

FINAL REPORT

ASSESSMENT OF DROUGHT IMPACTS ON SELECTED FISH AND WILDLIFE SPECIES IN THE SOUTHWESTERN UNITED STATES

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SECTION 1. ADMINISTRATIVE INFORMATION

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SECTION 2. PUBLIC SUMMARY:

The responses of individual species to environmental changes can be manifested at multiple levels that range from individual-level (i.e., behavioral responses) to population-level (i.e., demographic) impacts. Major environmental changes that ultimately result in population level impacts are often first detected as individual-level responses. For example, herbivores respond to limited forage availability during drought periods by increasing the duration of foraging periods and expanding home range areas to compensate for the reduction in forage. However, if the individual-level responses are not sufficient to compensate for reduced forage availability, reduced survival and reproductive rates may result. We studied the impacts of drought on desert bighorn sheep (*Ovis canadensis mexicana*), American pronghorn (*Antilocapra americana*), Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*), and scaled quail (*Callipepla squamata*), including assessments of individual- (e.g., desert bighorn sheep) and population-level (e.g., pronghorn, cutthroat trout, scaled quail) responses to drought.

Nutritional ecology forms the interface between environmental variability and large herbivore behaviour, life history characteristics, and population dynamics. Forage conditions in arid and semi-arid regions are driven by unpredictable spatial and temporal patterns in rainfall. Diet selection by herbivores should be directed towards overcoming the most pressing nutritional limitation (i.e., energy, protein, moisture). We investigated the influence of precipitation-induced shifts in forage nutritional quality and subsequent responses of desert bighorn sheep (*Ovis canadensis mexicana*, DBS) across widely varying precipitation conditions. Succulents were consistently high in moisture but low in protein and grasses were low in protein and moisture until the wet period. Protein and moisture content of shrubs and forbs varied among seasons and climatic periods, whereas trees had consistently high nitrogen and moderate moisture levels. Shrubs, trees and succulents composed most of the seasonal sheep diets but had little variation in energy content. Across all seasons during drought and during summer with average precipitation, forages selected by sheep were higher in protein and moisture than that of available forage. During drought, desert bighorn relied on a few key forage species including palo verde (*Parkinsonia microphylla*, *P.florida*) and ironwood (*Olneya tesota*) trees. Overall, forage selection was more strongly associated with protein and moisture content than energy content.

Wildlife managers often provide supplemental water to help desert ungulates endure the hottest, driest periods. When surface water is unavailable, the only source of water for ungulates comes from the forage they consume, and they must make resourceful foraging decisions to meet their daily requirements. We calculated water and nutrient intake and metabolic water production from forage intake and forage moisture to determine whether

desert bighorn sheep could meet their seasonal daily water requirements solely from forage. Under drought conditions without any surface water available desert bighorn would be unable to meet their daily water requirements in all seasons, except winter. We determined that DBS could achieve water and nutrient balances in all seasons by shifting their total diet proportions by 8–55% from lower to higher moisture and nitrogen forage species.

Climate often drives ungulate population dynamics, and as climates change, some areas may become unsuitable for species persistence. Therefore determining the relationships between climate and population dynamics can contribute to more informed management and conservation decisions. Growth rates of American pronghorn (*Antilocapra americana*) populations are particularly sensitive to climatic conditions. We analyzed long-term pronghorn population, precipitation, and temperature data from 18 populations in the southwestern United States and used these relationships to project population trends through 2090 under two climate change scenarios. Fifteen of the pronghorn populations declined in abundance since the 1990s. Sixteen populations demonstrated a significant relationship between precipitation and population growth. Models predicted that nine populations would be extirpated or approaching extirpation by 2090. In the southwestern United States, the climate underpinning pronghorn populations is shifting, making conditions increasingly inhospitable to pronghorn persistence.

Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*, RGCT), the southernmost subspecies of cutthroat trout, is endemic to the Rio Grande, Canadian, and Pecos River basins of Colorado and New Mexico. The subspecies is reduced to less than 11% of its historic range with most populations occupying isolated high elevation headwater streams. One of the greatest threats to its survival is the effect that low stream flow due to drought will have on this coldwater trout. We set out a specialized datalogger across 54 sites in 29 populations of RGCT to measure temperature and intermittency (no flow) over one year. While few RGCT populations experienced intermittency because of the serendipitous wet cycle from 2013 to 2014, the loggers provided water temperature data deemed comparable to more sophisticated and expensive temperature loggers. Thus, these intermittency loggers offer a low-cost and long-duration (battery can be replaced) solution that not only provides unambiguous and continuous water temperature, but also provides continuous intermittency information of stream flow. An important caveat of our research is that while RGCT populations may not experience intermittency during average to above average precipitation years, very little is known of their vulnerability during below average precipitation years.

Grassland birds are among the most imperiled bird guilds in North America. Scaled quail (*Callipepla squamata*) are a semi-arid grassland bird whose populations have declined over the past half century. We monitored scaled quail in New Mexico to study the effects of habitat, temperature and precipitation on survival of scaled quail adults, nests, and broods. Seasonal nest survival (39.4%) had a positive relationships with increasing average weekly maximum temperature and grass density, and negative relationships with increasing average minimum temperature and percent bare ground. Seasonal brood survival (49.0%) had a negative relationship with increasing average weekly minimum and maximum temperature, and with increasing precipitation. These results illustrate the importance of managing ground cover for scaled quail to ensure adult survival and successful recruitment. Ground cover provides protection from thermal and precipitation related stress, as well as for visual obstruction from predators.

