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November 30, 2017

Superintendent Sarah Creachbaum
Olympic National Park
600 East Park Avenue
Port Angeles, WA 98362-6798

RE: New additional information regarding mountain goats for the EIS

Sent via US Mail

Dear Superintendent Creachbaum:

On October 10, 2017, we submitted comments on the *Draft Mountain Goat Management Plan/Environmental Impact Statement.* Since that time, new research on mountain goats was published online (late October) that would have implications for the management plan.

The attached study, *Projecting the future of an alpine ungulate under climate change scenarios,* shows that mountain goat populations are very vulnerable to climate change and this may affect Olympic National Park and surrounding wildlands. This information has a direct bearing on how or whether to remove goats, especially if habitat changes render the Olympics unsuitable or less suitable for the species, as well as on the potential effects from the No Action alternative.

Since this is new information, it should be considered in any decision, included in the Final EIS or be used to reopen the comment period with additional alternatives.

Sincerely,

Gary Macfarlane
Board Member

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PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Projecting the future of an alpine ungulate under climate change scenarios

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Abstract

Climate change represents a primary threat to species persistence and biodiversity at a global scale. Cold adapted alpine species are especially sensitive to climate change and can offer key "early warning signs" about deleterious effects of predicted change. Among mountain ungulates, survival, a key determinant of demographic performance, may be influenced by future climate in complex, and possibly opposing ways. Demographic data collected from 447 mountain goats in 10 coastal Alaska, USA, populations over a 37-year time span indicated that survival is highest during low snowfall winters and cool summers. However, general circulation models (GCMs) predict future increase in summer temperature and decline in winter snowfall. To disentangle how these opposing climate-driven effects influence mountain goat populations, we developed an age-structured population model to project mountain goat population trajectories for 10 different GCM/emissions scenarios relevant for coastal Alaska. Projected increases in summer temperature had stronger negative effects on population trajectories than the positive demographic effects of reduced winter snowfall. In 5 of the 10 GCM/representative concentration pathway (RCP) scenarios, the net effect of projected climate change was extinction over a 70-year time window (2015–2085); smaller initial populations were more likely to go extinct faster than larger populations. Using a resource selection modeling approach, we determined that distributional shifts to higher elevation (i.e., "thermoneutral") summer range was unlikely to be a viable behavioral adaptation strategy; due to the conical shape of mountains, summer range was expected to decline by 17%–86% for 7 of the 10 GCM/RCP scenarios. Projected declines of mountain goat populations are driven by climate-linked bottom-up mechanisms and may have wide ranging implications for alpine ecosystems. These analyses elucidate how projected climate change can negatively alter population dynamics of a sentinel alpine species and provide insight into how demographic modeling can be used to assess risk to species persistence.

KEYWORDS
Alaska, alpine ecosystems, climate change, conservation, general circulation models, habitat change, mountain goat, *Oreamnos americanus*, population modeling, resource selection function

1 | INTRODUCTION

Climate change represents a primary threat to species persistence and biodiversity at a global scale; 7.9% of species are predicted to become extinct due to climate change (Urban, 2015). Thus, a mechanistic understanding of how climate influences population dynamics and viability is critical for forecasting, and potentially mitigating, deleterious effects of climate change. Identification of species and ecosystems that are particularly sensitive to climatic variability, along with the development of associated quantitative tools, can help expedite knowledge that is urgently needed to stem this conservation threat. In this regard, study of cold adapted alpine species that are especially sensitive to climate change (Dullinger et al., 2012; Gentili, Hemant, & Birks, 2015) and experiencing disproportionately rapid changes in climate (Christensen et al., 2013; Shanley et al., 2015), offer key opportunities to gain critical insights into broad-scale, forthcoming effects.

Alpine herbivores exhibit specialized strategies in order to survive and persist in highly seasonal and climatically extreme environments (Hoffman, 1974). Such species are sensitive to variation in climate during both summer and winter (Beever, Ray, Mote, & Wilkening, 2010; Bonardi, Corlatti, Bragalanti, & Pedrotti, 2017; Jacobson, Provenzale, von Hardenberg, Bassano, & Festa-Bianchet, 2004; Pettorelli, Pelletier, von Hardenberg, Festa-Bianchet, & Côté, 2007; Willisch et al., 2013). Recent studies determined that survival of mountain goats (*Oreamnos americanus*) in coastal Alaska, USA was negatively related to both higher summer temperature and higher winter snowfall (White et al., 2011). This occurs because summer temperature can influence the energy balance of mountain ungulates directly, via behavioral responses to thermoregulatory stress, and indirectly, through effects on plant nutritional characteristics and availability (Aublet, Festa-Bianchet, Bergero, & Bassano, 2009; Fox, 1991; Lenart, Bowyer, Ver Hoef, & Ruess, 2002). For example, warm summer temperatures resulting in heat stress lead to reduced foraging rates and altitudinal shifts to suboptimal foraging habitats in alpine ungulates, such as ibex (*Capra ibex*) (Aublet et al., 2009). Warm summer conditions also influence the nutritional quality of food resources by accelerating growth and lignification of plant cell walls, which reduce digestible protein concentration of forage resources (Doiron, Gauthier, & Levesque, 2014; Lenart et al., 2002). At a landscape scale, such dynamics are further amplified by rapid melting of snow fields and subsequent protraction of green-up, a period when high-quality, early-phenological stage forages are most readily available (Fox, 1991). Variation in summer forage quality, even when small, can have a strong influence on herbivore nutritional condition and productivity due to multiplier effects (McArt et al., 2009; White, 1983). Such effects can be particularly pronounced in highly seasonal environments when nutritional reserves that animals accumulate during the summer growing season influence their subsequent vulnerability to malnutrition during the following winter (Mautz, 1978). During winter, deep snow significantly elevates energetic costs of locomotion and restricts availability of important winter forages through burial (Dailey & Hobbs, 1989; Fox, 1983; White, Pendleton, & Hood, 2009). The interactive effects of summer and winter climate on mountain goat survival are expected to have strong demographic consequences (Parker, Barboza, & Gillingham, 2009) and thus provide mechanistic insight into how climate influences alpine herbivores.

Assessing the “winners” and “losers” of climate change is a profound and critical conservation objective that has been addressed in a variety of different ecosystems (Bateman et al., 2015; Brodie et al., 2017; LaRue et al., 2013; Thompson, Handel, Richardson, & McNew, 2016). Yet, the effect of projected future changes in climate on most alpine vertebrates is unclear. General circulation models (GCMs) predict that coastal Alaska will experience warmer summer temperatures but less snowy winter conditions (Shanley et al., 2015). Since predicted summer and winter changes result in opposite effects on mountain goat survival, the net change in survival is likely to be related to the strength, range, and directionality of the respective summer (i.e., negative) and winter (i.e., positive) effects (White et al., 2011). For example, change in summer climate may be more influential than winter because the increase in summer temperature spans a larger continuum of the effect curve, as compared to winter snowfall (Shanley et al., 2015; White et al., 2011). However, since the winter effect on survival is stronger than the summer effect (i.e., the slope of the response curve), decreased winter snowfall may partially or completely compensate for predicted summer warming (Shanley et al., 2015; White et al., 2011). This example illuminates the potential complexity of climate change effects, and highlights the challenges associated with identifying the “winners” and “losers” of climate change. Derivations of realistic and actionable prognoses require detailed quantitative analyses based on a strong mechanistic understanding of species’ and climate relationships.

Demographic models are a powerful tool for integrating multiple sources of population data, including survival and reproductive data and associated ecological relationships. In the context of climate change, implementation of mechanistic modeling approaches offers the potential to provide realistic demographic outcomes that can be directly acted upon in conservation policy arenas (Pacifici et al., 2015). For example, the ability to project population sizes and trajectories for a given area at key points in time enables direct evaluation of conservation objectives (i.e., population status) and subsequent development of proactive conservation policy. For species with high human value, such as alpine ungulates, population status information represents the basic currency through which management decisions are made and conservation policy implemented.

In this study, we develop a sex- and age-structured population modeling approach designed to examine how climate affects population dynamics. We parameterize the model using data from a well-studied alpine ungulate system (mountain goats in coastal Alaska; White et al., 2011) and climate change model (i.e., GCMs) predictions to examine scenarios about how populations are expected to change in the future. Specifically, we examine the net result of reduced winter snowfall, which improves mountain goat survival, and increased summer temperature, which reduces survival, across a range of regionally relevant climate change and emissions scenarios (sensu Shanley et al., 2015) on mountain goat population dynamics. Finally, we implemented a resource selection function (RSF) modeling approach to assess the degree to which increasing summer temperature would constrict available summer habitat. This provided a means to gauge whether behavioral adaptation (i.e., distributional shifts to higher elevation) could mediate effects of increased warming in extant summer ranges.

