Multichannel Microwave Radiometer, Special Sensor Microwave-Imager, and Special Sensor Microwave Imager-Sounder (Kim et al. 2016). For each day, the MEaSUREs product indicates whether each grid cell was frozen or thawed in the morning and in the afternoon. We counted a freeze-thaw event any time the status of a grid cell switched from frozen to thawed. We summed the number of events for each cell over the whole season, and then averaged over all the cells within a site to obtain a site-specific FTF for each season. Because there is some evidence that icing events in fall have a strong adverse effect on ungulates by impeding access to forage all winter long (Stien et al. 2010), we included both FTF in the whole winter and just October, the month with the most freeze-thaw events, as covariates.

Finally, we included the NDVI as an indicator of vegetation productivity. We used data from the NOAA Climate Data Records, which provide daily NDVI derived from surface reflectance data acquired by the Advanced Very High Resolution Radiometer sensor at a 500-m spatial resolution (Vermote et al. 2017). The study sites were mostly snow-covered in winter, so we used the maximum NDVI during summer only, which we estimated by finding the maximum NDVI for each grid cell during summer and averaging that value for all cells within each study site.

Data Analysis

We analyzed data for lambs and adults separately because lamb data were available from only 2 sites and there are generally large differences between neonate and adult ungulate survival rates (Eberhardt 1977, Gaillard et al. 2000). We defined adults as individuals ≥1 year. We estimated annual survival rates for biological years beginning 1 May, because Dall's sheep females tend to initiate birth in early to mid-May (Nichols 1978). We used the R package survival (Therneau 2014) to generate survival estimates using Cox proportional hazard regression (Cox 1972). This method is particularly useful for analyses of animals captured at different times because it allows for staggered entry and right censoring, so that individuals can enter and exit the sample population at any point in time during the study. For lambs, we truncated the data on 1 May to avoid introducing a bias in the survival rates of the next year by including lambs that are almost 12 months old.

We investigated how survival was affected by sex for both age classes, how lamb survival was affected by birth mass (indexed by body mass at capture; Arthur and Prugh 2010), and how adult survival was affected by age. For both age classes, we also tested for a cohort effect by including birth year as a fixed effect. We fitted single-variable and double-variable additive and interactive models and used Akaike's Information Criterion (AIC; Akaike 1973) to rank the models. We used the subset of data for which information on sheep density was available to test for density dependence in survival rates by using adult sheep density as a predictor for survival within sites. For both lambs and adults, we used the best fitting model with the lowest AIC from these analyses as a base model to investigate the effect of the environmental variables.

To identify the most important climatic predictors of lamb and adult survival, we compared the relative effects of environmental variables measured during summer, winter, and during the previous winter. For example, we tested the relationships between survival during 1 May 2010–30 April 2011 and the environmental covariates during winter 2009–2010, summer 2010, and winter 2010–2011. We used the R package MuMIn to create a full additive model set (the base model plus 1 or 2 environmental covariates) and calculate the relative variable importance (RVI) of each variable (Bartón 2018). We considered variables with RVI >0.5 to be important predictors (Burnham and Anderson 2002). To examine spatial correlations among important predictors, we estimated the correlations among sites for the variables that had highest RVIs for lambs and adults.

We used a model selection approach to find the most parsimonious model. We combined environmental variables that were uncorrelated (correlation coefficient <0.7) with the base model into additive and interactive models, and ranked the models based on AIC. We compared the base model with and without site as a random effect to determine if survival rates varied among sites. We then compared the fit of the top model with and without a random effect of site to determine whether the included covariates adequately accounted for these differences.

If predators kill individuals that were predisposed to die from other, climate-related causes, there could be a relationship between predation rates and environmental conditions. Therefore, we examined if there was a relationship between important predictors of survival and cause of mortality. We used binomial regression to investigate how the proportion of mortalities from each cause was affected by the environmental variable with the highest RVI for each age class (lambs and adults). We performed all analyses using R version 3.3.1 (R Development Core Team 2016).

RESULTS

We radio-collared 311 adult sheep >1 year of age at all 9 sites combined, and 187 lambs at the Alaska Range and Brooks Range sites. Sheep density estimates were available from surveys in the Alaska Range, Yukon-Tanana Uplands, and Yukon-Charley. The likely cause of death was determined for 64 out of 174 adult mortalities and 88 out of 113 lamb mortalities.