SECTION 3. PROJECT SUMMARY:

This project is comprised of 4 subprojects on: 1) desert bighorn sheep (*Ovis canadensis mexicana*), 2) American pronghorn (*Antilocapra americana*), 3) Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*), and 4) scaled quail (*Callipepla squamata*).

SUBPROJECT 1.

Influence of Extreme Climatic Variability and Drought on Habitat and Forage Selection of Desert Bighorn Sheep.

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Purpose and Objectives: Our overall goal was to assess the influence of climate variability and extreme drought on desert bighorn sheep on the Cabeza Prieta National Wildlife Refuge in southwestern Arizona. Climatic conditions 2002 to 2005 spanned the range of variability observed in the Sonoran Desert and ranged from the worst drought on record for the area, through periods of average precipitation and ending during a wet period. Our specific objectives were to investigate: 1) seasonal habitat selection patterns across widely differing climatic periods to determine if desert bighorn sheep use certain habitat features and or behavioral mechanisms to cope with extreme drought; 2) changes in diet selection across climatic periods to determine which forage species are used a buffer resources to maintain populations during droughts; 3) nutritional intake resulting from dietary shifts across climatic periods; and 4) whether desert bighorn sheep can maintain water and nutrient balance (particularly during the hottest, driest periods and during drought) without free-standing water.

Organization and Approach:

Objective 1.

We captured 37 adult female desert bighorn sheep from 2002 to 2004 with a net gun fired from a helicopter and fitted them with global positioning system (GPS) telemetry collars that record locations every 13 hours; GPS locations were transmitted via the Argos satellite system every three days. All capture and handling procedures followed acceptable methods (Sikes et al. 2011) and were approved by the University of Arizona Animal Care and Use Committee (Protocols 01-191 and 04-180).

We classified climatic conditions based on Standardized Precipitation Index (SPI, Guttman 1999), which represents the number of standard deviations observed cumulative precipitation deviates from the long-term average (McKee et al. 1993). We classified diel periods as night (reference), twilight (3 hours following civil twilight in the morning and prior to civil twilight in the evening) and day (US Naval Observatory 2015).

We used ArcGIS 10.3 with Spatial Analyst extension (ESRI, Redlands, CA, USA) to develop spatial models of the area used by desert bighorn sheep. We used Geospatial Modelling Environment program (Beyer 2015) to generate 95% kernel density estimates of home range around locations for each individual female ($n = 69-1884$) and minimum convex polygon estimates of home range around all sheep locations for each population (Cabeza Prieta: $n = 10650$; Sierra Pinta: $n = 10565$). We considered all habitat within 100% MCP home range polygons as available for use by sheep, and generated random points for locations within each home range polygon.

We derived elevation (m) and all other topographic features at each desert bighorn sheep location from a 10-m resolution digital elevation model (U.S. Geological Survey 2015). We determined distance (km) from each location to the nearest perennial water source (i.e., man-made water catchment). As part of a separate study, water catchments on SP were

maintained empty commencing March 2004, and thus, sheep locations from the SP population during this period (individual home range level: $n = 6146$; population level: $n = 6195$) were not included in analyses. We used the Land Facet Corridor 1.2.9 extension (Jenness et al. 2013) for ArcGIS to classify topographic position index (TPI) as valley, slope (reference) and ridgeline, using a 3 x 3 cell neighbourhood. We used the Benthic Terrain Modeler 3.0 extension (Wright et al. 2012) for ArcGIS to derive slope ($^{\circ}$), aspect and terrain ruggedness. Aspect was trigonometrically transformed to a metric representing relation to north using the equation $\text{northness} = \cos((\text{aspect} \times \pi)/180)$, resulting in values ranging from -1 (south) to 1 (north, Roberts 1986). Since aspect-influencing exposure increases towards mid-slope (i.e., flatter areas at lower slopes and shading at higher slopes reduce the influence of exposure on aspect), we accounted for this by always including aspect as a product with a quadratic term for slope. Terrain ruggedness is a vector ruggedness measure ranging from 0 (flat) to 1 (most rugged; Sappington et al. 2007), and was calculated using a 3 x 3 cell neighborhood. We scaled ruggedness values in our study are to range from 0 to 1.

We compiled daily minimum and maximum land surface temperatures for the study period from 1-km² grids across the study area (Thornton et al. 2014). We estimated diurnal hourly temperatures by fitting the daily minimum and maximum temperatures to a cosine curve representing temperature patterns throughout the day for a given date. Although these temperature data are high spatial resolution, the rugged topography of desert bighorn sheep habitat suggests there would be high variation in surface heat load among sheep locations; therefore, we factored in the effect of solar radiation on daytime temperatures. For the date and time of each sheep location, we derived solar radiation values using the ArcGIS Solar Radiation tool (ESRI, Redlands, CA, USA), which accounts for atmospheric effects, daily and seasonal shifts in the angle of the sun, latitude, elevation, slope, aspect, and effects of shadow cast by surrounding topography. Transmittivity and diffuse proportion were set for clear skies, because we considered temperature measurements adequately conveyed the influence of cloud cover, which occurs infrequently in the study area. The solar radiation algorithm does not account for topographic shielding and shadowing, and thus, may overestimate radiation in certain parts of the landscape, particularly those associated with south-facing convergent areas that may experience morning shading from adjacent north-facing slopes. Therefore, for each sheep location, we took the ratio of solar radiation with topography to solar radiation from a flat surface, and applied this ratio to estimated hourly temperatures to derive a topographically-adjusted temperature for each sheep location (Rasmussen et al. 2015).

