

Association between weather and Dall's sheep *Ovis dalli dalli* harvest success in Alaska

Authors: Leorna, Scott, Brinkman, Todd, McIntyre, Julie, Wendling, Brad, and Prugh, Laura

Source: *Wildlife Biology*, 2020(2)

Published By: Nordic Board for Wildlife Research

URL: <https://doi.org/10.2981/wlb.00660>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.



Association between weather and Dall's sheep *Ovis dalli dalli* harvest success in Alaska

Scott Leorna, Todd Brinkman, Julie McIntyre, Brad Wendling and Laura Prugh

S. Leorna (<https://orcid.org/0000-0001-8689-8197>) ✉ (sleorna@alaska.edu) and T. Brinkman, *Inst. of Arctic Biology, Univ. of Alaska Fairbanks, Fairbanks, AL 99775, USA.* – J. McIntyre, *Dept of Mathematics and Statistics, Univ. of Alaska Fairbanks, Fairbanks, AL, USA.* – B. Wendling, *Alaska Dept of Fish & Game, Division of Wildlife Conservation, Fairbanks, AL, USA.* – L. Prugh, *School of Environmental and Forest Sciences, Univ. of Washington, Seattle, WA, USA.*

Although extensive research has been conducted on a variety of factors that influence wildlife harvest rates, few studies have quantified the impact of weather on harvest success. As global warming continues to contribute to unprecedented changes in local weather regimes, particularly in arctic and alpine ecosystems, understanding how these changes impact human–wildlife interactions will become increasingly important and relevant for wildlife managers. Therefore, we used a long-term dataset (1999–2015) on Dall's sheep *Ovis dalli dalli*, an alpine species in Alaska, USA, as a case study to explore how changes in local daily weather has affected hunter harvest success. We used generalized linear mixed models to estimate relationships between daily harvest count and weather variables using three separate models; all hunters, resident hunters and non-resident hunters. Weather variables included daily mean relative humidity, precipitation, air temperature and wind speed. For our model including all hunters, which excluded wind, we estimated that a mean increase in relative humidity, precipitation and temperature from one day to the next resulted in an 11.7, 4.3 and 2.9% decrease in daily harvest, respectively. The effect of relative humidity influenced harvest count two to three times more than all other weather variables across models. This study contributes to a limited body of knowledge on quantifying the impact of weather on harvest success and about how changes in weather affect hunter and wildlife behavior. Advancing knowledge on how weather influences variation in harvest may facilitate effective strategies for adapting hunting regulations to meet harvest and population goals.

Keywords: climate change, harvest management, hunting, wildlife management, wild sheep

Hunting has been used as a wildlife management tool to regulate and conserve game populations in North America since the beginning of the twentieth century (Heffelfinger et al. 2013). Extensive research has been conducted on the effects of hunting on game population dynamics (Leopold 1933), and a growing body of research has assessed factors that influence harvest success (Bhandari et al. 2006). Prior research on harvest success has mainly evaluated the effects of hunter characteristics (e.g. experience level), habitat and access (Gratson and Whitman 2000, Cooper et al. 2002). Despite decades of the wildlife studies implying that weather conditions influence harvest opportunity (Fobes 1945, Hansen et al. 1986, Brinkman et al. 2016), few studies have quantified the impact of weather on harvest success and

those findings have been mixed concerning weather–harvest associations. Rivrud et al. (2014) noted that weather may affect harvest patterns through game and hunter behavior, but the interactions were complex and may be less important than hunter preference and harvest quotas. Lebel et al. (2012) suggested that harvest was weakly related to weather conditions when game density is high. Stafford et al. (2010) reported that temperature was an important predictor of waterfowl hunter success, with harvest increasing as average low temperature decreased.

With amplified climate change (Winton 2006, Serreze et al. 2009, Stuecker et al. 2018), it is plausible that unseasonable and irregular weather conditions will have an increasingly important influence on hunter success by altering either or both hunter and wildlife behavior. Accounting for variance in harvest explained by weather factors may provide insight on why actual harvest outcomes differ from expected outcomes. Discrepancies between realized and intended harvest numbers related to wildlife management plans has been referred to as implementation uncertainty

This work is licensed under the terms of a Creative Commons Attribution 4.0 International License (CC-BY) <<http://creativecommons.org/licenses/by/4.0/>>. The license permits use, distribution and reproduction in any medium, provided the original work is properly cited.

(Bischof et al. 2012). Quantifying causes of implementation uncertainty may address factors contributing to harvest instability, reduce unexpected outcomes related to hunter behavior, and help managers better translate policy into practice (Hunt 2013, Nuno et al. 2014). We anticipate that allocating more attention to weather–harvest associations will become increasingly important to wildlife managers as harvest management adapts to a shifting climate. Here, we assess the effects of daily weather conditions on harvest success using a long-term dataset on Dall’s sheep *Ovis dalli dalli* hunter harvests in Alaska, USA.

Dall’s sheep are broadly distributed across Alaska and northwestern Canada in high-elevation alpine and sub-alpine environments. These steep, dry and windswept areas are dominated by grasses and low shrubs. Generally, Dall’s sheep populations migrate seasonally between summer and winter ranges following forage availability (Bowyer et al. 2000). These high-elevation habitats are gradually being impacted by shrubification and upward advancement of the tree line due to a warming climate (Pauli et al. 1996, Dirnböck et al. 2003, Ernakovich et al. 2014, Greenwood and Jump 2014, Dial et al. 2016). As encroachment of the tree line persists, fragmentation of suitable Dall’s sheep habitat may reduce connectivity and gene flow between populations (Worley et al. 2004). Changes in winter and spring snow conditions are also thought to be affecting Dall’s sheep population dynamics (Mahoney et al. 2018, Rattenbury et al. 2018).