Overall annual survival rates were 0.29 ± 0.13 (SE) and 0.84 ± 0.02 for lambs and adults, respectively. In our base model without climate variables, the top model for lamb survival included an effect of birth mass, and the top model for adult survival included an effect of age (Table S2, available online in Supporting Information). We report hazard ratios (HR) with robust standard errors (SE) for scaled covariates. A hazard ratio of 1 indicates no effect, whereas hazard ratios <1 indicate a positive effect and hazard ratios >1 a negative effect. Lamb survival was positively affected by birth mass ($\mathrm{HR} = 0.81 \pm 0.09$), and adult survival was negatively affected by age ($\mathrm{HR} = 1.82 \pm 0.11$; Fig. 2A–B). The subset of data for which estimates of sheep density were available did not suggest a relationship between density of adult sheep and survival rates for either lambs ($\mathrm{HR} = 1.06 \pm 0.12$) or adults ($\mathrm{HR} = 0.97 \pm 0.17$).

Maximum summer NDVI had the highest RVI for lamb survival ($\mathrm{RVI} = 0.73$; Table 3). As maximum summer NDVI increased, so did lamb survival ($\mathrm{HR} = 0.64 \pm 0.09$; Fig. 2C). The FTF in the previous winter was the most important factor affecting adult survival ($\mathrm{RVI} = 0.991$), followed by mean temperature in the previous winter ($\mathrm{RVI} = 0.701$). The FTF negatively affected adult survival ($\mathrm{HR} = 1.48 \pm 0.11$; Fig. 2D), whereas adult survival increased following relatively warm winters. The average correlation among sites was 0.47 for both maximum summer NDVI and FTF, and 84% and 81% of the site combinations were correlated at a level <0.7, respectively (Fig. S1, available online in Supporting Information).