The Normalized Difference Vegetation Index (NDVI) uses satellite imagery to predict primary production, and can be used to assess timing of forage emergence and senescence (Pettoirelli 2005). We compiled all annual 8-day, 250 x 250 m Moderate-resolution Imaging Spectroradiometer (MODIS) raw reflectance images (Didan et al. 2015), extracted sheep location-specific raw reflectance values, calculated NDVI and scaled values to range from 0 to 1. We used NDVI values and NDVI rates (i.e., percent changes over the previous 8, 16 and 32 days) as proxies for available forage biomass and quality, respectively.

We ran generalized linear mixed-effects logistic regression models in R 3.3.1 (R Development Core Team 2016) using the *lme4* package (Bates et al. 2015) to assess the relationship between topographic, environmental and forage variables and seasonal resource selection in desert bighorn sheep. Every model included a fixed effect for range to account for variation among populations and random effects for females to account for individual variation among sheep. We examined third-order selection analysing sheep locations within their home range and second-order selection analysing sheep home ranges within the population range (Johnson 1980). We constructed a set of 23 candidate models (Table 1.1) and evaluated model performance using second-order Akaike's Information Criterion

corrected for small sample size (AIC_c ; Burnham and Anderson 2002) and predictive performance using K -fold cross-validation (Boyce et al. 2002). We ran separate model sets for drought and non-drought conditions within each season and at each spatial scale. Continuous data were scaled prior to analysis by subtracting the mean and dividing by two standard deviations so that we could compare the relative influence of each predictor variable on habitat selection.

We assessed the potential for non-linear relationships between sheep use and elevation, slope and ruggedness by comparing models with linear terms to those with quadratic terms and used the better predictor (i.e., from the model with the lowest AIC_c) in subsequent models. We expected high variability among seasons and between climatic conditions in relationships between forage components (i.e., abundance and quality) and sheep selection. Therefore, we conducted preliminary analyses to determine the best combination of NDVI (linear or quadratic term) and NDVI rate (i.e., previous 8, 16 and 32 days) for predicting sheep selection during drought and non-drought within each season, and incorporated those covariates as the parameter ‘Forage’ in subsequent models (Tables 1.1 & 1.2).

Table 1.1. Candidate models for testing desert bighorn sheep seasonal resource selection under drought and non-drought conditions in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005).

Model name ^a	Model covariates ^b
TOPO	Elevation ² + Ruggedness ² + TPI + Aspect
TOPO Diel	Elevation ² + Ruggedness ² + TPI*Diel + Aspect*Diel
ENV	Temp + Water
ENV Diel	Temp*Diel + Water
ENV Aspect	Temp*Aspect + Water
ENV Aspect Diel	Temp*Aspect + Temp*Diel + Water
FOR	Forage
FOR Diel	Forage*Diel
FOR Water	Forage + Water
FOR Water Diel	Forage*Diel + Water
FOR-ENV	Forage + Temp
FOR-ENV Diel	Forage*Diel + Temp*Diel
FOR-ENV Water	Forage + Temp + Water
FOR-ENV Water Diel	Forage*Diel + Temp*Diel + Water
FOR-ENV Aspect	Forage*Aspect + Temp*Aspect
FOR-ENV Aspect Diel	Forage*Aspect + Forage*Diel + Temp*Aspect + Temp*Diel
FOR-TOPO	Forage + Water + Elevation ² + Ruggedness ² + TPI + Aspect
FOR-TOPO Diel	Forage*Diel + Water + Elevation ² + Ruggedness ² + TPI*Diel + Aspect*Diel
ENV-TOPO	Temp + Elevation ² + Ruggedness ² + TPI + Aspect
ENV-TOPO Diel	Temp*Diel + Elevation ² + Ruggedness ² + TPI*Diel + Aspect*Diel
GLOBAL	Forage + Water + Temp + Elevation ² + Ruggedness ² + TPI + Aspect
GLOBAL Diel	Forage*Diel + Water + Temp*Diel + Elevation ² + Ruggedness ² + TPI*Diel + Aspect*Diel
NULL	[fixed effects for Range and Slope ² ; random effects for individual females]

^a TOPO, topography; FOR, forage; ENV, environmental

^b TPI, topographic position index (slope/ridgeline/valley); Aspect, Slope²*Northness; Diel, diel period (night/twilight/day); Temp, topographically-adjusted temperature; Water, distance to perennial water (km)

All models include fixed effects for Range (Cabeza Prieta/Sierra Pinta) and Slope², and random effects for individual females.

Models with quadratic terms also include the linear term (e.g., a² refers to a + a² as fixed effects).

Models with interaction terms also include main effects (e.g., a*b refers to a + b + a*b as fixed effects).

See Table 2 for covariates represented by Forage; Forage*Diel only includes interactions between forage biomass (NDVI or NDVI²) and diel period – interactions between forage quality (NDVIRate) and diel period were not tested.