Dall’s sheep rams are highly sought after by Alaska resident and non-resident hunters. Over the course of this study (1999–2015), the number of sheep hunters participating annually in Alaska ranged from 2191 to 3135, and annual harvest of rams ranged from 660 to 923 (ADF&G 2017). Non-residents represented 19% of sheep hunters but accounted for 39% of the annual harvest. Higher harvest success rates among non-residents are likely related to a regulation stipulating that all non-resident sheep hunters must hire a professional hunting guide unless the non-resident is hunting with a resident that they are related to within the second degree of kindred (ADF&G 2014). Guides can be hired for roughly \$10 000–20 000 USD per hunter. The general hunting season is open from 10 August through 20 September, and the majority of harvest (~50%) occurs within the first 10 days of the season (ADF&G 2014).

Dall’s sheep hunting serves as an ideal case study for the evaluated association between weather and harvest success for several reasons. First, climate-related changes are amplified at northern latitudes (Overland et al. 2013) within Dall’s sheep range, which may intensify weather–harvest interactions. Second, Dall’s sheep occupy relatively remote and inaccessible alpine environments that lack anthropogenic infrastructure (e.g. maintained roads, permanent shelter) that may shield hunters from weather conditions that can impede access or create unsatisfactory conditions while in the field. Third, many sheep hunters access hunting areas by small airplane where poor flight conditions may delay or prevent hunters from getting in or out of hunting areas. Fourth, after arriving at the hunting area, sheep hunters are usually committed to staying in remote field camps for extended

periods of time (10–14 days), rather than returning home and attempting the hunt at a later date with more favorable weather conditions. Finally, while hunting, inclement weather may also obstruct a hunter’s ability to see and stalk sheep or may present safety concerns because of the steep and rugged terrain that Dall’s sheep inhabit. While these weather-related challenges are likely common knowledge to hunters and intuitive to Dall’s sheep managers, no published studies have quantified the influence of weather on sheep harvest.

Quantifying the effects of weather on sheep harvest has important management implications. Dall’s sheep hunting is currently one of the most contentious wildlife management issues in Alaska (Brinkman 2014). Conflict among stakeholders (resident hunters, non-resident hunters, commercial guides and transporters) has intensified in recent years, and consensus on an acceptable resolution has not been achieved. The Alaska Board of Game has made recent changes to hunting regulations in an effort to reduce conflict, such as prohibiting the use of aircraft to locate sheep during the open sheep hunting season, and restricting non-resident hunters to one ram with full-curl horn or larger every four regulatory years (Alaska Board of Game 2016). Adding to this management dilemma are insufficient biological data on sheep population trends and social data on hunter concerns. Dall’s sheep populations in Alaska are thought to represent roughly a quarter of all wild sheep populations in North America, including both thinhorn sheep *Ovis dalli* subsp. and bighorn sheep *Ovis canadensis* subsp. (WAFWA 2019). Population demographic data on Dall’s sheep are spatially and temporally limited throughout much of the animal’s range, and survey methods currently employed (e.g. minimum counts) are considered insufficient to adequately track population trends in most areas with precision. Nearly ubiquitous full-curl harvest regulations have been thought to create sufficient hunting opportunity, while preventing hunter harvest from having a significant additive effect on annual mortality. However, peer-reviewed data supporting this hypothesis are absent (Whitten 2001), and several sources of variation (e.g. weather, habitat carrying capacity) likely contribute to implementation uncertainty of the full-curl management control. Studies have explored the attitudes and perceptions of Alaska sheep hunters and guides (Brinkman 2014), but published data on factors affecting Dall’s sheep harvest success are absent. Considering the intense hunter controversy, advancing knowledge on factors that affect Dall’s sheep harvest would likely be instrumental to informing the dialogue among stakeholders and may contribute to Dall’s sheep management decisions.

We anticipate that our research may also inform a broader audience interested in interactions between weather and hunter harvest. Optimizing hunter harvest will continue to be an important tool for maintaining wildlife populations at densities that are socially and ecologically acceptable (Cote et al. 2004, Gortázar et al. 2006). Incorporating weather variables into harvest management models may prove useful when trying to identify the optimal timing of hunting seasons and for interpreting variability in daily and annual harvest data.

Methods

Study area

The Alaska Department of Fish and Game (ADF&G) uses Game Management Unit (GMU) subunits as spatial boundaries for which hunting regulations and management is based. Our study was conducted using sheep harvest and weather data from 26 GMU subunits, which were combined into five major mountain regions within Alaska: Alaska Range East, Alaska Range West, Brooks Range, Talkeetna Mountains and Wrangell-St. Elias Mountains (Fig. 1). Three mountain regions were excluded because: 1) changes in harvest regulations (e.g. any ram harvest, change from general season to draw hunts) during the study period likely altered harvest rates

(Chugach mountain region), 2) low harvest rates prevented a sufficient sample size for analysis (Yukon-Tanana Uplands and Kenai mountain regions) and 3) a lack of weather stations to estimate daily weather variables on dates for which harvest occurred (Yukon-Tanana Uplands mountain region). The majority of sheep hunting opportunities in these mountain regions are open to both resident and non-resident hunters with a general harvest ticket. However, certain areas within some mountain regions (e.g. the Tok Management Area and the Delta Controlled Use Area within Alaska Range East) are managed under a draw hunt system for varying reasons (e.g. the opportunity to harvest trophy rams and hunting in aesthetically pleasing conditions). Rigorous sheep population estimates for these mountain regions are not available. Therefore, identifying fluctuations in sheep abundance over