2 | MATERIALS AND METHODS

2.1 | Study system

Mountain goats are an iconic alpine ungulate species distributed throughout coastal and interior regions of western North America. Due to the extreme environments in which they inhabit, mountain goats have a conservative life-history strategy, relative to other temperate ungulates (Festa-Bianchet & Côté, 2008). Mountain goats are typically not physically and sexually mature until 4–6 years of age, rarely exhibit twinning, and have an average life span of 8 years (maximum age 15–18 years; Festa-Bianchet & Côté, 2008). A majority of mountain goats in North America live in northern temperate coastal areas in environments characterized by cool, wet summers, and snowy winters. In coastal areas, mountain goats typically exhibit seasonal migrations from high-elevation alpine summer habitat to lower elevation forested environments (Fox, Smith, & Schoen, 1989; Shafer et al., 2012; White & Gregovich, 2017). Seasonal migration to low-elevation, forested habitats during winter benefits mountain goats due to the reduced snow depths in such areas (Fox, 1983). Mountain goats are highly adapted for life in steep, rugged terrain, and exhibit strong selection for such terrain during both summer and winter (Fox et al., 1989; Shafer et al., 2012; White & Gregovich, 2017).

We modeled mountain goat population dynamics using climate data and projections for Juneau, Alaska, an area located near the geographic center of coastal mountain goat distribution and considered to be representative of North American coastal populations (Figure 1). Mountain goats in this region have been extensively studied (Fox, 1983, 1991; Fox et al., 1989; Shafer et al., 2012; White & Gregovich, 2017; White et al., 2011), and our previous research in this region has linked climate to mountain goat survival (White et al., 2011; Figure 1). Additionally, the Juneau International Airport (JIA) has a relatively long (1943–2014) time series of National Weather Service climate data, and served as the geographic reference for our climate data analyses and projections.

2.2 | Modeling approach

We developed a dual-sex, postbreeding, age-structured population model with 20 age classes (kids to 19+) to explore the impact of projected climate change from five GCMs and two emissions scenarios (details below; Figures 2 and 3). The population model is parameterized using published vital rates estimates and density-dependent relationships that vary at each annual time step in response to population density and summer/winter climate inputs (Houston & Stevens, 1988; Houston, Stevens, & Moorhead, 1994; Rice & Gay, 2010; White et al., 2011). Because temporal variation in adult survival can have a disproportionate influence on demographic outcomes (Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000), the goal of our modeling efforts was to assess how change in projected climate influences adult survival and resultant demographic outcomes. To assess climate effects on long-term demography, we conducted a population viability analysis to determine the probability of quasi-extinction for mountain goats using three initial population sizes (at equal population density) for each GCM and emissions scenario.

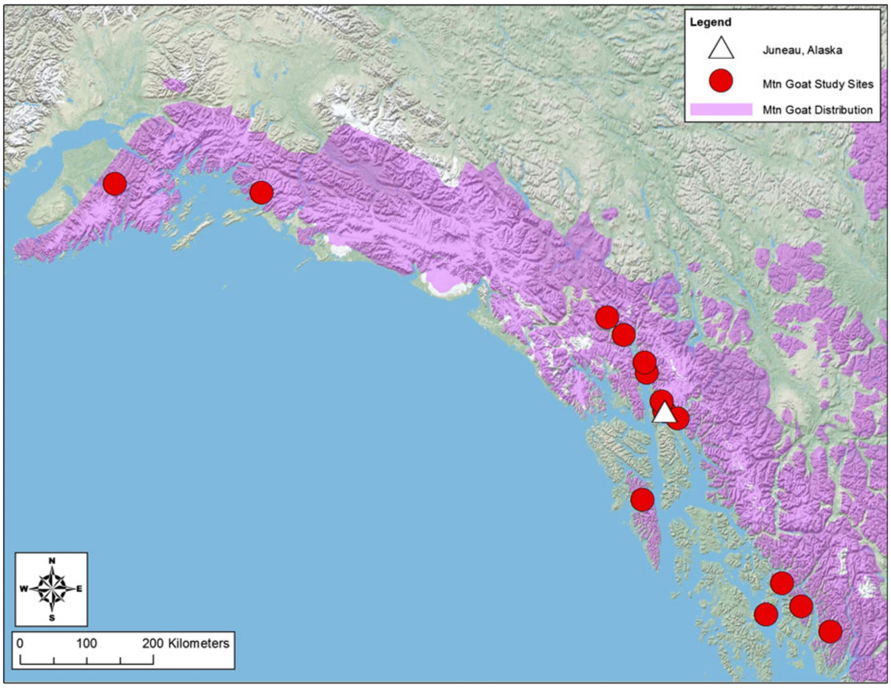

FIGURE 1 Map depicting mountain goat distribution in Alaska, USA and northwestern Canada. Study sites where field data were collected to parameterize mountain goat survival models are depicted by red circles (White et al., 2011, K. S. White, unpublished data). Juneau, Alaska is depicted by the white triangle and was used as the reference area for population simulations. Juneau, Alaska roughly coincides with the geographic center of mountain goat distribution in Alaska

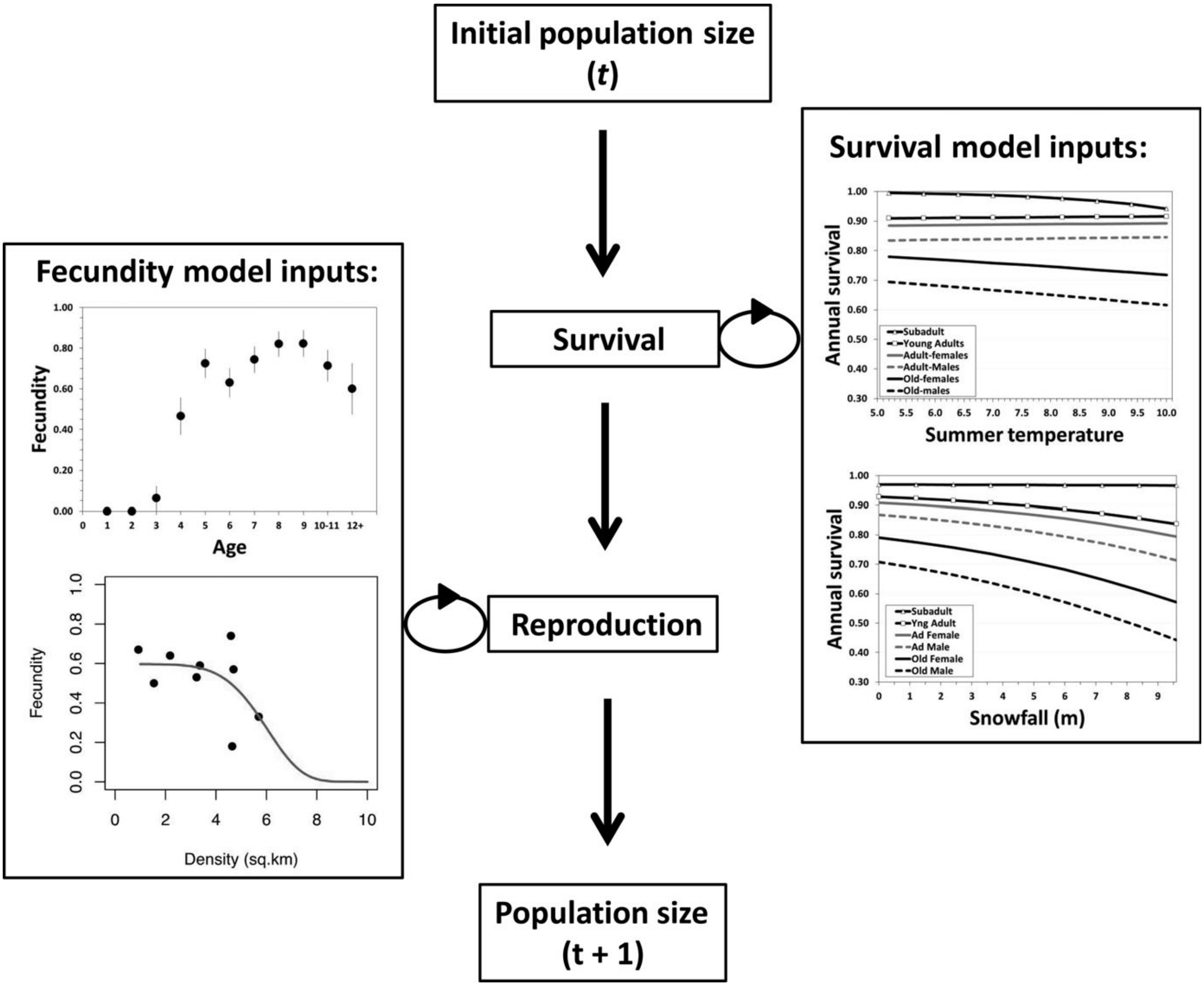

FIGURE 2 Conceptual diagram describing the dual-sex, postbreeding, age-structured population model used to examine demographic responses to GCM/RCP-based climate change scenarios. The model adjusts mountain goat survival for each sex and age class based on GCM predicted winter snowfall and summer temperature inputs for each annual time step. Mountain goat survival vs. climate relationships are based on White et al. (2011) and simulated based on the beta coefficient error distributions. Environmental stochasticity is simulated based on the statistical distributions of actual snowfall and summer temperature measurements recorded at the Juneau International Airport, Juneau, AK, USA, 1943–2014. Age-specific fecundity is modified based on density-dependent relationships. GCM, general circulation models; RCP, representative concentration pathway

Since we hypothesized that mountain goat populations would decline due to negative effects of increasing summer temperatures, we further examined a scenario involving the implications of behavioral adaptation to increasing temperature. Given that mountain goats are capable of shifting to higher elevations in order to mediate thermal stress, we used a habitat modeling approach to calculate how shifts to demographically thermoneutral elevations (i.e., the elevation that coincided with temperatures values required for $\lambda = 1.0$) reduced summer range carrying capacity. In this manner we were able to assess the implications of mountain goat adaptation to climate change.