Table 1.2. Normalized Difference Vegetation Index (NDVI) covariates represented by ‘Forage’ in the candidate models (see Table 1.1) from the best-fit models from preliminary analyses testing forage components against desert bighorn sheep seasonal resource selection under drought and non-drought conditions in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005).

Selection scale	Season	Climatic conditions	Covariates ^a	
Third order	Winter	Drought	NDVI + NDVIRate16	
		Non-drought	NDVI ² + NDVIRate16	
	Early summer	Drought	NDVI	
		Non-drought	NDVI ² + NDVIRate32	
	Late summer	Drought	NDVI	
		Non-drought	NDVI ²	
	Autumn	Drought	NDVIRate8	
		Non-drought	NDVI ² + NDVIRate32	
	Second order	Winter	Drought	NDVI + NDVIRate32
			Non-drought	NDVI ² + NDVIRate32
Early summer		Drought	NDVI ² + NDVIRate32	
		Non-drought	NDVI ² + NDVIRate32	
Late summer		Drought	NDVI + NDVIRate32	
		Non-drought	NDVI ²	
Autumn		Drought	NDVI + NDVIRate8	
		Non-drought	NDVI ² + NDVIRate32	

^a NDVI², NDVI + NDVI²; NDVIRate8, NDVI change over previous 8 days; NDVIRate16, NDVI change over previous 16 days; NDVIRate32, NDVI change over previous 32 days.

Objectives 2 and 3. We investigated how precipitation variability influences forage nutritional quality, assessed changes in diet breadth and forage selection in response to precipitation-induced shifts in forage quality, and determined the relationship between forage selection and specific nutritional limitations across widely varying precipitation conditions. We used GPS positions from peak morning and afternoon foraging periods of sheep to identify areas for assessing forage availability and collecting forage samples to determine nutritional content (Cain et al. 2008). From 2002 through 2005, we sampled forage plots seasonally and estimated percent cover of each plant species in the foraging areas.

We collected ≥ 100 g of agave (*Agavi deserti*), barrel cactus (*Ferocactus* spp.), big galleta grass (*Pleuraphis rigida*), brittlebush (*Encelia farinosa*), catclaw acacia (*Senegalia greggii*), desert lavender (*Hyptis emoryi*), fishhook cactus (*Mammillaria* spp.), globemallow (*Sphaeralcea* spp.), ironwood (*Olneya tesota*), palo verde (*Parkinsonia microphyllum* and *P. florida*), ratany (*Krameria* spp.), rough jointfir (*Ephedra aspera*), silverbush (*Ditaxis lanceolata*), three-awn (*Aristida* spp.), Wright’s buckwheat (*Erigonum wrightii*), and white bursage (*Ambrosia dumosa*). These 16 species constituted 73–98% ($\bar{x} = 85.4\% \pm 7.9\%$ SD) of the seasonal diets of desert bighorn sheep in our study ranges (Cain et al. 2008). We classified each forage species as grass, forb, succulent, shrub or tree to assess differences in forage moisture and nutritional content related to forage type. We then determined forage moisture, nitrogen (N), neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid

detergent lignin (ADL). We used dry matter digestibility (DMD) as a proxy for energy content of forage, as calculated by Mould and Robbins (1982) for white-tailed deer (i.e., desert bighorn sheep are primarily browsers, and thus, have a diet more similar to deer than to domestic sheep).

We collected 10–20 pellet groups per season per mountain range from adult female desert bighorn to estimate percent diet composition using microhistological analysis. Using data collected at the foraging plots and diet composition, we estimated forage selection in relation to forage availability using Jacobs' modified electivity D index (Jacobs 1974) and estimated diet breadth using Levins Niche Breadth index (Levins 1968).

If N, DMD, or moisture were limiting, we would expect desert bighorn sheep to select diets to compensate for this nutritional limitation assuming there were sufficient forages with suitable nutritional conditions available. Therefore, we would expect higher values for a limiting nutritional metric in forages selected by desert bighorn sheep than in the available forage as a whole. To assess differences in nutritional metrics between diets consumed by desert bighorn sheep and available forage, we calculated weighted means for each nutritional metric for each season and precipitation period.

We used ANOVA to assess differences in nutritional quality in relation to precipitation period (drought, average, and wet conditions), season (winter, early summer, late summer, and autumn), and forage type (succulent, grass, shrub, tree, and forb). We conducted separate analyses, each with N, DMD, or moisture as the response variable, precipitation period, season, and forage type as factors, and topographic position (drainage, slope, and ridgeline) as a blocking factor. We used ANOVA to determine differences in diet breadth across seasons and precipitation periods. We used Levins Niche Breadth as the response variable and season and precipitation period were entered as factors.

We assessed the relationships between forage selection (i.e., Jacobs' D) and nutritional content (N, DMD, and moisture) and precipitation periods (reference level – wet) using generalized linear models. To account for the potentially conflicting limitations in desert bighorn sheep diets (e.g., protein vs. water), we developed an initial set of 18 *a priori* models (Appendix 1, Table A1). All models included precipitation period as a fixed effect and some models tested the interaction between forage quality metrics and precipitation period. In addition, to assess the potential for a nonlinear relationship between diet selection and moisture content, we included a quadratic term for moisture. We evaluated models using Akaike's Information Criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). We calculated model-averaged parameter estimates (\pm SE) and 95% confidence intervals for variables in the highest ranking models using multi-model averaging (Burnham and Anderson 2002) across all *a priori* models except for those excluded due to uninformative parameters.