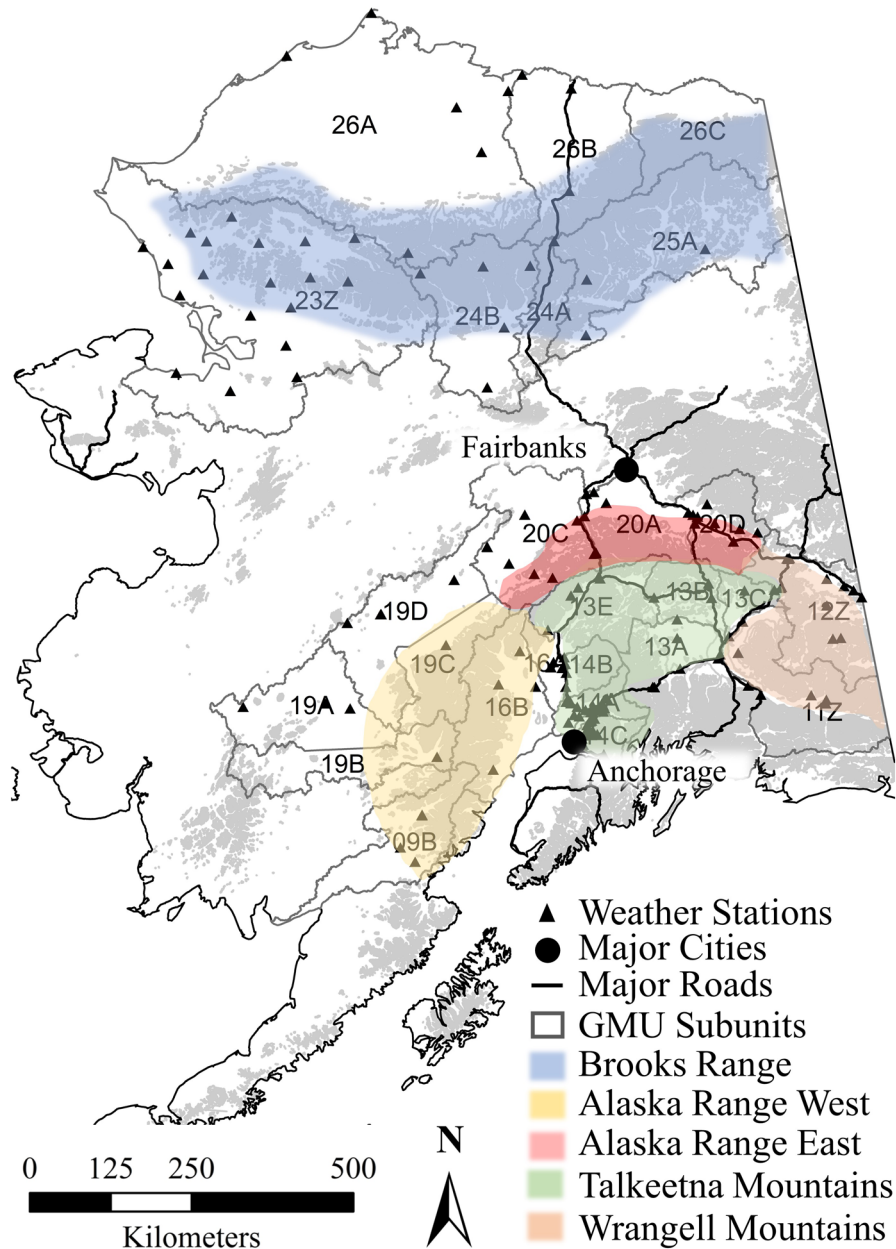


Figure 1. Mountain regions within Alaska, USA included in our analysis of the effects of weather variables on Dall's sheep harvest between 1999 and 2015. Included within mountain regions are weather station locations and Game Management Unit (GMU) subunits from which weather and harvest data were compiled.

the course of this study was not possible. However, ADF&G management biologists periodically perform minimum count surveys in small portions of the major mountain regions. This information, in addition to management objectives, management activities and harvest statistics can be found in ADF&G's management and harvest reports (ADF&G 2020).

Data management

Hunter harvest data

Through a memorandum of agreement with the ADF&G, we received all individual hunter harvest data between the years 1999 and 2015. ADF&G's database provided information on the GMU subunit in which the harvest occurred (i.e. harvest location), the date of the kill, and whether the hunter was a resident or non-resident. To prepare the harvest data for analysis, we summed the total number of sheep harvested on each day, during each year, in each mountain region. Although harvest data were available prior to 1999 and in other GMU subunits, daily weather station data were too limited to include those data in our analysis.

Weather data

We compiled daily weather data from 10 Aug to 20 Sep between 1999 and 2015 from 210 weather stations across our study area (Western Regional Climate Center 2017). The weather variables in our dataset included daily mean relative humidity (%), precipitation (cm), air temperature ($^{\circ}\text{C}$) and wind speed (m s^{-1}) on a day that sheep harvest occurred. We identified and removed erroneous weather data (e.g. daily average precipitation > 5 cm, temperature $> 38^{\circ}\text{C}$, wind speed $< 0 \text{ m s}^{-1}$) using the 1st and 99th percentiles of each dataset. This cutoff sufficiently discarded nonsensical weather measurements while retaining extreme but physically plausible weather characteristics. We excluded other weather variables (snowfall, snow depth and barometric pressure) due to excessive missing data and small sample sizes.

To connect weather data to harvest, we first used ArcGIS to assign the corresponding GMU subunit to each weather station based on its GPS location. We then used all available data from weather stations within each GMU subunit where harvest occurred to calculate average daily weather values at the GMU subunit scale. These average daily weather values were then connected to each individual harvest using the date of kill and GMU subunit where the harvest occurred. Finally, the dataset used for analysis was generated by summing all harvest within each mountain region, on each day, in each year, and averaging the associated daily weather from the GMU subunits where harvest occurred, accounting for the number of harvest in each GMU subunit (i.e. weather data from GMU subunits where more harvest occurred within each region received more weight in the calculation). Weighted average weather calculations were restricted to days for which at least one sheep was harvested within a region and the GMU subunit where the harvest occurred had available weather data. Few weather stations were located in high-elevation sheep habitat and the exact location of harvest could not be determined from harvest data. Therefore, our averages of weather station variables within the GMU subunits where harvest occurred were considered the best available representation of weather conditions within the mountain region.