To summarize, we first examine demographic outcomes for mountain goats in their current range. We then allow mountain goats to adapt to increasing summer temperatures and shift to higher elevations, which we use to quantify the extent to which adaptation reduces summer range carrying capacity. Our adaptation results are conservative because of the expected temporal mismatch, or delay, between increasing temperature and growing season length and the subsequent soil development and plant colonization following high-elevation glacial recession (i.e., the highest elevation predicted habitats are unlikely to be immediately utilized by mountain goats, even if temperatures are suitable; sensu Jumpponen, Brown, Trappe, Cázares, & Strömmer, 2012).

2.3 | Sex- and age-structured population model

We used field data, literature values, and a statistical survival model based on 1,179 mountain goat-years to parameterize a sex- and

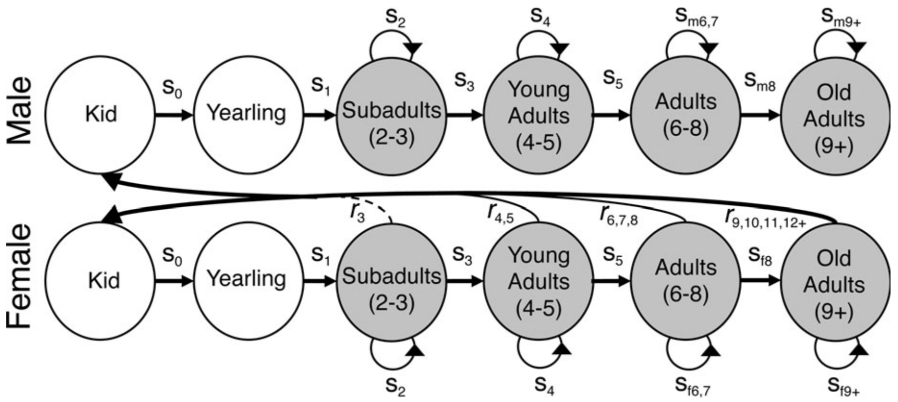

FIGURE 3 Mountain goat life cycle graph describing the dual-sex, postbreeding, age-structured population model used to examine demographic responses to GCM/RCP-based climate change scenarios. The model was implemented with 20 age classes (kids to 19+) for each sex but is simplified as a stage-structured model in the life cycle diagram for display purposes. Model description: S_0 = kid survival (no sex or climate effect; based on values from Rice & Gay, 2010), S_1 = yearling survival (no sex or climate effect; White et al., 2011), $S_{2,3}$ = 2- and 3-year-old survival (no sex effect, climate effects apply; White et al., 2011); $S_{4,5}$ = 4- and 5-year-old survival (no sex effect, climate effects apply; White et al., 2011), $S_{m6,7,8}/S_{f6,7,8}$ = 6-, 7-, and 8-year-old survival (sex and climate effects apply; White et al., 2011); S_{m9+}/S_{f9+} = 9+-year-old survival (sex and climate effects apply; White et al., 2011); r_{3-12+} = age-specific fecundity (Table S3) (no climate effect; density-dependent effects apply [Houston & Stevens, 1988; Houston et al., 1994, Fig. S4]). GCM, general circulation models; RCP, representative concentration pathway

age-structured stochastic population model (Figures 2 and 3, Appendix S1). To derive survival estimates we used the known-fates model in program MARK and RMARK (Cooch & White, 2016, Appendix S1). Specifically, we used the top model (determined via AIC model selection procedures; sensu Burnham & Anderson, 2002) published by White et al. (2011) in order to parameterize the effects of climate on sex- and age-specific mountain goat survival for all age classes, except kids. Estimates of kid survival were based on the average survival across studies reported by Rice and Gay (2010). Nonkid survival estimates were derived based on field data collected between 1977 and 2014 (1,179 goat-years, 447 radio-marked goats) in 10 different study areas located in coastal Alaska (White et al., 2011, K. S. White, unpublished data; Table S2a–b). White et al. (2011) estimated survival based on summer temperature and winter snowfall for all nonkid age classes. Overall, these models indicated that survival varied with respect to sex and age class. Furthermore, winter survival was negatively affected by the previous summer temperature (during July–August) and total winter snowfall (White et al., 2011). Fecundity was based on age-specific estimates derived from field data collected in coastal Alaska (K. S. White, unpublished data; Table S4) and modified based on previously described density-dependent relationships (Houston & Stevens, 1988; Houston et al., 1994; see below).

To account for uncertainty, we sampled from within the error distribution surrounding the beta coefficients (i.e., the effect of summer temperature and winter snowfall on survival) accounting for covariance structure among coefficients using the RMark package in R (Laake, 2013). We ran 1,000 iterations of our population model for each GCM and emissions scenario using stochastic annual survival estimates for each sex and age to propagate uncertainty in the relationship between climate variables and survival. Each GCM and emissions scenario provided the expected change in temperature and precipitation as snow for the years 2025, 2055, and 2085; values for intervening years were interpolated. To implement environmental stochasticity around these expected values, we modeled temperature as a normally distributed random variable and precipitation as snow as a lognormally distributed random variable. The standard deviation of both distributions was parameterized using the observed variance in the residuals around a trend fit to summer temperature and ln(winter precipitation as snow) using the JIA temperature record from 1943 to 2014. To reduce initial transient effects, we initialized each model based at the stable age distribution from a density-independent model run with the mean survival estimates.

We implemented density-dependent fecundity to more accurately project the mountain goat population through time and assess the probability of quasi-extinction by 2085 (quasi-extinction threshold of $N < 2$ individuals). Density-dependent effects reduced fecundity according to a statistical relationship fit to data from Houston and Stevens (1988) and Houston et al. (1994) following the S-shaped function from the per-capita formulation of the Ricker discretization of the theta-logistic model. This model has the desirable properties of a wide shoulder maintaining high fecundity at low population densities followed by a decline in fecundity toward zero at high densities, given by

$$F(D) = F_0 e^{-\left(\frac{D}{K}\right)^{\theta}} \tag{1}$$

$F(D)$ is the fecundity of females at population density (population size/km^2) D, F_0 is the maximum fecundity, which occurs as density approaches 0, and K and θ are parameters that determine the shape of density-dependent declines in fecundity. Maximum likelihood estimates for F_0, K, and θ were fit with simulated annealing using the *likelihood* package in program R with data from Houston and Stevens

(1988) and Houston et al. (1994) (Fig. S4). We then used field data from mountain goat populations in southeast Alaska to incorporate age-specific maximum fecundity (Appendix S3, Table S3) using the equation:

$$F_a(D) = F_a(0)\mathrm{e}^{-\left(\frac{D}{K}\right)^{\theta}}, \tag{2}$$

where $F_a(0)$ is a field-derived estimate of maximum fecundity for female mountain goats with age a, $F_a(D)$ is the density- and age-dependent fecundity, and K and θ remain unchanged.

For each GCM and emissions scenario, we used the proportion of 1,000 model runs that fell below $N = 2$ to estimate the probability of quasi-extinction by 2085. Because the probability of extinction depends on the initial population size, we ran each model with initial small, average, and large mountain goat populations ($N = 50$, 300, 1,000; defined based on field surveys from coastal Alaska, K. S. White, unpublished data). All models began with a population density of one mountain goat per km^2, well below the onset of significant density-dependent reductions in fecundity, so that we could understand the effect of climate change rather than site-specific effects due to densities that approach carrying capacity. Initial climate values (total winter snowfall [m] and mean daily temperature [°C]—July/August) were based on the average values for the JIA during the 20 years preceding our start time (1994–2014).

2.4 | General circulation models

To examine the effects of climate change on mountain goat population demography, we considered five different GCMs determined to perform well for coastal Alaska (Radic & Clarke, 2011; Walsh, Chapman, Romanovsky, Christensen, & Stendel, 2008) and previously used to assesses ecological implications of climate change in the North Pacific (Shanley et al., 2015). These models (CCSM4, GFDL-CM3, GISS-E2-H, IPSL-CM5B-LR, and MRI-CGCM3) were each parameterized based on two different ("worst case" and "best case") representative concentration pathway (RCP) scenarios: (1) RCP4.5 which assumes low–medium emissions and (2) RCP8.5 which assumes a "business-as-usual" high emissions scenario. Models were run using the ClimateWNA software (version 4.85; Wang, Hamann, Spittlehouse, & Murdock, 2012) to derive annual estimates (2015–2085) of precipitation as snow (PAS; mm) and mean temperature (°C) during July/August for the JIA. Since our mountain goat survival models required estimates of total annual snowfall and July/August temperature at 914 m (i.e., average mountain goat elevation during summer), we used historic data from the JIA (1943–2014) to calculate total annual snowfall based on PAS (Fig. S5), and adjusted JIA summer temperature estimates using the standard environmental lapse rate (−6.5°C/1,000 m; Barry & Van Wie, 1974), following White et al. (2011). The resulting summer and winter climate estimates were then input into the population model at annual time steps to derive sex- and age-specific survival estimates and model mountain goat demographic performance for each GCM and emission scenario.