Objective 3 and 4. We compared two desert bighorn sheep populations in southwestern Arizona, U.S.A.: a treatment population with supplemental water removed, and a control population (access to supplemental water). We examined whether sheep altered their seasonal diets without supplemental water and we determined water and nutrient balance for non-reproductive females, reproductive females and males. As described above for objectives 2 and 3, we collected key forage samples seasonally and analyzed them for nutrient and moisture content and simultaneously collected fecal pellet samples to assess diet composition. Only pellet groups in which identified forage species made up $\geq 90\%$ of the total diet composition were used to calculate seasonal water and nutrient intake. For estimations of water and nutrient intake of the unknown portion of the diet, we used seasonal mean water and N content by plant type from the known portion of the diet, and at seasonal proportions found in the known portion of the diet. Seasonal water and nutritional content of forage

species not analyzed and lipid content of all forage species were taken from the literature. We determined water and nutrient balance for non-reproductive females, reproductive females and males. The DBS lambing season lasts from late December to early April (Karsch 2014), with peaks in January and March (Russo 1956, Witham 1983, Karsch 2014). Therefore, we designated reproductive females as early breeders (i.e., late gestation and early lactation correspond with autumn and winter, respectively) and late breeders (i.e., late gestation and early lactation correspond with winter and early summer, respectively).

We used seasonal dry matter intakes (DMI) on captive desert bighorn sheep from Mazaika et al. (1992). Daily DMI for a 78 kg male was 3.87 kg in early summer, 2.66 kg in late summer, 2.91 kg in autumn and 4.25 kg in winter (Mazaika et al. 1992). Thus, after adjusting for metabolic weight, daily DMI for a 52 kg non-reproductive female was 2.86 kg in early summer, 1.96 kg in late summer, 2.15 kg in autumn and 3.14 kg in winter. We increased DMI for reproductive females by 17% during lactation (Weston 1988).

Daily water intake in the absence of free-standing water is the total of preformed water (i.e., water contained in forage) and metabolic water. Daily preformed water intake was estimated using the product of the seasonal diet composition, DMI and forage moisture content and metabolic water produced was estimated based on Houpt (1970) and Robbins (1993). We assumed utilizable metabolic water by DBS to be about half of the total metabolic water produced, after accounting for water lost through excretion (urination and defaecation), from respiration and evaporation from the body surface (Houpt 1970). Previous water deprivation trials determined that daily maintenance water requirements for DBS were 4% of bodyweight during early summer and 3% of bodyweight in the remaining seasons (Turner 1973). Research on Awassi (*Ovis aries*), a desert-adapted sheep breed, showed that daily water turnover rates in females increased by 11% and 30% during late gestation and lactation, respectively (Degen 1977); we adjusted minimum daily water requirements for reproductive females accordingly. Daily N requirements for DBS were 0.89% DMI for maintenance in all seasons for non-reproductive females and males, and 1.5% DMI during late gestation and lactation for reproductive females (Hebert 1973, DeYoung et al. 2000).

To test for the impacts of water removal on DBS diet selection and quality of forage consumed, we compared parameters among ranges (i.e., SP treatment and CP control) and treatment periods. We used general linear models to test for differences in diet composition (by plant type) and forage quality (moisture and N content) among ranges, seasons and treatment periods.

We estimated DBS water and nutrient balances on SP (treatment range) during the treatment period, when water catchments were maintained empty. When modelling water and nutrient balances, we assumed there was no surface water available to DBS during all seasons. We estimated DBS daily nutrient and preformed water intake, and metabolic water production for each season based on diet composition, forage quality and DMI. For seasons when a negative daily water balance was accompanied by a positive N balance, we examined if DBS could potentially meet their daily water and nutrient requirements by shifting part of their diet from forage species with lower moisture content to higher moisture species. For early summer, we systematically reduced the proportion in the diet of the lowest moisture species (i.e., big galleta [31%] and brittlebush [36%]) by 3% (i.e., percent of total diet), and shifted this to the three highest moisture species in the diets (i.e., barrel cactus [90%], desert agave [78%] and fishhook cactus [66%]), thereby increasing each of these species in the early summer DBS diet by 1%. We continued in increments of 3%, and at each stage adjusted estimates of DBS water and N intake accordingly. Shifting from the lowest moisture species ceased if the percentage of that species in DBS diet decreased to below 1%. The species with the next lowest moisture content was then selected for reduction (i.e., in this case Wright's buckwheat [37%]). Diet shifts were to the two highest moisture species in late summer (i.e.,

barrel cactus [93%] and fishhook cactus [66%]) and autumn (i.e., *Janusia* sp. [71%] and fishhook cactus [60%]), because only two higher moisture species occurred in DBS diets in these seasons. In winter, diet shifts were from the species in DBS diets with the lowest N content (i.e., big galleta [0.7%]) to the species with the most N (i.e., fairy duster [3.3%]).