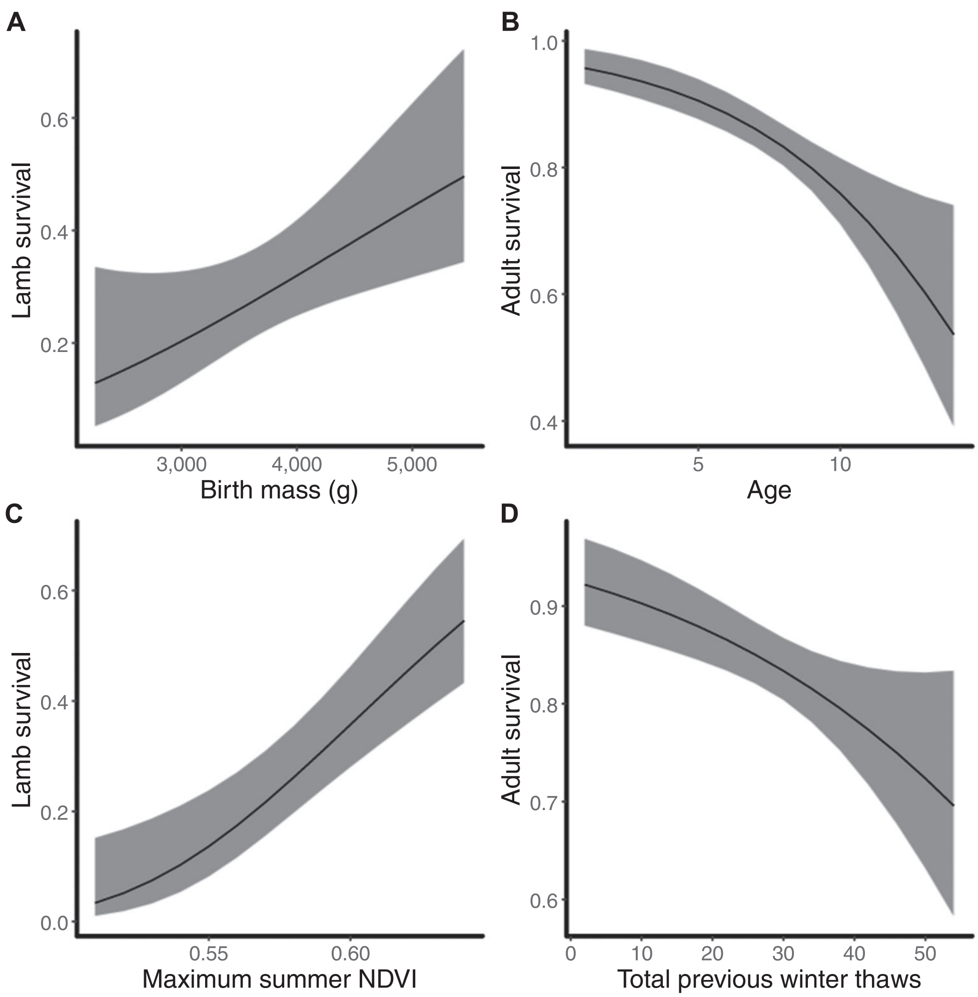

Figure 2. The relationship between A) birth mass and lamb survival, B) age and adult survival, C) maximum summer normalized difference vegetation index (NDVI) and lamb survival, and D) the number of thaws in the previous winter and adult survival for Dall's sheep at 9 locations throughout their range, Alaska, USA, 1997–2012. Shaded area represents 95% confidence interval.

Table 3. Relative variable importance (RVI) for the top 10 parameters for survival of Dall's sheep lambs and adults at 9 locations throughout their range, Alaska, USA, 1997–2012.

Age class	Parameter[a]	RVI
Lambs	NDVI summer	0.730
	FTF winter	0.417
	Temp summer	0.230
	Precip summer	0.075
	PDO winter	0.065
	SWE winter	0.060
	SWE summer	0.056
	FTF October	0.053
	AO winter	0.034
	Temp previous winter	0.028
Adults	FTF previous winter	0.991
	Temp previous winter	0.701
	FTF winter	0.107
	Temp winter	0.079
	FTF October	0.040
	Precip summer	0.021
	NDVI summer	0.007
	Temp summer	0.006
	Precip previous winter	0.005
	SWE.Summer	0.004

[a] NDVI = normalized difference vegetation index, FTF = freeze-thaw frequency, temp = temperature, precip = precipitation, PDO = pacific decadal oscillation, SWE = snow water equivalent, AO = arctic oscillation.

When we included environmental variables in the model selection process, the top model for lamb survival included an interactive effect of summer NDVI and winter temperature, with an additive effect of birth mass (Table 4). Survival was highest when high NDVI in summer was followed by a warm winter, lowest when low NDVI in summer was followed by a warm winter, and generally increased with birth mass (Table 5; Fig. 3A). The top model for adult survival included an interactive effect of the FTF in the previous winter and the temperature in the previous winter, with an additive effect of age (Table 4). Survival was highest when the temperature was high but the FTF was low, lowest when both the FTF and temperature were high, and generally decreased with age (Table 5; Fig. 3B).

Table 5. Hazard ratios and robust standard errors (SE) for each variable included in the top model for survival of Dall's sheep lambs and adults at 9 locations throughout their range, Alaska, USA, 1997–2012.

Age class	Covariate[a]	Hazard ratio	SE
Lambs	Birth mass	0.79	0.10
	NDVI summer	0.64	0.09
	Temp winter	0.98	0.11
	NDVI summer × temp winter	0.78	0.13
Adults	Age	1.98	0.12
	FTF previous winter	1.84	0.17
	Temp previous winter	0.67	0.17
	FTF previous winter × temp previous winter	1.25	0.11

[a] NDVI = normalized difference vegetation index, temp = temperature, FTF = freeze-thaw frequency.

Adding a random effect of site to the base survival models, which included birth mass for lambs and age for adults but did not include environmental covariates, improved the model AIC by 1.09 and 0.82 for lamb and adult survival, respectively. The environmental covariates in the top models accounted for the majority of the variation among sites; adding a random effect of site to models with these covariates did not improve the model fit. However, the difference in AIC between the top model without a random effect and the top model with a random effect of site was ≤2 for lamb and adult survival, indicating that substantial variation remained (Table S3, available online in Supporting Information).