Statistical analysis

We used R (www.r-project.org) to fit generalized linear mixed models to estimate relationships between daily harvest count and weather variables for all hunters, as well as separate models for resident and non-resident hunters. The majority ($> 80\%$) of sheep harvested in Alaska during our study period were harvested under general harvest regulations, where there are no quota restrictions put on the number of sheep that can be harvested or limits to the number of hunters who can sheep hunt within a given year. Considering the harvest data available, there was no reliable way to control for hunter effort (i.e. how many total hunters were hunting in each area, on each day of the season) since date specific information was not collected from hunters unless they harvested a sheep; in which case the date of kill was reported. However, we included the day of season (i.e. 10 Aug = 1; 20 Sep = 42) when harvest occurred in our models which is strongly associated with hunter effort (i.e. more hunters in the beginning of the season) (ADF&G 2014). Also, since no hunter data were recorded on days when no harvest occurred, there was no way to distinguish between days where there were hunters in the area, but no successful hunters (i.e. no sheep harvested), or no hunters at all in the field leading to no sheep being harvested. Due to this ambiguity for zero-harvest days, models were fit using the zero-truncated Poisson response using R package glmmTMB (Brooks et al. 2017, Magnusson et al. 2017). Random effects were included for the yearly trend between harvest count and day of season, allowing for potential random annual variation in both the slope and intercept of the trend line.

We attempted to investigate region specific differences using mountain region as a fixed effect, but model output was unnecessarily complicated and we did not have social or biological explanations for the results (e.g. why would changes in weather affect hunters differently in different regions?). Therefore, we chose to examine weather effects at a statewide scale (i.e. effects of weather averaged over all regions) fostering results with practical interpretations, rather than gaining greater specificity by including region effects. We modeled the harvest count response for each hunter group independently using subsets of resident ($n = 1975$ days with harvest) and non-resident ($n = 1702$ days with harvest) data. All models were fit using only records that had no missing values for any of the covariates. For model diagnostics, we examined plots of residuals vs. fitted values and histograms of harvest count by year and observed what would be expected from a zero-truncated Poisson response variable (i.e. increased variability as fitted values increased and histograms showed a right-skewed distribution with only positive counts). We used Akaike's information criterion (AIC) to select the best models (Burnham and Anderson 2002). We used a backward elimination process, starting with selection of random effects, followed by consideration of fixed effect terms. If model AIC values were within two points, we selected the simpler model. We used McFadden's Pseudo- R^2 to measure model fit (McFadden 1974). Different from normal R^2 value, McFadden's Pseudo- R^2 should not be interpreted as the proportion of variance explained. In general, Pseudo- R^2 values between 0.2–0.4 indicate a strong model fit (McFadden 1977).

Our best-fit models provided estimated coefficients for each weather covariate. We used model coefficients to

Table 1. Average daily Alaska sheep harvest and weather by region from 1999 to 2015.

Region		Sheep harvested	Wind (ms ⁻¹)	Temp. (°C)	Rel. hum. (%)	Precip. (cm)
Alaska Range West	Mean (SD)	3.54 (2.89)	1.44 (0.58)	11.54 (3.47)	79.47 (11.62)	0.19 (0.36)
Alaska Range East	Mean (SD)	4.34 (4.17)	1.08 (0.59)	10.58 (3.43)	71.10 (12.59)	0.15 (0.24)
Wrangell Mountains	Mean (SD)	4.52 (4.95)	1.67 (0.74)	9.14 (3.28)	69.56 (11.14)	0.15 (0.26)
Talkeena Mountains	Mean (SD)	3.84 (3.68)	1.39 (1.03)	10.64 (2.80)	75.89 (12.44)	0.22 (0.36)
Brooks Range	Mean (SD)	6.46 (5.89)	2.83 (1.35)	8.25 (3.17)	65.43 (14.48)	0.10 (0.19)
Total	Mean (SD)	4.64 (4.71)	1.67 (1.09)	9.81 (3.39)	71.11 (13.12)	0.16 (0.28)

These values are based on the dataset used for analysis (i.e. includes only records where at least one sheep was harvested and weather data was available for all variables on a particular day). Therefore, harvest data on days where weather data was not available for all variables is excluded from the average daily harvest calculation. Likewise, weather data on days where there was no harvest data is excluded from the average daily weather calculations.

estimate how a daily change in each weather variable affected the percent change in daily harvest using the formula (Weisberg 2014):

$$\%change = 100 \times (exp(dB) - 1)$$

where B is the estimated coefficient for the weather variable and d is its daily change. Calculations were carried out with two different degrees of daily change for each weather variable. The first used the mean daily increase and decrease in each weather variable and the second used the value at two standard deviations above or below the means for each weather variable. The degrees of daily change (i.e. mean and two standard deviation) for each weather variable were calculated using data where there were consecutive days of weather and harvest count data. The second degree of change provides an estimate of an abrupt and large change in the weather from one day to the next. The delta method was used to compute approximate standard errors for each estimate of percent change in daily harvest.

Results

Our dataset included 2287 days when at least one harvest occurred within a given mountain region (total harvest of 10 612 sheep) and weather data were available for all variables. Maximum and mean daily sheep harvest was 46 and 4.6 (SD=4.7), respectively. During the hunting season (10 Aug–20 Sep) over the study period (1999–2015), mean daily precipitation, air temperature, wind speed and relative humidity was 0.16 cm (SD=0.28), 9.8°C (SD=3.39), 1.7 ms⁻¹ (SD=1.09) and 71% (SD=13.1), respectively (Table 1). Mean daily increase in precipitation, air temperature, wind speed and relative humidity was 0.17 cm (SD=0.23), 1.2°C (SD=1.1), 0.6 ms⁻¹ (SD=0.7) and 8.2% (SD=7.4), respectively. Mean daily decrease in precipitation, air temperature, wind speed and relative humidity was -0.2 cm (SD=0.2), -1.3°C (SD=1.2), -0.6 ms⁻¹ (SD=0.6) and -7.9% (SD=6.5), respectively.