2.5 | Habitat modeling simulations

Resource selection function models (sensu Boyce, Vernier, Nielsen, & Schmiegelow, 2002; Fieberg, Matthiopoulos, Hebblewhite, Boyce, & Frair, 2010) were developed for a 300-km^2 study area in the Kakuhan Range, AK (60–100 km north of the JIA) by White and Gregovich (2017), and used to estimate the amount of summer range habitat. RSF models predicted the relative probability of use of mountain goats for given 5-m pixels across the landscape and were based on empirically derived mechanistic relationships between mountain goat use and availability for multiple covariates such as elevation, distance to cliffs, slope, terrain ruggedness, and solar exposure (an index of plant productivity in wet, coastal environments). These variables represent biologically relevant correlates of ecophysiologic niche requirements of mountain goats as they relate to foraging conditions, predation risk, thermal constraints, and winter snow conditions. Specifically, RSF modeling indicated that mountain goats selected areas with high elevation, close proximity to cliffs, moderate-steep slopes, high terrain ruggedness, and high solar exposure during summer (White & Gregovich, 2017). Models had high predictive performance based on *k*-fold cross-validation analysis criteria (Boyce et al., 2002; White & Gregovich, 2017). Rasterized RSF surfaces were postprocessed to determine the amount of important summer habitat using methods described by Fedy et al. (2014).

We coupled this habitat modeling framework with GCM/RCP population modeling outputs to determine the extent to which mountain goat summer habitat is reduced if mountain goats adapt to climate warming by shifting to higher, "thermoneutral" elevations. Thermoneutral elevations were defined as the mean elevation that mountain goats currently inhabit in the Kakuhan Range case study area (mean elevation = 896 ± 163 m, $n = 104$ GPS collared mountain goats between 2005 and 2015); due to the current existence of mountain goats in this distribution we consider such areas to be demographically stable, or thermoneutral. First, we determined the predicted change in summer temperature for each GCM between 2015 and 2085. We then multiplied that quantity by the standard environmental lapse rate (−6.5°C/1,000 m; Barry & Van Wie, 1974) to determine how many meters a mountain goat would need to shift upslope to occupy an environment thermally identical to the mean summer elevation that mountain goats use during the current (2005–2015) time period (i.e., the current thermoneutral elevation). The estimated upslope altitudinal shift for each GCM/RCP scenario was added to the digital elevation model raster input layer for each customized GCM/RCP model run. The resulting RSF model output assumed that future mountain goat resource selection patterns for all model covariates would be identical to the current time period with the exception of elevation, which was shifted upslope to a degree dictated by the GCM/RCP under consideration. Finally, we compared how the amount of summer range differed between each GCM/RCP scenario—that is, how the amount of summer range available for mountain goats would be reduced in order for mountain goats to occupy a thermoneutral environment in the future.

3 | RESULTS

3.1 | General circulation models

All GCMs predicted similar trends in climate change between 2015 and 2085, however the degree of change differed between each GCM/RCP scenario (Table 1). Specifically, GCMs predicted that winter snowfall will decrease between 0.4 and 1.6 m (mean = 1.1 m) and summer temperature will increase between 1.3 and 6.0°C (mean = 3.5°C) between 2015 and 2085. As expected, the RCP8.5 emissions scenarios resulted in greater change than the RCP4.5 scenarios. Among the GCMs, the CCS, GDFL, and IPSL models predicted greater changes (i.e., "worst case scenarios") than the MRI and GISS models (i.e., "best case scenarios").

3.2 | Population projections

Mountain goat demographic performance was negatively influenced by predicted changes in future climate for all GCMs considered (Table 2, Figure 4). The CSS, GFDL, and IPSL climate modeling scenarios all resulted in simulated populations with a mean trajectory reaching extinction by 2085; the GISS and MRI models resulted in greatly reduced densities by 2085 relative to the baseline (i.e., the "no climate change" scenario), but the mean mountain goat population trajectory did not yet fall to extirpation (Table 2, Figure 4). As expected, higher emissions scenarios (RCP8.5) resulted in higher likelihood and faster rates of extinction than the low emission scenarios (RCP4.5; Table 2). In cases where populations went extinct for a given GCM for both RCP emission scenarios, populations went extinct 17 years sooner, on average, for the RCP8.5 scenario, as compared to the RCP4.5 scenario (Table 2). Given that GCMs predicted a decline in total annual snowfall and increase in average daily summer temperature between 2015 and 2085, our population simulations indicate the negative effects of increasing summer temperature exert a stronger effect on mountain goat population demography than the positive effects of decreasing winter snowfall.

TABLE 1 Observed and predicted mean daily summer temperature (July–August) and total annual snowfall for Juneau, AK, USA. Observed baseline values (i.e., 2015) represent the mean values for the preceding 20-year period (1995–2015). Predicted values (i.e., 2085) were derived based on 10 general circulation model (GCM) and representative concentration pathway (RCP) scenarios (Wang et al., 2012); GCM/RCP emission scenarios span a continuum of "best case" to "worst case" scenarios. Temperature values were adjusted using the standard environmental lapse rate and represent predicted temperature at 912 m (i.e., mean elevation of mountain goat summer range). These climate values were used as inputs to mechanistically model the effects of climate on mountain goat survival (via White et al., 2011) and population demography

	Temperature (°C)			Snowfall (m)		
GCM scenario	2015	2085	Change	2015	2085	Change
RCP 4.5						
CCS	7.4	11.2	3.8	2.3	1.3	−1.0
GFDL	7.4	10.9	3.5	2.3	1.2	−1.1
IPSL	7.4	10.2	2.9	2.3	1.3	−1.1
MRI	7.4	8.9	1.5	2.3	1.5	−0.8
GISS	7.4	8.7	1.3	2.3	2.0	−0.4
RCP 8.5						
CCS	7.4	13.4	6.0	2.3	0.8	−1.5
GFDL	7.4	12.5	5.2	2.3	0.9	−1.4
IPSL	7.4	13.2	5.8	2.3	0.7	−1.6
MRI	7.4	10.3	3.0	2.3	1.1	−1.2
GISS	7.4	9.7	2.3	2.3	1.4	−1.0
Average	7.4	10.9	3.5	2.3	1.2	−1.1

3.3 | Initial population size

A larger initial population size reduced the likelihood that a population fell to quasi-extinction (Table 2, Figure 4). A higher proportion of model simulations resulted in extinction for small (0.50; 5/10 scenarios), relative to medium (0.30; 3/10), and large population sizes (0.30; 3/10; Table 2, Figure 4). However, in the CCS-RCP4.5 and GFDL-RCP4.5 scenarios, 92.5%–99.9% of simulated populations went extinct for medium- and large-sized populations suggesting that extinction would likely occur over slightly longer time frames than considered in our analyses (Table 2, Figure 4). Small populations also tended to go extinct sooner than larger populations (Table 2, Figure 4). In the three scenarios where all-sized populations went extinct, small populations went extinct 6–8 years sooner than medium-sized populations and 9–12 years sooner than large-sized populations (Table 2, Figure 4).

3.4 | Habitat modeling simulations

At current conditions, RSF modeling indicated that 179 km^2 of important summer habitat existed in the 300 km^2 Kakuhan Range reference study area. Summer temperature lapse rate/elevation shift simulations indicated that the relationship between summer temperature and summer habitat was nonlinear due to the variable, but generally conical, shape of the mountain landscape (Figures 5 and 6). Specifically, the amount of summer habitat slightly increased as summer temperature increased up to 0.9°C above the baseline temperature (7.39°C), but then decreased rapidly; a temperature increase of 8.45°C resulted in complete elimination of existing summer range habitat conditions (Figure 5). Depending on the GCM/RCP scenario considered, the simulated change in summer habitat varied between a net loss of 153 km^2 (86% decline) and a net gain of 3 km^2 (1% increase) between 2015 and 2085 (Figure 5). Overall, 9 of 10 scenarios resulted in a net loss of summer habitat and 7 of 10 scenarios resulted in a net loss of 17%–86% of summer habitat (Figure 5).

4 | DISCUSSION

General circulation models predict that mountain goat populations in our coastal Alaska study area will experience increases in summer

TABLE 2 Projected mountain goat demographic responses to climate change scenarios over a 70-year time period (2015–2085), referenced on Juneau, AK, USA. Populations were simulated for three different initial population sizes (i.e., small, medium, and large) across 10 different GCM/emission scenario combinations. Initial population sizes coincide with observed naturally occurring populations sizes. Populations were simulated 1,000 times for each combination and varied based on model-based and climatic stochasticity. GCM/RCP emission scenarios span a continuum of "best case" to "worst case" scenarios

	% Extinct by 2085[a]			Years to extinction[b]			Years to 50% extinction[c]		
	Initial pop size			Initial pop size			Initial pop size		
GCM	50	300	1,000	50	300	1,000	50	300	1,000
RCP 4.5									
CCS	100.0	99.9	98.5	63	>70	>70	43	53	59
GFDL	100.0	99.3	92.5	68	>70	>70	45	56	63
IPSL	65.8	7.8	0.4	>70	>70	>70	68	>70	>70
MRI	0.0	0.0	0.0	>70	>70	>70	>70	>70	>70
GISS	0.0	0.0	0.0	>70	>70	>70	>70	>70	>70
RCP 8.5									
CCS	100.0	100.0	100.0	45	53	56	35	41	46
GFDL	100.0	100.0	100.0	53	60	65	40	48	52
IPSL	100.0	100.0	100.0	55	61	64	43	50	53
MRI	2.9	0.1	0.0	>70	>70	>70	>70	>70	>70
GISS	0.0	0.0	0.0	>70	>70	>70	>70	>70	>70
Baseline	0.0	0.0	0.0	>70	>70	>70	>70	>70	>70

GCM, general circulation model; RCP, representative concentration pathway.