The majority of lamb mortality (76%) took place in summer, whereas the majority of adult mortality (72%) took place in winter (Fig. 4). Predation was the largest source of

Table 4. Model selection table showing the model, the number of parameters (*K*), the difference in Akaike's Information Criterion (ΔAIC), and model weight for the top 10 models for survival of Dall's sheep lambs and adults at 9 locations throughout their range, Alaska, USA, 1997–2012.

Age class	Model[a]	*K*	ΔAIC	Weight
Lambs	Mass + temp winter × NDVI summer	4	0.00	0.30
	Mass + FTF winter × NDVI summer	4	0.97	0.19
	Mass + FTF October × NDVI summer	4	2.79	0.08
	Mass + precip summer × FTF October	4	3.29	0.06
	Mass + temp previous winter × NDVI summer	4	4.17	0.04
	Mass + NDVI summer × PDO winter	4	4.68	0.03
	Mass + precip summer × NDVI summer	4	5.24	0.02
	Mass × NDVI summer × temp winter	7	5.33	0.02
	Mass × FTF October × precip summer	7	5.87	0.02
	Mass + FTF winter + NDVI summer	3	5.97	0.02
Adults	Age + temp previous winter × FTF previous winter	4	0.00	0.46
	Age + temp previous winter + FTF previous winter	3	2.20	0.15
	Age × FTF previous winter + temp previous winter	4	3.09	0.10
	Age + precip summer × AO summer	4	3.30	0.09
	Age × FTF previous winter × temp previous winter	7	3.79	0.07
	Age × temp previous winter + FTF previous winter	4	4.12	0.06
	Age × AO summer × precip summer	7	5.91	0.02
	Age × PDO summer × FTF October	7	6.13	0.02
	Age × FTF previous winter × precip previous winter	7	10.56	0.00
	Age + precip previous winter × FTF previous winter	4	10.72	0.00

[a] Temp = temperature, NDVI = normalized difference vegetation index, FTF = freeze-thaw frequency, precip = precipitation, PDO = pacific decadal oscillation, AO = arctic oscillation.