All hunters model

Our best-fit model (Psuedo $R^2=0.268$) that pooled all hunters included year and day of season as random effects (random slopes and intercepts), and temperature, precipitation and relative humidity as fixed effects. The importance of

day of season was anticipated given that approximately half of the total harvest occurred during the first 10 days of the season across our study area and period. Thereafter, harvest gradually decreased throughout the remainder of the season.

Daily changes in relative humidity had the largest effect on change in percent daily harvest (Fig. 2, Table 2). Changes in weather variables had an inverse relationship with percent daily harvest (Fig. 2, Table 2). A mean daily increase in relative humidity, precipitation and temperature from one day to the next resulted in an 11.7, 4.3 and 2.9% decrease in daily harvest, respectively. A mean decrease in relative humidity, precipitation and temperature resulted in a 12.8, 4.4 and 3.4% increase in daily harvest, respectively. A two standard deviation daily increase from the mean in relative humidity, precipitation and temperature resulted in a 29.5, 15.1 and 8.0% decrease in daily harvest, respectively. A two standard deviation decrease from the mean in relative humidity, precipitation and temperature resulted in a 37.4, 17.8 and 9.6% increase in daily harvest, respectively (Table 2).

Resident and non-resident hunter models

Our best-fit model for resident (Psuedo $R^2=0.219$) hunters included random effects for both slope and intercept and for non-resident (Psuedo $R^2=0.162$) hunters included only a random intercept. Both models included all weather variables as fixed effects. The direction of the effect between daily weather variables and harvest were similar between residents and non-residents, with the exception of wind speed (Fig. 2, Table 2). Wind speed had an opposite effect on daily harvest for non-residents compared to residents; harvest decreased with increasing wind speeds for residents, whereas harvest increased with increasing wind speeds for non-residents. We found relative humidity, wind speed and precipitation had slightly greater effects on resident harvest as compared to non-resident harvest. Temperature had slightly less of an effect on resident daily harvest as compared to non-resident harvest.

For residents, a mean daily increase in relative humidity, precipitation, wind speed and temperature resulted in a 13.1, 4.4, 3.2 and 2.5% decrease in daily harvest, respectively. A mean daily decrease in relative humidity, precipitation, wind speed and temperature resulted in 14.6, 4.5, 3.3 and 2.8% increase in daily harvest, respectively. A two standard deviation daily increase from the mean in relative humidity, precipitation, wind speed and temperature resulted in a 32.6, 15.4, 9.4 and 6.8% decrease in daily harvest, respectively. A two standard deviation decrease from the mean in

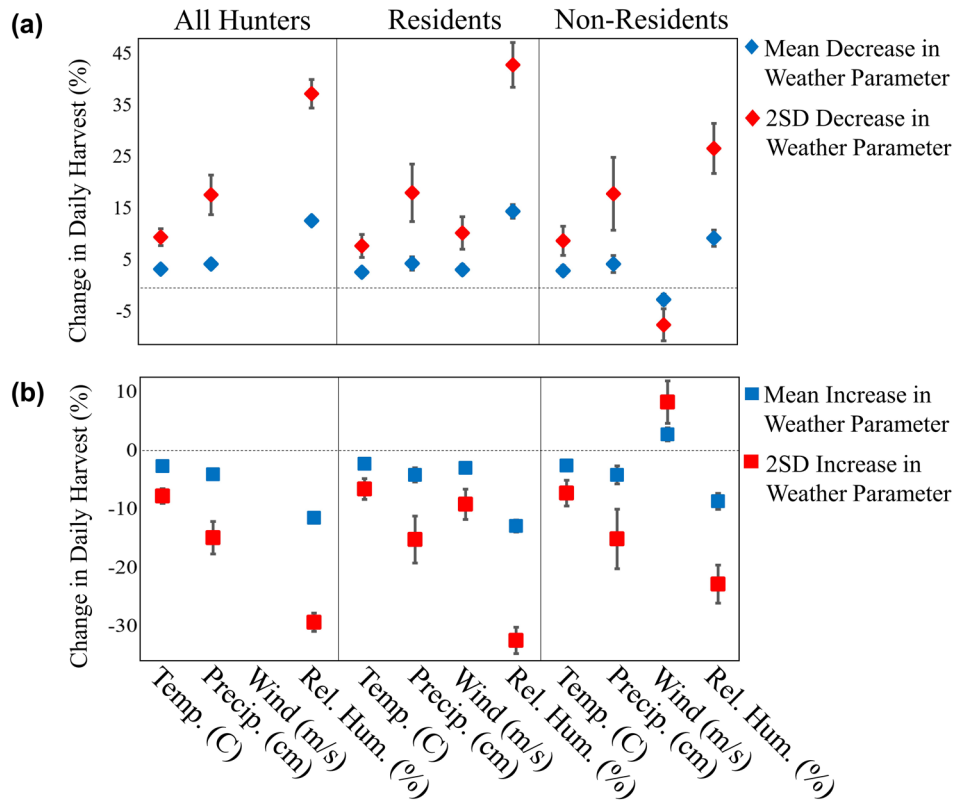


Figure 2. Estimates for all hunter, resident and non-resident models for how a mean and two standard deviation from the mean decrease (a) and increase (b) in each weather parameter affects percent change in daily Dall's sheep harvest in Alaska, USA. Error bars represent the standard error calculated using the delta method.

relative humidity, precipitation, wind speed and temperature resulted in a 43.0, 18.2, 10.4 and 7.9% increase in daily harvest, respectively (Table 2).