[a] % of population simulations going extinct by 2085.

[b] Number of years until 100% of population simulations go extinct.

[c] Number of years until 50% of population simulations go extinct.

temperature, which should negatively influence survival, and decreases in winter snowfall, which should improve survival. Our mountain goat population models predict that climate change will exert negative demographic effects on mountain goat populations in all scenarios. Specifically, population modeling predicted that climate change would result in lower mountain goat population densities in all scenarios compared to the baseline (i.e., no climate change) scenario. In addition, analyses predicted a net decline in mountain goat populations by 2085 in 9 of 10 scenarios, and a mean trajectory indicating extirpation in 5 of 10 scenarios. Overall, these findings indicate that negative changes linked to increasing summer temperature are more important in influencing mountain goat population demography than positive changes associated with decreasing winter snowfall.

4.1 | Importance of summer vs. winter effects

The predicted negative demographic outcomes of climate change result from the magnitude and directionality of change in summer vs. winter climate. For example, in the "worst case" scenario (CCS/RCP8.5) survival of old female mountain goats (9+year-old, the female age class most sensitive to climate effects) was predicted to decline 9% due to the predicted 6°C increase in summer temperature (2015 = 7.4°C, 2085 = 13.4°C), but only increase 2% due to the predicted 1.5 m decrease in winter snowfall (2015 = 2.3 m, 2085 = 0.8 m). Quantitatively, this outcome occurs because the change in summer temperature spans a range of values where the slope of the effect curve is steeper, relative to winter snowfall. Consequently, future changes in snowfall are expected to have small, declining effects, whereas summer temperature is expected to exert increasingly stronger and negative effects on mountain goat survival and ultimately population dynamics.

Herbivore survival in highly seasonal alpine environments requires substantial accumulation of endogenous energetic reserves during the summer growing season (up to 25%–30% of total body mass in mountain goats; K. S. White, unpublished data) in order to survive winter seasons characterized by severe nutritional deprivation (Mautz, 1978; Parker et al., 2009). Consequently, summer growing season conditions have important implications for survival during the following winter (White et al., 2011). Warm summer temperatures can negatively influence herbivore nutrient assimilation via direct and indirect ecological mechanisms. For example, during cool summers slower plant growth and reduced lignification of cell walls lead to production of more digestible forages and higher quality animal diets (Bo & Hjeljord, 1991; Doiron et al., 2014; Lenart et al., 2002; Weladji, Klein, Holand, & Mysterud, 2002). Small changes in forage nutritional characteristics can lead to disproportionately large responses in animal nutritional condition and productivity via multiplier effects (McArt et al., 2009; White, 1983). Warm growing season temperature can also accelerate snow melt and lead to a more rapid green-up (Pettorelli et al., 2007), particularly if preceded by mild winter conditions. This results in an overall reduction in the

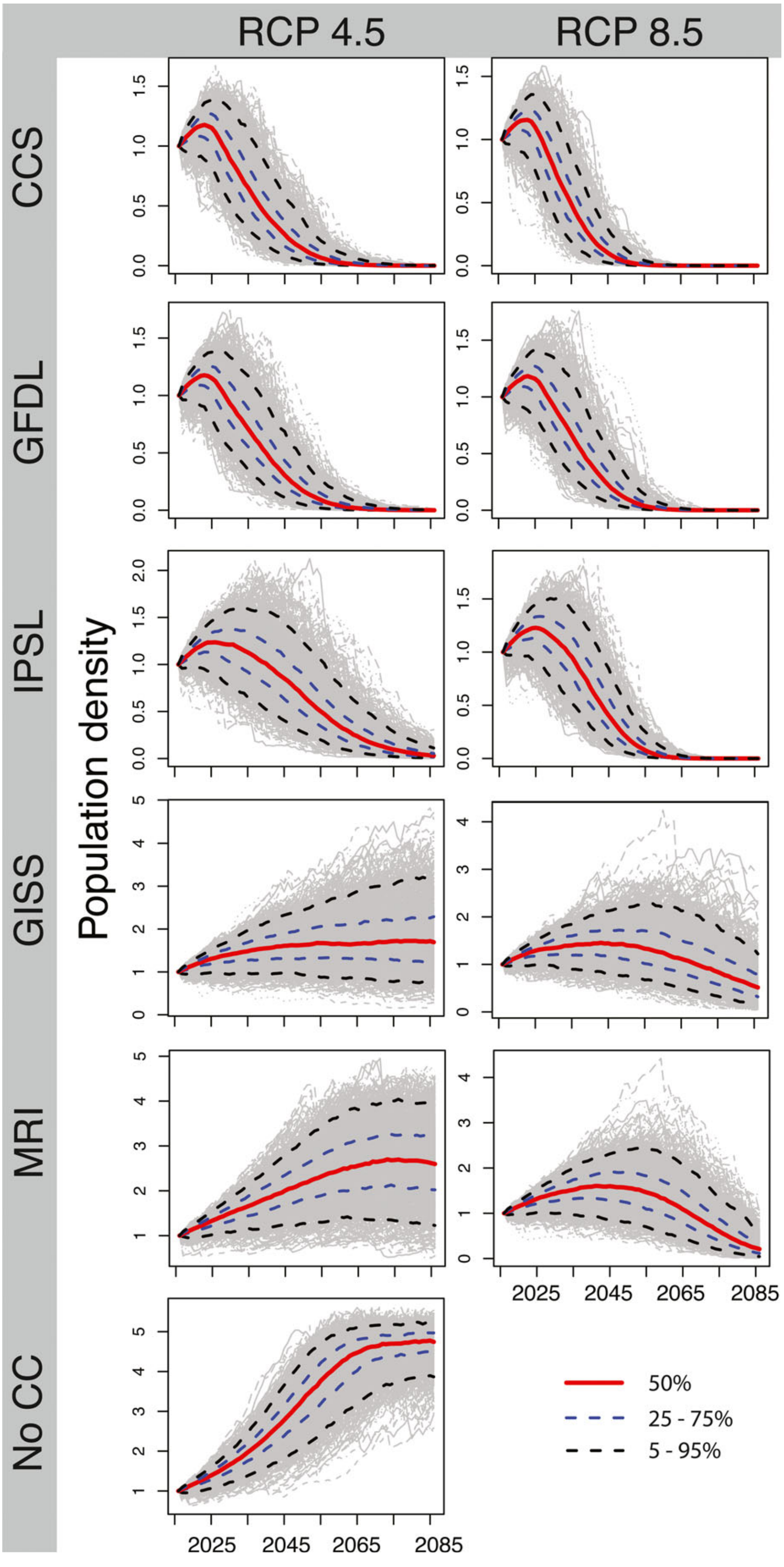

FIGURE 4 Projected mountain goat demographic responses to climate change scenarios over a 70-year time period (2015–2085); climate scenarios are referenced on Juneau, AK, USA. Populations were simulated for three different initial population sizes (i.e., small, medium and large) across 10 different GCM/emission scenario combinations. Initial population sizes coincide with observed naturally occurring populations sizes. In this example, relationships are described for medium-sized (n = 300) populations. GCM/emission scenarios span a continuum of "best case" to "worst case" scenarios. GCM, general circulation models

temporal availability of high-quality early-phenological stages forages across alpine landscapes which can negatively influence juvenile growth and survival in alpine ungulates (Pettorelli et al., 2007). Yet, summer temperature not only influences the availability of high-quality food resources across the landscape, but also the efficiency through which herbivores can procure them. Cold-adapted large mammalian herbivores are physiologically sensitive to heat stress (Renecker & Hudson, 1986) and during hot summer periods may reduce foraging rates and shift to suboptimal foraging habitats (Aublet et al., 2009). Overall, the net effect of warm summer temperatures on mountain goat survival is linked to environmental and behavioral processes that regulate assimilation of nutrient reserves needed to survive long winter periods. While extreme winter conditions (i.e., high snowfall) can exert strong negative effects on mountain goat survival, our modeling results indicate that the positive effects of mild winter conditions are relatively weak and not able to completely compensate for the deleterious effects of predicted future increases in summer temperature.