Project Results, Analysis and Findings:

Our data spanned a period of exceptional drought (January through October 2002 being the driest period on record for this region at the time of the study), transitioning through a period with near average precipitation and into an abnormally wet period. Based on SPI, we classified January 2002 through February 2003 and July 2004 through October 2004 as drought; March 2003 through June 2004 and May to September 2005 were classified as average. November 2004 through April 2005 were classified as wet; Fig 1.1).

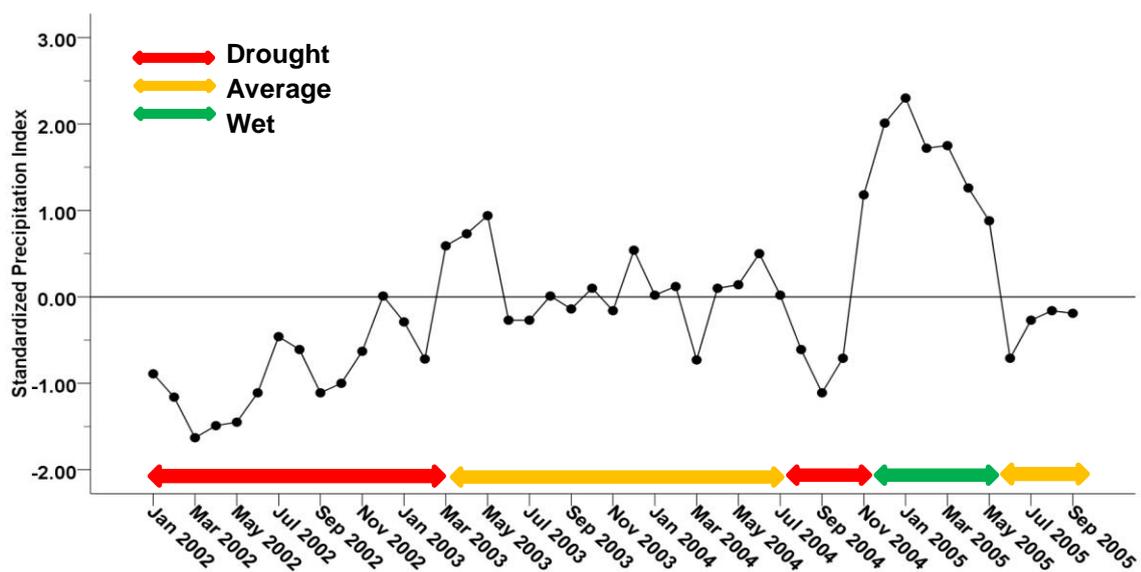


Figure 1.1. Three-month Standardized Precipitation Index (SPI; i.e., the number of standard deviations that observed cumulative precipitation deviates from the long-term climatological average) calculated from long-term (1969-2005) precipitation data from Tacna, Arizona (Western Regional Climate Center 2005). We defined a drought event when the SPI was consistently negative and reaches ≤ -1.0 with the drought event beginning when the SPI fell below 0, and ending when the SPI becomes positive. We defined wet periods as when the SPI was continuously positive and reached a value ≥ 1.0 and periods near average when the SPI fluctuated near 0, not becoming consistently positive or negative.

Concentration of N in forage available to desert bighorn sheep differed among precipitation periods ($F_{2,1103} = 16.63, p < 0.001$), seasons ($F_{3,1103} = 6.37, p < 0.001$), and forage types ($F_{4,1103} = 74.38, p < 0.001$). Differences in N content between precipitation periods depended on season (precipitation period \times season interaction; $F_{4,1103} = 3.34, p = 0.010$). Forage N content did not differ between seasons during drought, but was higher during winter and autumn of average and wet periods than during drought (Fig. 1.2a). Seasonal N levels in forage during all seasons in drought and in summer during average precipitation were between minimum levels to prevent loss of body condition and minimum level for accretion of lean body mass, and only winter and autumn N levels during average and wet precipitation periods met minimum levels for accretion of lean body mass. The highest N levels occurred in winter under wet conditions (25% and 36% higher than in winter during

average and drought conditions, respectively; 40–46% higher than in summer during average precipitation; 52–61% higher than other seasons in drought). Autumn N levels were also high in the average and wet precipitation periods; during the wet period, 26–29% higher than in summer under average conditions and 19–42% higher than in all seasons in drought (Fig. 1.2a).

Differences in N content between precipitation periods also depended on forage type (precipitation period × forage type interaction; $F_{8,1103} = 3.90$, $p < 0.001$). Mean N content of succulents and trees did not differ across precipitation periods, that of grasses was similar between periods of drought and average precipitation, and forb and shrub N content increased with precipitation (Fig. 1.2b). Mean N content of succulents was below sheep minimum maintenance levels to prevent loss of condition during all climate periods, and grasses only exceeded this level under wet conditions. Nitrogen content of grasses was 42–55% higher during the wet period than during drought and average precipitation, but was significantly lower than shrubs, trees and forbs across climate periods (Fig. 1.2b). Nitrogen content of shrubs and forbs were positively correlated with precipitation, increasing from drought to average precipitation (shrubs – 14%; forbs – 35%) and from average to wet conditions (shrubs – 30%; forbs – 60%; Fig. 2). In every precipitation period, N levels in shrubs, forbs and trees were above sheep minimum maintenance requirements, but forbs were the only plant type that met all reproductive requirements of female sheep, and only under wet conditions (Fig. 1.2b). Mean N content of trees was generally high, meeting sheep lactation requirements during non-drought periods.