For non-residents, a mean daily increase in relative humidity, precipitation and temperature resulted in an 8.9, 4.4 and 2.8% decrease in daily harvest, respectively. However, a mean daily increase in wind speed increased daily harvest by 2.5%. A mean daily decrease in relative humidity, precipitation and temperature resulted in a 9.4, 4.4 and 3.1% increase in daily harvest, respectively. Mean daily decrease in wind speed

resulted in a 2.5% decrease in harvest. A two standard deviation increase from the mean in relative humidity, precipitation and temperature resulted in a 23.0, 15.3 and 7.5% decrease in daily harvest, respectively. A two standard deviation increase from the mean in daily wind speed increased harvest by 8.0%. A two standard deviation decrease from the mean in relative humidity, precipitation and temperature resulted in a 26.8, 18.0 and 8.9% increase in daily harvest, respectively. A two standard deviation decrease from the mean in daily wind speed decreased daily harvest by 7.4% (Table 2).

Table 2. Effects of daily weather on change in daily Dall's sheep harvest in Alaska, USA.

Model	Weather	Coefficient	SE	% change in daily harvest from decrease in weather variable		% Change in daily harvest from increase in weather variable	
				Mean (SE)	2SD (SE)	Mean (SE)	2SD (SE)
All hunters	Relative humidity (%)	-0.0152	0.0010	12.8 (0.86)	37.4 (2.76)	-11.7 (0.69)	-29.5 (1.56)
	Precipitation (cm)	-0.2617	0.0521	4.4 (0.89)	17.8 (3.84)	-4.3 (0.84)	-15.1 (2.77)
	Temperature (°C)	-0.0249	0.0040	3.4 (0.55)	9.6 (1.62)	-2.9 (0.47)	-8.0 (1.24)
	Wind speed (ms ⁻¹)	Not in best model					
Resident	Relative humidity (%)	-0.0171	0.0014	14.6 (1.32)	43.0 (4.33)	-13.1 (1.03)	-32.6 (2.25)
	Precipitation (cm)	-0.2662	0.0754	4.5 (1.29)	18.2 (5.58)	-4.4 (1.21)	-15.4 (4.00)
	Wind speed (ms ⁻¹)	-0.0515	0.0148	3.3 (0.96)	10.4 (3.15)	-3.2 (0.89)	-9.4 (2.58)
	Temperature (°C)	-0.0208	0.0056	2.8 (0.76)	7.9 (2.22)	-2.5 (0.65)	-6.8 (1.76)
Non-resident	Relative humidity (%)	-0.0114	0.0018	9.4 (1.58)	26.8 (4.84)	-8.9 (1.36)	-23.0 (3.23)
	Precipitation (cm)	-0.2646	0.0954	4.4 (1.64)	18.0 (7.06)	-4.4 (1.53)	-15.3 (5.07)
	Temperature (°C)	-0.0234	0.0071	3.1 (0.96)	8.9 (2.82)	-2.8 (0.82)	-7.5 (2.20)
	Wind speed (ms ⁻¹)	0.0400	0.0174	-2.5 (1.06)	-7.4 (3.10)	2.5 (1.11)	8.0 (3.62)

Estimates from best-fitting models for all hunters, resident hunters and non-resident hunters with all mountain regions combined of how a mean and two standard deviation from the mean daily change in weather variables affect percent change in daily harvest of Dall's sheep in Alaska, USA. Weather variables are ordered from greatest to least effect within models.

Discussion

We modeled the effects of weather on Dall's sheep harvest in Alaska and determined that several weather variables influenced daily success rates. Our interpretations are restricted to daily weather and its effects when at least one sheep was harvested. Relative humidity had the largest effect on harvest, with average daily changes having two to three times as strong an effect on harvest as changes in precipitation, temperature or wind speed (Fig. 2, Table 2). Relative humidity may be especially important because high relative humidity can increase the likelihood of fog in alpine areas (Hansen et al. 1986, Gonser et al. 2012, Haeffelin et al. 2013, YiHui and YanJu 2014). Fog hinders hunters' visibility of sheep and may introduce a safety risk when navigating steep and complex terrain. Because sheep hunting occurs in remote areas with challenging access, hunters are committed to remaining in the field and planes are grounded when visibility is limited. Therefore, it is logical that a decrease or increase in relative humidity would help or hinder harvest, respectively. For example, after fog limits visibility and forces hunters to be less mobile, a decrease in relative humidity may result in an increase in hunter effort to make up for lost time and opportunity from previous days. Generally, increases in weather variables from one day to the next had slightly less effect than decreases on daily harvest across all models (Fig. 2, Table 2).

Precipitation had the second largest effect across models. Similar to the consequences of high relative humidity, precipitation also may limit visibility and create safety risks when traversing steep rocky terrain that provides escape cover to sheep. Also, other research suggests that hunter motivation decreases in poor weather leading to decreased effort (Fobes 1945, Hansen et al. 1986, Rivrud et al. 2014). Precipitation may have had a reduced effect on daily harvest compared to relative humidity because hunters can better adapt to days of precipitation with the aid of rain gear if visibility is not impaired.

Temperature and wind speed had relatively small effects on change in daily harvest compared to the other variables (Fig. 2, Table 2). Temperature and wind are less likely to affect visibility and a hunter's ability to spot and stalk sheep as compared to fog or low cloud ceilings that may occur on rainy days or when relative humidity is high. However, high temperatures can cause mountain ungulates to move to higher elevations, seek shade in rugged terrain, and become less active (Aublet et al. 2009), which may impede a hunter's ability to spot sheep. Increases in daily temperature consistently reduced harvest success rates. Other research suggests that game becomes less active when temperatures are high (Rivrud et al. 2014, Street et al. 2015), which could reduce chances of encountering or seeing sheep bedded in cover.

Wind speed was not included in the best model for all hunters and had opposite effects on hunter groups; daily harvest increased for non-residents and decreased for residents with increased wind speeds. Increased winds may improve harvest success by masking sound and improving predictability of how scent travels (Cherry and Barton 2017), two factors hunters commonly account for when in the field. A potential explanation for increased non-resident daily harvest

may be related to professional guides' relatively high-level of experience who accompany most non-residents. Guides commonly hunt the same area year after year and may have better knowledge of how winds behave in their area. The increased financial investment of hiring a guide may also motivate more effort during poor weather, and the advanced local knowledge of the professional guide may enhance non-residents ability to navigate the hunting area. We speculate that advanced knowledge of the hunting area may explain why non-residents were less affected by relative humidity, the most influential weather variable. In general, harvest data indicates that non-resident hunters are proportionally more successful than resident hunters (ADF&G 2014).