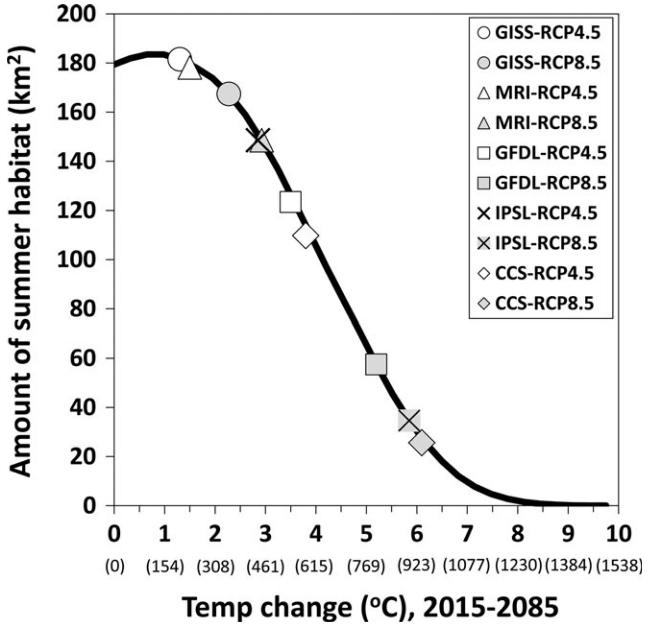

FIGURE 5 Relationship between predicted summer temperature change and the amount of summer habitat (based on RSF modeling) predicted for 10 different GCM/RCP scenarios in the Kakuhan Range, AK, USA. Temperature change represents the difference between mean daily summer temperatures (July–August) observed in 2015 and predicted values for 2085 based on GCM/RCP models. Standard environmental lapse rates (−6.5°C/1,000 m) were used to calculate altitudinal shifts (in parentheses on *x*-axis; meters) required by mountain goats to inhabit environments thermally equivalent to 2015 distributions. GCM, general circulation models; RCP, representative concentration pathway

4.2 | Initial population size effects and environmental stochasticity

Population size can exert strong effects on population persistence and extinction (Lande, 1988) and such effects may be more pronounced in large bodied mammals with slow life-history strategies (Cardillo et al., 2005). In alpine ungulates, small populations exhibit greater vulnerability to extinction than large populations (Berger, 1990; Hamel, Côté, Smith, & Festa-Bianchet, 2006). This occurs because smaller populations exhibit heightened sensitivity to demographic and environmental stochasticity. Consistent with such expectations, our analyses documented increased extinction risk in small populations due to negative effects of climate change over a relatively short (70 years) time period. Mountain goats are capital breeders that exhibit slow life-history strategies (i.e., late age at first reproduction, small litter size, frequent reproductive pauses, long

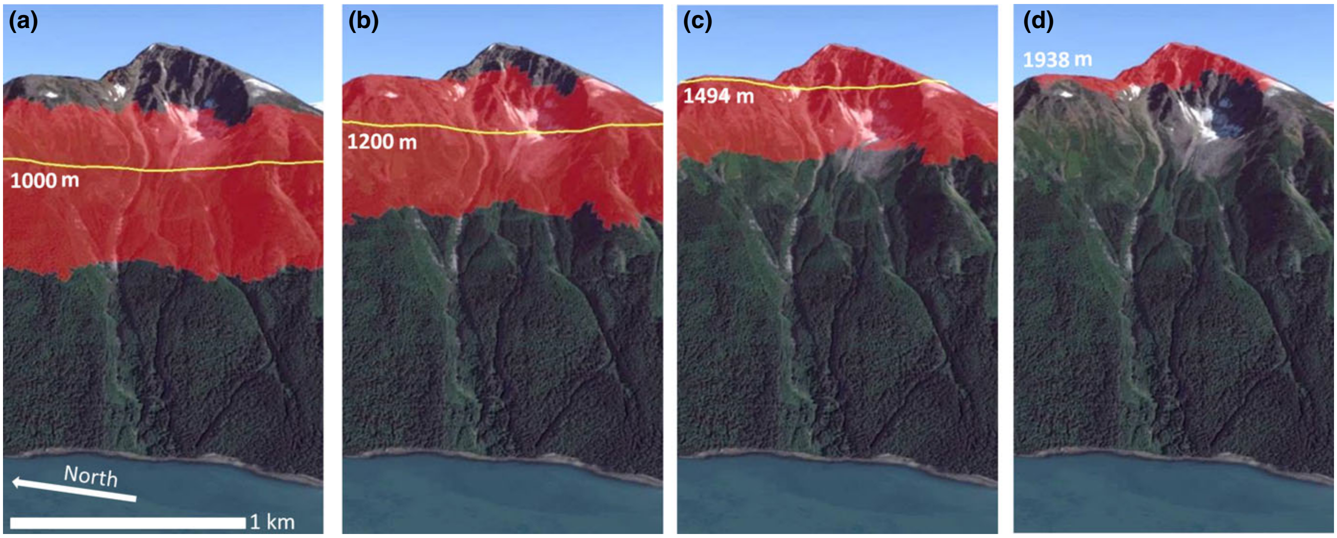

FIGURE 6 Resource selection function modeling output describing predicted changes in mountain goat summer habitat distribution for four scenarios: (a) current distribution (2005–2015 baseline conditions), (b) year 2085, GCM-GISS-RCP4.5 ("best case scenario"), (c) year 2085, GCM-MRI-RCP8.5/GCM-GFDL-RCP4.5 midpoint ("intermediate scenario), and (d) year 2085, GCM-CCS-RCP-8.5 ("worst case scenario")

generation times), relative to other similar sized ungulates (Festa-Bianchet & Côté, 2008). These characteristics result in relatively low reproductive productivity and influence the capability of populations to rapidly recover from deleterious stochastic events. When populations are small, short interval recurrence of negative stochastic events can lead to rapid extinction due to the limited demographic capability to recover via reproduction. Climate change can thus have multidimensional effects on mountain goat demography. For example, our findings have emphasized the long-term negative effects of slow, incremental increases in mean summer temperature. However, extreme stochastic events in summer temperature and winter snowfall can both have short-term, but severe, negative demographic consequences that can require extended periods for population recovery. In contrast, extreme stochastic events that positively influence mountain goat demography are likely exert modest, or negligible population responses, due to the slow life-history strategy and low reproductive capability of the species which influence their ability to capitalize on favorable conditions. Consequently, these dynamics are likely to become increasingly relevant to the viability of mountain goats, and other similarly affected alpine species, if the likelihood of extreme stochastic events that negatively influence population demography increases over time—a prominent prediction of recent global climate change analyses (IPCC, 2012).

4.3 | Habitat change and behavioral adaptation

Large mammalian herbivores commonly track phenological or other beneficial environmental changes that occur spatially and temporally across seasonally dynamic landscapes (Armstrong, Takimoto, Schindler, Hayes, & Kauffman, 2016; Bischof et al., 2012; Hebblewhite, Merrill, & McDermid, 2008). In mountainous environments, species such as mountain goats exhibit seasonal migrations from low-elevation winter ranges to high-elevation alpine summer ranges in order to track the availability of high-quality, early-phenological stage forages as they emerge at the edge of melting snow patches (Fox, 1991; Pettorelli et al., 2007). Such altitudinal migrations also enable animals to inhabit cooler summer environments, where heat stress events which negatively influence nutritional intake are less common (Aublet et al., 2009). Our population models suggest that under most climate change scenarios mountain goat populations are likely to decline, often to extinction, due to increases in summer range temperature (i.e., a proxy of nutritional and thermoregulatory constraints; White et al., 2011). Yet, our population models are based on population performance at average elevational distribution used by mountain goats during 1977–2014 and do not explicitly consider the consequences of mountain goats mitigating future summer warming by shifting to higher elevations where temperatures would more closely resemble current, thermoneutral conditions. We investigated the implications of this behavioral adaptation using a novel RSF modeling approach that enabled us to determine the amount of change in areal extent of summer range for each GCM/RCP scenario over a 70-year time horizon. These simulations predicted that under nearly all scenarios thermoneutral mountain goat summer range would contract across our reference landscape. Consequently, we conclude that behavioral adaptation to summer warming by shifting to higher elevations could result in demographic stability, but would result in net reductions in summer range carrying capacity. Under the most extreme scenario, mountain goat summer range carrying capacity would decline by 86%. We consider our analyses to be conservative because a portion of the predicted "new" highest elevation habitat may not actually be suitable because of time lags between the occurrence of warmer temperatures (that facilitate plant primary productivity) and the development of soils and vegetation colonization of recently deglaciated or barren landscapes (Jumpponen et al., 2012). Furthermore, our analyses do not directly account for habitat shrinkage effects on fragmentation and connectivity—dynamics that would be expected to further reduce functional carrying capacity and utilization of future summer range (Bennett, 2003). Overall, behavioral adaptation can be considered a stopgap measure and is unlikely to fully mitigate summer range climate change effects on mountain goat demography, though dynamics are likely to be complex.