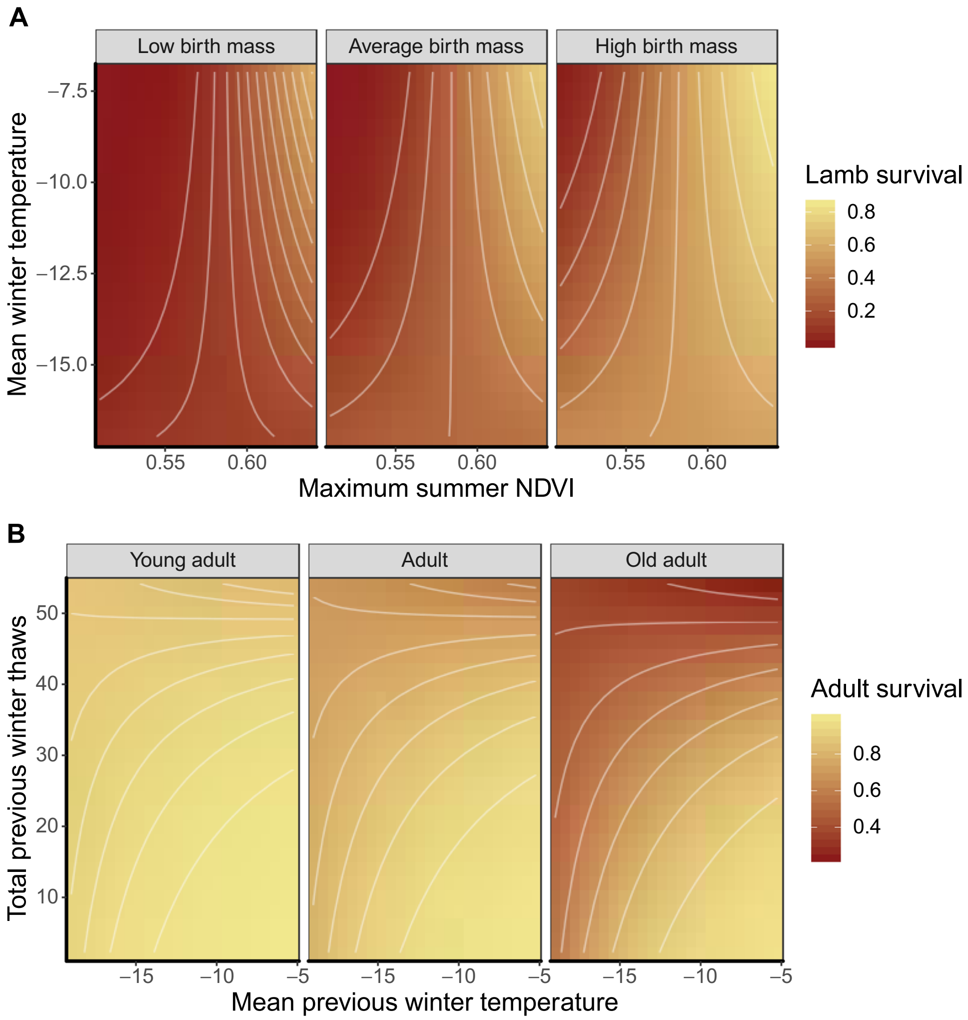

Figure 3. A) The relationship between survival, birth mass, mean winter temperature (°C), and maximum summer normalized difference vegetation index (NDVI) as predicted by the top model for Dall's sheep lambs (low, average, and high birth mass are 2,250 g, 3,750 g, and 5,250 g, respectively), and B) the relationship between survival, age, total previous winter thaws, and mean previous winter temperature as predicted by the top model for Dall's sheep adults (young adults, adults, and old adults are 3 yr, 7 yr, and 11 yr, respectively) at 9 locations throughout their range, Alaska, USA, 1997–2012.

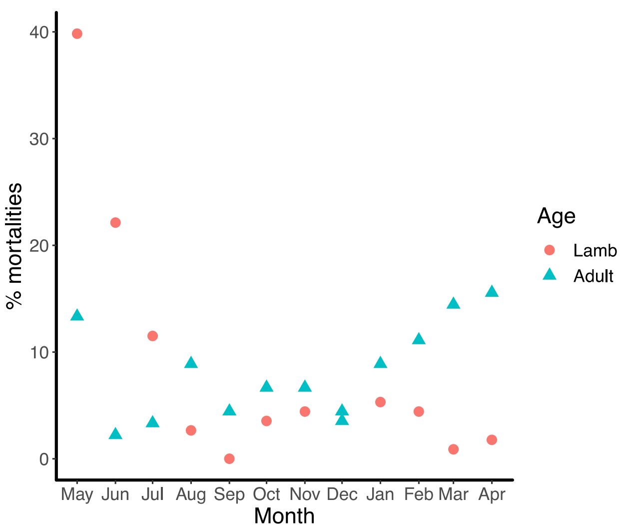

Figure 4. The proportion of mortality occurring in each month of the year for Dall's sheep lambs and adults at 9 locations throughout their range, Alaska, USA, 1997–2012.

mortality, accounting for 87% and 74% of known causes of lamb and adult mortality, respectively (Table S4, available online in Supporting Information). We included only data from the Alaska Range to examine the relationship between summer NDVI and coyote predation of lambs because that was the only study site with documented coyote predation (coyotes were rare in the Brooks Range site). The number of lamb mortalities from predation by coyotes (slope $= -0.74 \pm 0.23$, $P < 0.01$) and golden eagles (slope $= -0.48 \pm 0.22$, $P = 0.03$) decreased with increasing NDVI, but we found no significant relationship between maximum summer NDVI and other mortality sources. For adults, we did not find any significant relationships between FTF in previous winter and any causes of mortality.

DISCUSSION

We investigated how survival rates of Dall's sheep populations were affected by a variety of environmental factors across portions of their range. We found major stage-specific differences in the importance of direct and indirect climatic variables on survival that were consistent with the timing of mortality. In our models, the index of summer vegetation productivity had the strongest effect on lamb survival and frequency of winter freeze-thaw events had the strongest effect on adult survival. In addition, these remotely sensed environmental factors interacted with meteorological factors to affect survival, such that effects of winter temperature varied with changes in productivity (summer NDVI) and the frequency of freeze-thaw events (FTF). These findings highlight the utility of remotely sensed environmental conditions for ungulate management, and indicate that evaluating the effects of climate change on ungulate survival will require accounting for multiple interacting climate factors.