Management implications and future research

As climate-related changes in weather continue to intensify, accounting for weather factors on hunter success rates may improve wildlife management by helping to explain variation in harvest. Unknown causes of variation in harvest force managers and hunters to speculate about factors influencing changes in harvest success. These factors are often contentious and can lead to controversial management policies (e.g. predator control, differences in permit allocation among different stakeholder groups) (Boertje et al. 2010, Brinkman 2018). Precise estimates of factors influencing harvest models may help define and resolve conflict among stakeholders and inform game management decisions.

Several opportunities remain for future research on the relationship between weather and harvest. First, we recommend studies account for the relative effect of weather compared to other factors known to cause variation in harvest (e.g. game abundance, nutrition, habitat quality, anthropogenic disturbance, predation). Second, as confidence is enhanced in daily associations, studies may scale up to seasonal assessments to identify seasons with 'good' or 'poor' weather. Seasonal harvest statistics are typically used as an index of abundance (Imperio et al. 2010, Wolfe et al. 2015). Therefore, understanding the seasonal impact of weather on harvest may inform other population metrics. Third, to more precisely assess the localized effects of weather, a more intensive grid of weather stations in remote alpine areas where hunting occurs is needed. Averaging weather data from surrounding areas may not capture the localized conditions experienced by hunters. Due to insufficient data, we excluded snowfall and snow depth from our analysis. Snow accumulation likely affects Dall's sheep hunting opportunities, and we suggest future analyses account for this variable as the spatial and temporal resolution of snow station data improves (Boelman et al. 2019). Lastly, we recommend wildlife agencies increase information they collect from unsuccessful hunters. Historically and currently, successful hunters report more detailed spatial and temporal information on effort. Information from unsuccessful hunters would greatly enhance sample sizes for statistical assessments of weather-harvest associations.

The quantitative effects of weather on hunter harvest is a relatively unexplored topic for all game species but may be a critical component to effective harvest management in a shifting climate regime. As seasonal norms in weather shift,

assessing the associations between weather and harvest may provide insight into effective strategies for adapting hunting regulations and meeting harvest goals. To our knowledge, our study represents one of the few that has quantified the effects of weather on ungulate harvest. Additional exploration of this understudied topic may help optimize hunting as a wildlife management tool.

Acknowledgements – We thank the Alaska Department of Fish & Game for providing Dall's sheep harvest records.

Funding – This study was funded by the NASA ABoVE project (award no. NNX15AU21A).