4.4 | Modeling considerations, constraints, and inference

Our modeling approach represents a powerful tool for quantifying explicit effects of climate change on population size—a universally meaningful currency required to assess conservation threats, successes, and failures. This approach is based on mechanistic field-derived relationships between species demographic rates and climate that rely on extensive, long-term data collection and explicitly account for parameter uncertainty at multiple stages of analyses. This framework allows for evaluation of consistent and strongly directional demographic responses across multiple climate modeling scenarios and thereby enable a robust determination of effects. The resulting population-level inference associated with this approach can significantly improve our capability to address conservation challenges relative to alternative methods such as correlative species distribution and bioclimate envelope modeling that may be better suited for complementary analyses (Pacifici et al., 2015; Pearson & Dawson, 2003). Furthermore, our mechanistic modeling approach is flexible and can be used for multiple applications involving conservation of mountain ungulates as well as other alpine or nonalpine species. While our analyses have highlighted relatively long time-horizon modeling outputs (i.e., 70 years), the modeling framework can be easily adapted to address "real-time" applications such as those required to make short-term population conservation and management decisions. Thus, possible modeling applications can range from the assessment of long-term effects of climate change on alpine ecosystems to the short-term effects of climate conditions in 1 year on resultant population performance the following year.

Parameterization of mechanistic population models is data intensive and can constrain model inference. In this study, our goal was to directly assess the effects of climate change on mountain goat survival and resultant demographic outcomes using previously published mechanistic models from our study system derived from an extensive long-term data collection effort (White et al., 2011). Given that variation in adult survival typically exerts the strongest influence on ungulate demographic outcomes (Gaillard et al., 2000), we consider our modeling outcomes to be realistic yet certain constraints apply. Specifically, our models would be strengthened if data were available within our study system to model mechanistic relationships between climate and age-specific reproduction, kid survival, and density dependence. In addition, our models do not incorporate meta-population dynamics and thus the spatial-demographic context of our reference study site and surrounding landscape is not considered. Our models are also specific to mountain goat populations inhabiting coastal environments, and it is unclear whether populations living in drier, colder interior climates are influenced by climate in a comparable manner. Finally, we considered extinction to occur when a simulated population dropped below two individuals, yet genetic- or demographic-linked effects of small population size may begin to occur when populations are larger than our predefined extinction threshold. Overall, we expect our modeling approach to substantially improve the capability to address conservation challenges associated with climate change and species conservation yet future refinements will be beneficial and expand its utility and enable a broader range of conservation applications.

4.5 | Conservation implications

Global climate change is considered to be among the most profound conservation challenges of our generation (Intergovernmental Panel on Climate Change, 2012). To a significant degree, existing analyses suggest the prognosis for many species and ecosystems is negative (Urban, 2015). In alpine and arctic environments change is occurring at a particularly rapid rate, relative to other ecosystems, and may have far-reaching implications. Mountain ungulates are iconic species that have high ecological and human value. Due to their unique adaptations for living in mountain environments they occupy a specialized ecophysiological niche that tightly overlaps alpine ecosystems. In such environments, mountain goat population dynamics are linked to climate via direct effects on thermoregulation and energetics, and indirectly through climate effects on plant phenology, population dynamics, and community ecology. In this context, mountain ungulates are sentinel species of alpine environments and population status can be considered a barometer of ecosystem function, viability, and resilience. Yet based on our analyses, the future viability of mountain goat populations is uncertain due to the opposing demographic effects of projected reductions in winter snowfall and increasing summer temperature.

Consideration of multiple GCMs and emissions scenarios provided a comprehensive assessment of future demographic outcomes for mountain goats inhabiting North Pacific coastal environments. Overall, our simulations indicated that mountain goat quasi-extinction probabilities were more influenced by the GCM considered than associated RCP emissions scenario, suggesting that modest emissions reductions may not be sufficient to maintain viable mountain goat populations within their current range. Mountain goat quasi-extinction probabilities were higher for the most pessimistic GCMs and associated emissions scenarios, but all climate change scenarios resulted in significant reductions in population size and growth rate, including complete extirpation for 3 of the 5 GCMs for the 70-year time frame investigated. For the two GCM scenarios not resulting in extinction (on average), population trajectories remained largely negative, indicating that extirpation from current range is likely, given a longer time frame. These effects may be partially ameliorated by mountain goat range expansion upslope, but upward migration leads to reductions in the areal extent of summer range and may not be possible on the time scale of climate warming due to the multidecadal delay of soil development and plant colonization following glacial recession. While our projections were spatially constrained, and also subject to other considerations (see above), they are likely relevant to a broad array of populations given our analyses were centered near the geographic center of the coastal mountain goat distribution. Overall, our results suggest that change in atmospheric policy leading to reduced emissions will marginally benefit mountain goat populations, perhaps providing time for higher elevation habitats to develop; although alpine ungulates already occupy the highest available elevation in many areas. Nonetheless, long-term strategic and effective conservation efforts focused on emissions reductions are likely to be beneficial and should be encouraged in order to maximize alpine ungulate, and ultimately ecosystem, viability, and resilience. In the near-term, research initiatives and conservation planning efforts focused on advancing mechanistic understanding of climate impacts on alpine ecosystems will foster human awareness and aid in mitigating undesirable consequences of climate change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Supporting Information

Appendix S1. Running population simulations using survival model input via the 'run.pop.simulations' function in program R.

All files necessary to run the goat population model are located within '`goat.sim.code.and.data.zip`'. The inputs for the main function '`run.pop.simulations`' come from both the '`goat.simulation.runner.script.R`' and the '`goat.simulation.data.R`' files. The arguments supplied within '`goat.simulation.runner.script`' are meant to be those most likely to be changed by a new user initially, while further data inputs that are sourced from '`goat.simulation.data.R`' can also be manipulated when the user becomes more familiar with the code.

There are a few inputs that originate from csv files and in one case an Rdata file ('`goat.mod`') that are all necessary to run the '`run.pop.simulations`' function.

The run.pop.simulations function takes the following arguments:

Argument values input via the script 'goat.simulation.runner.R':

`year.begin`—beginning year of simulation.
`year.end`—end year of simulation.
`initial.N`—initial total population size.
`n.ages`—number of ages of animals in the simulated population.
`n.runs`—the number of simulations to run of each climate scenario specified.
`area`—The area inhabited by animals simulated, which affects fecundity by way of density dependence.
`climate.scenario.nos`—which climate scenarios to run (1 through 11):
1 – no environmental change
2 — CCS_RCP45
3 — CCS_RCP85
4 — GFDL_RCP45
5 — GFDL_RCP85
6 — GISS_RCP45
7 — GISS_RCP85
8 — IPSL_RCP45
9 — IPSL_RCP85
10 — MRI_RCP45
11 — MRI_RCP85

`output.folder`—the folder under the working directory (perhaps 'goat.sim.code.and.data') to which a summary of results (graphs and csv files) will be output.

`density.dependence`—is density dependence implemented (TRUE or FALSE).
`update.betas.yearly`—should the Beta coefficients of the survival model by drawn from within their uncertainty interval every year (TRUE) or just once at the beginning of a simulation (FALSE).
`environmental.stochasticity`—apply stochasticity in climate parameter projections based on past patterns of variability in temperature and snowfall from near the study area (Juneau airport).
`demographic.stochasticity`—if TRUE, apply random noise to fecundity values to represent natural variability and uncertainty in parameters.

Arguments created in or imported by the 'goat.simulation.data.R' file:

`env.data`—A list of two matrices, one specifying June temperatures for each year of simulation, the other snow deposition in winter.
`F0vec`—Fecundity intercepts for each female age class.
`F1`—K from MLE fit to Olympic Nat'l Park data.
`F2`—theta from MLE fit to Olympic Nat'l Park data.
`goat.mod`—an RMARK model from which monthly survivals were obtained and transformed to yearly survivals.
`harvest.matrix`—an optional n.ages X n.sim.years matrix specifying harvest of animals by age and year (not implemented in current publication).
`scenario.names`—vector of the names of all potential climate scenarios investigated in White et al 2017.
`agest`—a vector of initial N for each age and sex to begin the simulation with, which are scaled to the total N specified by 'initial.N' above. The current publication uses the age structure obtained from the mouintain goat life history matrix in year 2015.

Appendix S2: Mountain goat survival modeling.

White *et al.,* (2011) modeled mountain goat survival in relation to age-, sex- and climate using data collected in 8 different coastal Alaska study areas during 1977–2008. This model was based on monthly monitoring data collected from 279 individual radio-marked mountain goats (643 "goat years"; Table S2a). Since the White *et al.,* (2011) analyses were completed, a significant amount of additional monitoring data (n = 168 individuals, 536 "goat years") were collected in four coastal Alaska study areas during 2008–2014 (Table S2a). In order to optimize the accuracy and precision of the survival model, we combined both data sets and re-calculated the model parameter estimates (Table S2b). We did not completely re-analyze the new, larger data set because we considered the original data set to be sufficient for identifying key modeling variables and estimating effects; instead we were interested in refining and reducing variation in parameter estimates. Thus, the data set used (via RMark) to model climate effects on sex- and age-specific survival is based on data collected from 447 individual mountain goats (1179 "goat years") located in 10 different study areas (two study areas overlapped original study areas) during 1977–2014.

Table S2a. Study area location, study period, and sample size of radio-marked mountain goats used to estimate sex, age, and climate effects on mountain goat survival in coastal Alaska, 1977–2014.