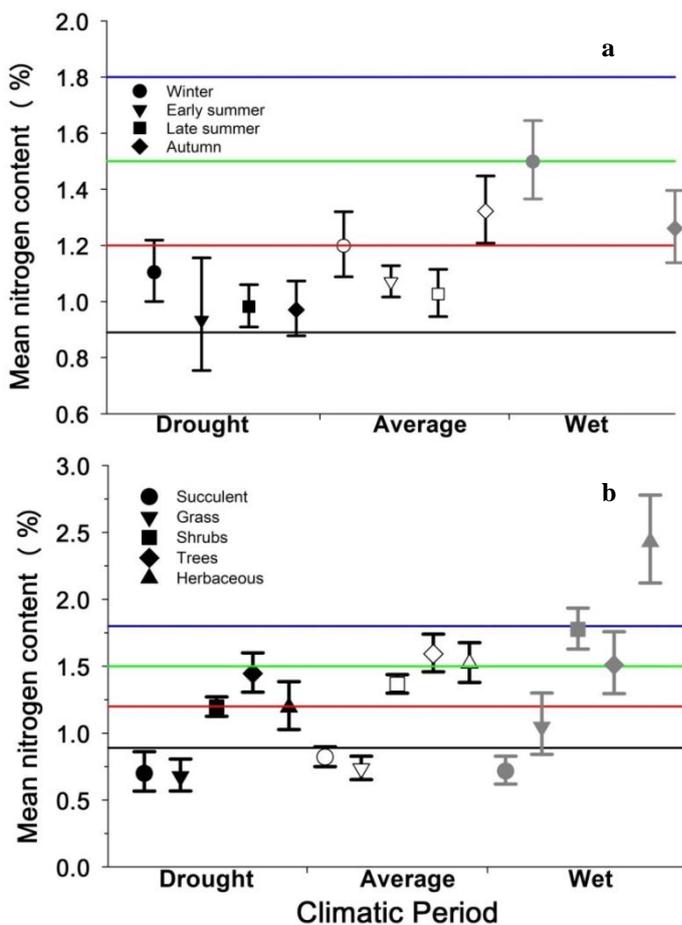


Figure 1.2. Mean nitrogen content of forage available to adult female desert bighorn sheep in Cabeza Prieta National Wildlife Refuge, Arizona, USA (20002–2005), by a) season and b) forage type in drought (closed black symbols), average (open symbols), and wet (closed grey symbols) conditions. Means and error bars are back-transformed estimated marginal means and 95% confidence intervals. Horizontal reference lines are forage N requirement levels for desert bighorn sheep (DeYoung et al. 2000): 0.89% minimum maintenance (black line), 1.2% accretion of lean body mass (red line), 1.5% lower limit for lactation (green line), and 1.8% minimum for weaned lamb growth (blue line).

Differences in moisture content of forage available to desert bighorn sheep between precipitation periods depended on season (precipitation period \times season; $F_{4,1106} = 8.55$, $p < 0.001$), forage type (precipitation period \times forage type; $F_{8,1106} = 11.50$, $p < 0.001$), and season by forage type (precipitation period \times season \times forage type; $F_{28,1106} = 3.54$, $p < 0.001$). As expected, succulents had the highest (>75% and as high as 92%) moisture content of any forage type throughout the study, and showed a slight increasing trend from the drought to the wet period. Grasses, forbs and shrubs had low to moderate moisture content, which increased across precipitation periods and during winter and autumn within precipitation periods; lowest moisture content was observed during summer in these forage types. Trees had moderate but consistent moisture content across seasons within precipitation periods and across precipitation periods (Appendix 1, Fig. A1).

Differences in DMD of forage available to desert bighorn sheep between precipitation periods depended on season (precipitation period \times season; $F_{4,1108} = 3.34$, $p = 0.010$), forage type (precipitation period \times forage type; $F_{8,1108} = 5.54$, $p < 0.001$), and season by forage type (precipitation period \times season \times forage type; $F_{16,1108} = 2.76$, $p < 0.001$). Within forage types, DMD levels were generally consistent across seasons and precipitation periods, although grasses and forbs demonstrated more variability (Appendix 1, Fig. A2). The lowest DMD in each precipitation period (43–62%) occurred in early summer and winter grasses under drought and wet conditions, respectively, and in forbs during average precipitation (Appendix 1, Fig. A2). Alternatively, the highest DMD in each climatic period occurred in succulents (80–81%); early summer in drought, late summer in average precipitation, autumn in wet conditions (Appendix 1, Fig. A3).

Shrubs and trees had the highest availability of all forage types at foraging sites of desert bighorn sheep (Table 1.3). Correspondingly shrubs and trees composed the bulk of sheep diets across all seasons and climatic periods; however, the proportion of the diet composed of tree species was always substantially higher than availability (winter in non-drought periods excepted), whereas the proportion of shrubs in diets were considerably lower than availability (Table 1.3). Succulent consumption was highest during drought (17–20%) and the proportion in the diet always exceeded availability (Table 1.3). With the exception of autumn, forb availability and consumption generally increased with precipitation, particularly during winter (Table 1.3).