References

- ADF&G (Alaska Dept of Fish & Game) 2014. Trends in Alaska sheep populations, hunting and harvests. – Division of Wildlife Conservation, Wildlife Management Report ADFG/DWC/WMR-2014-3, Juneau.
- ADF&G (Alaska Dept of Fish & Game) 2017. Dall's sheep news. – <www.adfg.alaska.gov/static/hunting/dallsheephunting/pdfs/dalls_sheep_news_winter_2017.pdf>, accessed 27 Aug 2019.
- ADF&G (Alaska Dept of Fish & Game) 2020. Management and harvest reports: sheep. Accessed January 2020 from <<http://www.adfg.alaska.gov/index.cfm?adfg=librarypublications.wildlifemanagement#sheep>>
- Alaska Board of Game 2016. Findings related to proposal 207: restrictions on the use of aircraft associated with sheep hunting. 5 AAC 92.085. – from <www.adfg.alaska.gov/static/regulations/regprocess/gameboard/pdfs/findings/16213.pdf>, accessed June 2018.
- Aublet, J. et al. 2009. Temperature constraints on foraging behavior of male Alpine ibex (*Capra ibex*) in summer. – *Oecologia* 159: 237–247.
- Bhandari, P. et al. 2006. Effort versus motivation: factors affecting antlered and antlerless deer harvest success in Pennsylvania. – *Hum. Dimens. Wildl.* 11: 423–436.
- Bischof, R. et al. 2012. Implementation uncertainty when using recreational hunting to manage carnivores. – *J. Appl. Ecol.* 49: 824–832.
- Boelman, N. et al. 2019. Integrating snow science and wildlife ecology in Arctic-boreal North America. – *Environ. Res. Lett.* 14: 1.
- Boertje, R. et al. 2010. Science and values influencing predator control for Alaska moose management. – *J. Wildl. Manage.* 74: 917–928.
- Bowyer, R. et al. 2000. Dall's and Stone's sheep. – In: Demarais, S. and Krausman, P. (eds), *Ecology and management of large mammals in North America*. Prentice Hall, pp. 491–544.
- Brinkman, T. 2014. Alaska sheep hunter survey: resident sheep hunter responses. – Alaska Dept of Fish & Game. – <www.adfg.alaska.gov/static/home/library/pdfs/wildlife/mgt_rpts/14_sheep_hunter_survey_report.pdf>, accessed Oct 2019.
- Brinkman, T. 2018. Hunter acceptance of antlerless moose harvest in Alaska: importance of agency trust, proximity of hunter residence to hunting area, and hunting experience. – *Hum. Dimens. Wildl.* 23: 129–145.
- Brinkman, T. et al. 2016. Arctic communities perceive climate impacts on access as a critical challenge to availability of subsistence resources. – *Clim. Change* 139: 413–427.
- Brooks, M. et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – *R J.* 9: 378–400.
- Burnham, P. and Anderson, R. 2002. Model selection and multi-model inference: a practical information-theoretic approach, 2nd edn. – Springer.
- Cherry, M. and Barton, B. 2017. Effects of wind on predator–prey interactions. – *Food Webs* 13: 92–97.
- Cooper, A. et al. 2002. Predicting hunter success rates from elk and hunter abundance, season structure and habitat. – *Wildl. Soc. Bull.* 30: 1068–1077.
- Cote, S. et al. 2004. Ecological impacts of deer overabundance. – *Annu. Rev. Ecol. Evol. Syst.* 35: 113–147.
- Dial, R. et al. 2016. Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. – *Global Change Biol.* 22: 1841–1856.
- Dirnböck, T. et al. 2003. A regional impact assessment of climate and land-use change on alpine vegetation. – *J. Biogeogr.* 30: 401–417.
- Ernakovich, J. et al. 2014. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. – *Global Change Biol.* 20: 3256–3269.
- Fobes, C. 1945. Weather and the kill of white-tailed deer in Maine. – *J. Wildl. Manage.* 9: 76–78.
- Gonser, S. et al. 2012. The relation between humidity and liquid water content in fog: an experimental approach. – *Pure Appl. Geophys.* 169: 821–833.
- Gortázar, C. et al. 2006. Disease risks and overabundance of game species. – *Eur. J. Wildl. Res.* 52: 81–87.
- Gratson, M. and Whitman, C. 2000. Characteristics of Idaho elk hunters relative to road access on public lands. – *Wildl. Soc. Bull.* 28: 1016–1022.
- Greenwood, S. and Jump, A. 2014. Consequences of treeline shifts for the diversity and function of high altitude ecosystems. – *Arct. Antarct. Alpine Res.* 46: 829–840.
- Haefelin, M. et al. 2013. A comparative study of radiation fog and quasi-fog formation processes during the ParisFog field experiment 2007. – *Pure Appl. Geophys.* 170: 2283–2303.
- Hansen, L. et al. 1986. Factors affecting daily and annual harvest of white-tailed deer in Illinois. – *Wildl. Soc. Bull.* 14: 368–376.
- Heffelfinger, J. et al. 2013. The role of hunting in North American wildlife conservation. – *Int. J. Environ. Stud.* 70: 399–413.
- Hunt, L. 2013. Using human-dimensions research to reduce implementation uncertainty for wildlife management: a case of moose (*Alces alces*) hunting in northern Ontario, Canada. – *Wildl. Res.* 40: 61–69.
- Imperio, S. et al. 2010. Investigating population dynamics in ungulates: do hunting statistics make up a good index of population abundance? – *Wildl. Biol.* 16: 205–214.
- Lebel, F. et al. 2012. Influence of habitat features and hunter behavior on white-tailed deer harvest. – *J. Wildl. Manage.* 76: 1431–1440.
- Leopold, A. 1933. *Game management*. – C. Scribner's Sons.
- Magnusson, A. et al. 2017. glmTMB: generalized linear mixed models using template model builder. – R package ver. 0.1.3.
- Mahoney, P. et al. 2018. Navigating snowscapes: scale-dependent responses of mountain sheep to snowpack properties. – *Ecol. Appl.* 28: 1715–1729.
- McFadden, D. 1974. Conditional logit analysis of qualitative choice behavior. – In: Zarembka, P. (ed.), *Frontiers in econometrics*. Academic Press, pp. 105–142.
- McFadden, D. 1977. Quantitative methods for analyzing travel behavior of individuals. – In: Hensher, D. and Stopher, P. (eds), *Behavioural travel modeling*. Cowles Foundation, pp. 279–318.
- Nuno, A. et al. 2014. Managing social-ecological systems under uncertainty: implementation in the real world. – *Ecol. Soc.* 19: 52.
- Overland, J. et al. 2013. Future arctic climate changes: adaptation and mitigation time scales. – *Earth's Future* 2: 68–74.
- Pauli, H. et al. 1996. Effects of climate change on mountain ecosystems-upward shifting of alpine plants. – *World Resource Rev.* 8: 3.

- Rattenbury, K. et al. 2018. Delayed spring onset drives declines in abundance and recruitment in a mountain ungulate. – *Ecosphere* 9: 1–15.
- Rivrud, I. et al. 2014. Interaction effects between weather and space use on harvesting effort and patterns in red deer. – *Ecol. Evol.* 4: 4786–4797.
- Serreze, M. et al. 2009. The emergence of surface-based Arctic amplification. – *Cryosphere* 3: 11–19.
- Stafford, J. et al. 2010. Factors associated with hunter success for ducks on state-owned lands in Illinois, USA. – *Wildl. Biol.* 16: 113–122.
- Street, G. et al. 2015. Mid-day temperature variation influences seasonal habitat selection by moose. – *J. Wildl. Manage.* 79: 505–512.
- Stuecker, M. et al. 2018. Polar amplification dominated by local forcing and feedbacks. – *Nat. Clim. Change* 8: 1076–1081.
- WAFWA (Western Association of Fish & Wildlife Agencies) 2019. Wild sheep pop est license harvest 1990–2018 ver 5_21_2019. www.wafwa.org/committees___groups/wild_sheep_working_group/resources/, accessed Aug 2019.
- Weisberg, S. 2014. *Applied linear regression*, 4th edn. – Wiley.
- Western Regional Climate Center 2017. – <http://wrcc.dri.edu>, accessed Oct 2018.
- Whitten, K. 2001. Effects of horn-curl regulations on demography of Dall's sheep: a critical review. – *Alces* 37: 483–495.
- Winton, M. 2006. Amplified arctic climate change: what does surface albedo feedback have to do with it? – *Geophys. Res. Lett.* 33: 1–4.
- Wolfe, M. et al. 2015. Evaluation of harvest indices for monitoring cougar survival and abundance. – *J. Wildl. Manage.* 9999: 1–10.
- Worley, K. et al. 2004. Population genetic structure of North American thinhorn sheep (*Ovis dalli*). – *Mol. Ecol.* 13: 2545–2556.
- YiHui, D. and YanJu, L. 2014. Analysis of long-term variations of fog and haze in China in recent 50 years and their relations with atmospheric humidity. – *Sci. China Earth Sci.* 57: 36–46.