Consistent with previous studies, our base model indicated that lamb survival was strongly affected by birth mass, and adult survival was strongly affected by age (Forchhammer et al. 2001, Prugh and Arthur 2015). Sex was not an important predictor of survival, indicating that the female bias of the adult data should not have a strong effect on our findings. Birth mass is important for lamb survival and is a good indicator of overall fitness (Arthur and Prugh 2010). The negative effect of age on adult survival indicates that senescence occurs in Dall's sheep, as in other ungulates (Loison et al. 1999). Adult survival was generally high and stable, whereas juvenile survival was low and variable, as is the general pattern for long-lived ungulates like Dall's sheep (Eberhardt 1977, Gaillard et al. 2000). We did not find any evidence of density dependence in survival of Dall's sheep lambs and adults, which indicates that survival patterns among our study populations were not strongly affected by differences in densities. It is possible we did not detect an effect because we derived sheep densities from counts. In converting counts to density estimates, we assumed the entire study area was sheep habitat, which is inaccurate and makes counts an imperfect index of density.

Maximum summer NDVI was the most important environmental covariate related to lamb survival and suggested a positive effect of greater net primary productivity and green biomass in alpine vegetation. Researchers have reported increased survival rates, body condition, and growth rates of Dall's sheep in areas and years with higher productivity (Hoefs and Cowan 1979, Bunnell 1980, Nette et al. 1984). The majority of nutrition during a lamb's first summer is from nursing, and the quality and quantity of milk produced by females are affected by their forage (Rachlow and Bowyer 1991). Milk that is high in protein accelerates weight gain, causing the lambs to outgrow the most vulnerable stage quicker (Whitten 1975). Predation by coyotes and eagles decreased substantially with increasing NDVI. We also found an unexpected interaction between NDVI and winter temperature, where high winter temperatures were beneficial following summers with high NDVI values, but detrimental following summers with low NDVI values. These results indicate that how lambs are affected by winter temperature might depend on their condition at the end of the summer. Joly (2011) reported reduced population growth and calf body condition of caribou during warm winters, and suggested increased predation risk and higher probability of ice crust formation as possible causes. For Dall's sheep, lambs in poor condition might struggle more to avoid predators and cope with reduced winter food. Our analysis of lamb survival was limited because lamb data were restricted to 2 study sites, so additional data are needed for stronger inference.

Although vegetation productivity (as measured by NDVI) is not considered a climatic variable, it is affected by climate and could affect survival through climate-related changes as an indirect climate effect (Mysterud and Østbye 2006). Studies addressing climate-influenced population dynamics in ungulates often suggest that effects of climate operate indirectly through changes in vegetation, but vegetation measures are rarely examined explicitly (Forchhammer et al. 1998, Wang et al. 2002, Griffin et al. 2011). Several researchers have reported a positive effect of earlier spring thaw and lengthening growing season on NDVI, reporting increases in NDVI ranging from 7–17% over 3 decades at high latitudes (Myneni et al. 1997, Jia et al. 2003). Besides increased productivity, the influence of higher maximum NDVI in the models could also be due to factors such as earlier spring thaws or green-ups and longer growing seasons. Additionally, it is possible that NDVI was related to survival because it does a better job of integrating climate effects than do more direct measurements of climate.

Survival of adult Dall's sheep was high and stable, but adults became increasingly sensitive to previous winter conditions as they aged. Although few researchers have examined delayed effects of climate conditions on ungulate survival, Sand et al. (1995) reported a significant correlation between previous winter conditions and adult body mass of moose in Sweden. Thus, delayed effects of weather variables may be important to test for in models of ungulate survival.