		Mountain goats			"Goat years"		
Study Area	Years	M	F	Total	M	F	Total
Original Data							
Echo Cove-Herbert Glacier	1977–1981	6	14	20	14	30	44
Kelsall River	1981–1984	6	6	12	11	13	24
North Kenai Mountains	1979–1983	16	25	41	49	82	131
Ketchikan	1980–1985	25	37	62	65	88	153
Prince William Sound	1989–1991	1	14	15	2	29	31
Lions Head	1990–1994	8	4	12	28	17	45
Sheep Creek	1991–1994	4	9	13	9	28	37
Lynn Canal	2005–2008	51	38	89	80	67	147
North Kenai Mountains	2006–2008	1	14	15	3	28	31
		118	161	279	261	382	643
New Data							
Lynn Canal[1]	2008–2014	37	39	76	156	144	300
Cleveland Peninsula[2]	2009–2014	6	6	12	18	26	44
Haines-Skagway[3]	2010–2014	32	17	49	69	43	112
Baranof Island[4]	2010–2014	21	10	31	54	26	80
		96	72	168	297	239	536
Grand Total		214	233	447	558	621	1179

[1] White, K. S. 2016. Mountain goat population monitoring and movement patterns near the Kensington Mine, Research Progress Report. Alaska Department of Fish and Game, Juneau, AK.

[2] White, K. S., B. Porter and S. Bethune. 2010. Cleveland Peninsula mountain goat population monitoring. Research Progress Report. Alaska Department of Fish and Game, Juneau, AK.

[3] White, K. S., A. Crupi, R. Scott and B. Seppi. 2014. Mountain goat movement patterns and population monitoring in the Haines-Skagway area, AK. Research Progress Report. Alaska Department of Fish and Game, Juneau, AK.

[4] White, K. S., P. Mooney and K. Bovee. 2013. Mountain goat movement patterns and population monitoring on Baranof Island. Research Progress Report. Alaska Department of Fish and Game, Juneau, AK.

Table S2b. Parameter estimates (β) and standard errors used to predict mountain goat survival in coastal Alaska, 1977–2014. Estimates reference the model receiving the highest support in White *et al.,* (2011).

Parameter	Estimate	SE	LCI	UCI
Intercept	3.351	0.866	1.653	5.050
Yearling	4.645	3.648	-2.506	11.796
Subadult	6.120	3.500	-0.739	12.979
Young adult	0.923	0.459	0.024	1.822
Adult	0.294	0.420	-0.530	1.117
Sex (adult, old)	0.381	0.182	0.025	0.737
June	0.647	0.848	-1.016	2.310
July	0.949	0.931	-0.877	2.774
August	1.271	0.949	-0.589	3.132
September	1.076	0.503	0.090	2.063
October	-0.217	0.366	-0.935	0.501
November	0.511	0.432	-0.335	1.358
December	0.610	0.445	-0.262	1.482
January	0.297	0.412	-0.511	1.105
February	0.201	0.328	-0.441	0.843
March	0.339	0.342	-0.332	1.011
April	-0.083	0.313	-0.697	0.531
Snowfall	-0.120	0.040	-0.199	-0.041
Snowfall (sub)	0.485	0.351	-0.203	1.173
Temp	-0.052	0.101	-0.249	0.145
Temp (sub)	-0.458	0.414	-1.269	0.353
Temp (yng ad, ad)	0.114	0.057	0.003	0.225

Variable definitions: age (yearling/ylg = 1-yrs, subadult/sub = 2-3 years, young adult/yng ad = 4-5 years, adult/ad = 6-8 years, old = 9+ years), month (June = 1, May = 12), snowfall = total annual snowfall (m; elevation: 0 m), temp = average daily temperature during July-August (^{o}C; elevation: 914 m/3000 ft).

Appendix S3. Age-specific fecundity

Mountain goat fecundity was estimated by monitoring known-age radio-marked females during monthly surveys using fixed-wing aircraft (usually a Piper PA-18 Super Cub) equipped for radio-telemetry tracking or via ground-based observations. During surveys, radio-marked adult female mountain goats were observed (typically using 14X image stabilizing binoculars) to determine whether they gave birth to offspring. Data were collected in three separate study areas in coastal Alaska during 2005-2014: Lynn Canal (n = 76, 223 "goat years"; White 2016), Haines-Skagway (n = 17, 56 "goat years"; White *et al.,* 2014) and Baranof Island (n = 10, 34 "goat years"; White *et al.,* 2013). Data were combined (n = 103, 313 "goat years") to derive average age-specific fecundity estimates for coastal Alaska (Table S3). These data were used to parameterize mountain goat population models, and modified based on density dependent relationships (as described in Eq 2, "Methods" section; also see Appendix S4).

References:

White, K. S. 2016. Mountain goat population monitoring and movement patterns near the Kensington Mine, Research Progress Report. Alaska Department of Fish and Game, Juneau, AK.

White, K. S., A. Crupi, R. Scott and B. Seppi. 2014. Mountain goat movement patterns and population monitoring in the Haines-Skagway area, AK. Research Progress Report. Alaska Department of Fish and Game, Juneau, AK.

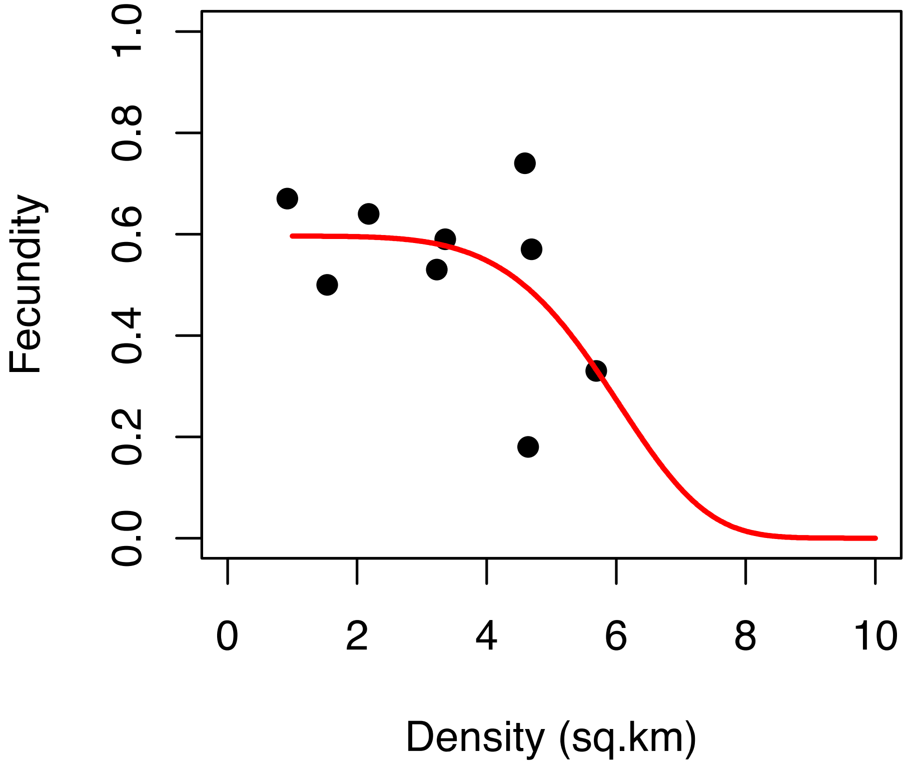
White, K. S., P. Mooney and K. Bovee. 2013. Mountain goat movement patterns and population monitoring on Baranof Island. Research Progress Report. Alaska Department of Fish and Game, Juneau, AK.

Table S3. Mountain goat age-specific fecundity estimates based on data from radio-marked females located in coastal Alaska, 2005-2014.

Age	n	Kid	No kid	Prop with kid	SE
1	3	0	3	0.00	0.00
2	8	0	8	0.00	0.00
3	16	1	15	0.06	0.06
4	30	14	16	0.47	0.09
5	40	29	11	0.73	0.07
6	46	29	17	0.63	0.07
7	47	35	12	0.74	0.06
8	39	32	7	0.82	0.06
9	34	28	6	0.82	0.07
10-11	35	25	10	0.71	0.08
12+	15	9	6	0.60	0.13
All ages	313	202	111	0.65	0.03

Appendix S4. Model describing density dependent effects on fecundity

Figure S4. Fit of the discrete per-capita theta-logistic model (Eq. 1) to density-dependent mountain goat fecundity data collected by Houston and Stevens (1988) and Houston *et al.,* (2004).



Appendix S5. Estimating total annual snowfall based on precipitation as snow
Mountain goat survival is negatively influenced by total annual snowfall, as measured at sea-level (White *et al.,* 2011). Our simulations required derivation of total annual snowfall measurements at the Juneau International Airport (JIA), Juneau, AK in order to estimate survival and project population trajectories. GCM models for the JIA generate precipitation as snow (PAS, mm), a corollary of total annual snowfall. To derive total annual snowfall, we derived a linear regression equation using PAS estimates and actual snowfall observation collected at the JIA during 1960–2014. The resulting equation ($y = 5.2203x + 407.11$; $r^2 = 0.51$) predicts total annual snowfall (y) based on PAS (x) and enables projection of total annual snowfall estimates into the future for each GCM/RCP scenario.

Figure S5. Relationship between precipitation as snow (PAS, mm) and total annual snowfall (mm) at the Juneau International Airport, Juneau, AK, 1960-2014.