We discovered an interactive effect of FTF and temperature in the previous winter on adult survival, indicating that warm winters were beneficial but only if FTF was low (Fig. 3). Northern mountain ranges often have areas that blow free of snow in winter (Mahoney et al. 2018), and we therefore did not expect freeze-thaw events to affect Dall's sheep as strongly as ungulates such as caribou and muskox that occur in regions with deeper, continuous snow cover. The strong effect of FTF that we detected indicates that freeze-thaw events, and the icing conditions that accompany them, may have strong negative effects on access to forage or forage quality even in areas with heterogeneous, non-continuous snow cover. Our results suggest that the increased frequency and spatial extent of freeze-thaw events that has been predicted by climate models (Intergovernmental Panel on Climate Change 2013) may lead to decreased survival of adult sheep (Putkonen and Roe 2003). The negative effects this would have on population growth rates could outweigh any positive effects of climate change on lamb survival, depending on the relative magnitudes of positive and negative effects.

Several environmental variables that other studies have found to be important for ungulate survival were not included in our top models. For example, large-scale temporal climate patterns such as the PDO and AO are related to population trajectories of caribou in Alaska (Joly et al. 2011). Our results suggest that these regional climate patterns do not affect Dall's sheep survival uniformly across the species' range, which may be the result of substantial spatial variability in local environmental conditions and differences in limiting factors among sites. The environmental variables were generally not highly correlated among sites. The low correlation among local climatic conditions might also explain why we did not find an effect of cohort or year on survival. Differences in factors such as elevation, slope, and latitude may lead to substantial variation in local conditions among sites, such that local, site-specific covariates were better predictors than regional, broad-scale climate cycles. Data spanning multiple decades would be required to adequately test the effect of a multi-decadal cycle, and our studies were limited in time. Therefore, it is possible that the effect of decadal oscillations would be more apparent given a longer time frame.

Our results indicate that 2 remotely sensed variables, NDVI and FTF, were stronger predictors of Dall's sheep survival than more commonly used variables such as precipitation and temperature. Therefore, our study highlights the usefulness of remote sensing data in understanding how environmental factors affect wildlife survival. Freeze thaw data derived from passive microwave data are particularly underused by wildlife biologists (Kim et al. 2016, 2018). We strongly recommend incorporating remotely sensed data in studies examining the responses of species to climate variables.

We found that the environmental variables in our top model explained most of the variation in survival rates among sites, indicating that spatial variation in environmental conditions may partially explain why some populations are declining while others appear stable or increasing. Dall's sheep in the Chugach Mountains of southcentral Alaska appear to be decreasing, whereas populations in much of the Brooks Range have experienced several periods of sharp decline interspersed with periods of slow increase (Alaska Department of Fish and Game 2011, 2014). Only 1 of our sites, Lake Clark, experiences a maritime climate similar to southcentral Alaska, and the FTF at this site was exceptionally high. In contrast, the Brooks Range is subject to a cold arctic climate, with infrequent winter thaws, relatively less snowfall, and low winter temperatures (Verbyla et al. 2017). Our results indicate that the low temperatures at the northern edge of the range of Dall's sheep and high FTF at the southern edge could both result in relatively low adult survival, potentially leading to population declines via different climate mechanisms.

MANAGEMENT IMPLICATIONS

Of the variables we used in our models, changes in winter temperatures, frequencies of freeze-thaw events, and vegetation productivity had the strongest effects on Dall's sheep survival. Climate change is predicted to alter these variables. According to our findings, the interactive effects of the projected changes might increase lamb survival and decrease adult survival, with net effects on population numbers that may vary substantially across their distribution based on local climate trends. This information may help managers prepare adaptive management strategies required to conserve Dall's sheep populations into the future. For example, new climate conditions may push Dall's sheep out of their documented range and alter population performance in their current range. Anticipating these changes will allow managers to understand new population levels and (re)define harvest objectives that are in line with what the environment can support in a given area. Additionally, prudent wildlife management should direct money and effort primarily to locations with suitable environmental conditions for Dall's sheep. If climate change makes an area unsuitable for sheep, resources can be directed to populations in more suitable locations. Finally, Dall's sheep are great bellwethers of alpine areas in the Arctic. Changes in the alpine environment that cause Dall's sheep populations to decline could be a signal for managers to monitor those areas more closely and initiate management actions directed at the sheep and other wildlife species. Such actions might include closure of certain areas during times of the year when lambs are born, or keeping people off of sensitive alpine vegetation.

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