With the exception of succulents, N content of forage types that made up the majority of seasonal sheep diets tended to be higher than the mean N averaged across available forages for each season and precipitation period (Table 1.3). Moisture content of forage types was similarly higher in sheep diets during summer, drought and the average precipitation period. Among forage types that made up the majority of seasonal sheep diets, there was little difference between DMD of diets and the within-season average DMD across forage types, and surprisingly, some predominant seasonal forage types in sheep diets (i.e., >20%) were actually lower in DMD than the within-season precipitation period average (Table 1.3).

Across all seasons in drought, the weighted mean N and moisture contents were 12–18% and 14–37%, respectively, higher in sheep diets than in available forage, and a similar pattern was found in summer under average precipitation conditions (Fig. 1.3). Winter during non-drought periods was the only season when N content was higher in available forage than in sheep diets (Fig. 1.3). Differences in DMD between sheep diets and available forage were minor (i.e., 0.1–4%) and showed no consistent pattern across seasons or precipitation periods (Fig. 1.3).

Each of the three nutritional metrics, N, DMD, and moisture, appeared in at least one model in the confidence set of models (i.e., models with $\sum w_i \geq 0.95$) for forage selection by desert bighorn sheep (Table 1.4). However our top model had 3 and 10 times more support

Table 1.3. Mean forage availability (Avail.), diet contribution (Diet), nitrogen (N), moisture (Moist.), and dry matter digestibility (DMD) of adult female desert bighorn sheep forage by forage type, season, and precipitation period in Cabeza Prieta National Wildlife Refuge, Arizona, USA. – = not available; during the study wet conditions did not occur during any summer seasons.

Season ^a	Forage	Drought					Average					Wet				
		Avail. ^b	Diet ^c	N	Moist.	DMD	Avail.	Diet	N	Moist.	DMD	Avail.	Diet	N	Moist.	DMD
ES	Forb	0.6	1.1	1.1	42.9	77.9	6.6	8.0	1.4	41.6	56.5	–	–	–	–	–
	Grass	1.5	6.1	0.5	16.9	57.1	2.2	1.1	0.7	20.9	59.7	–	–	–	–	–
	Shrub	71.8	25.9	1.2	33.6	71.6	63.3	27.1	1.3	42.3	62.2	–	–	–	–	–
	Succulent	1.6	19.9	0.8	66.6	71.1	2.7	13.3	0.8	77.4	66.5	–	–	–	–	–
	Tree	24.5	44.3	1.6	48.4	67.8	25.2	33.3	1.9	47.8	64.1	–	–	–	–	–
	Mean		1.0	41.7	69.1			1.2	46.0	61.8	–	–	–	–	–	
LS	Forb	1.9	2.9	1.3	28.4	74.0	4.2	7.2	1.7	36.1	44.2	–	–	–	–	–
	Grass	2.4	7.9	0.7	14.9	63.3	1.1	4.5	0.6	22.5	74.7	–	–	–	–	–
	Shrub	59.9	12.2	1.2	29.9	67.9	71.7	12.2	1.1	37.6	46.6	–	–	–	–	–
	Succulent	2.4	20.2	0.7	73.5	74.4	1.6	18.4	0.9	76.1	40.4	–	–	–	–	–
	Tree	33.3	41.7	1.6	45.2	71.9	21.2	39.9	1.6	45.8	43.3	–	–	–	–	–
	Mean		1.1	38.4	70.3			1.2	43.6	49.8	–	–	–	–	–	
A	Forb	8.9	6.3	1.2	25.5	64.4	3.0	3.9	1.7	52.4	63.9	4.9	17.1	1.9	61.5	62.2
	Grass	1.5	1.6	0.8	12.2	78.5	2.2	1.7	1.0	43.4	60.1	1.2	2.5	1.0	30.5	59.9
	Shrub	58.2	27.6	1.4	33.9	68.4	58.6	27.4	1.9	55.1	68.6	58.2	16.9	1.9	60.8	68.1
	Succulent	1.5	16.5	0.7	69.8	69.0	1.2	16.3	0.9	81.6	77.3	4.2	9.5	0.7	91.6	75.9
	Tree	29.9	40.8	1.5	47.1	72.5	35.0	42.1	1.6	52.9	67.5	31.5	42.1	1.6	52.8	69.1
	Mean		1.1	37.7	70.6			1.4	57.1	67.5			1.4	59.4	67.0	
W	Forb	4.8	4.6	1.4	33.0	65.9	6.9	15.3	1.6	51.7	73.5	22.3	13.9	3.5	70.1	51.3
	Grass	1.2	0.8	1.0	14.8	75.3	4.5	2.1	0.8	29.7	76.4	2.4	2.4	1.2	61.6	32.5
	Shrub	74.1	27.3	1.3	38.9	57.1	58.3	33.0	1.6	47.1	66.9	53.2	28.8	1.9	63.4	54.4
	Succulent	2.9	18.1	0.9	76.7	73.1	2.4	6.5	0.9	75.2	75.8	1.4	11.7	0.8	88.5	41.4
	Tree	16.4	43.2	1.5	42.3	62.1	27.9	19.2	1.6	42.5	73.4	20.4	19.1	1.5	42.6	36.7
	Mean		1.2	41.1	66.7			1.3	49.2	73.2			1.8	65.2	43.3	

^aSeason: ES = early summer, LS = late summer, A = autumn, W = winter.

^bAvail. = Percent forage availability.

^cDiet = Percent diet contribution.

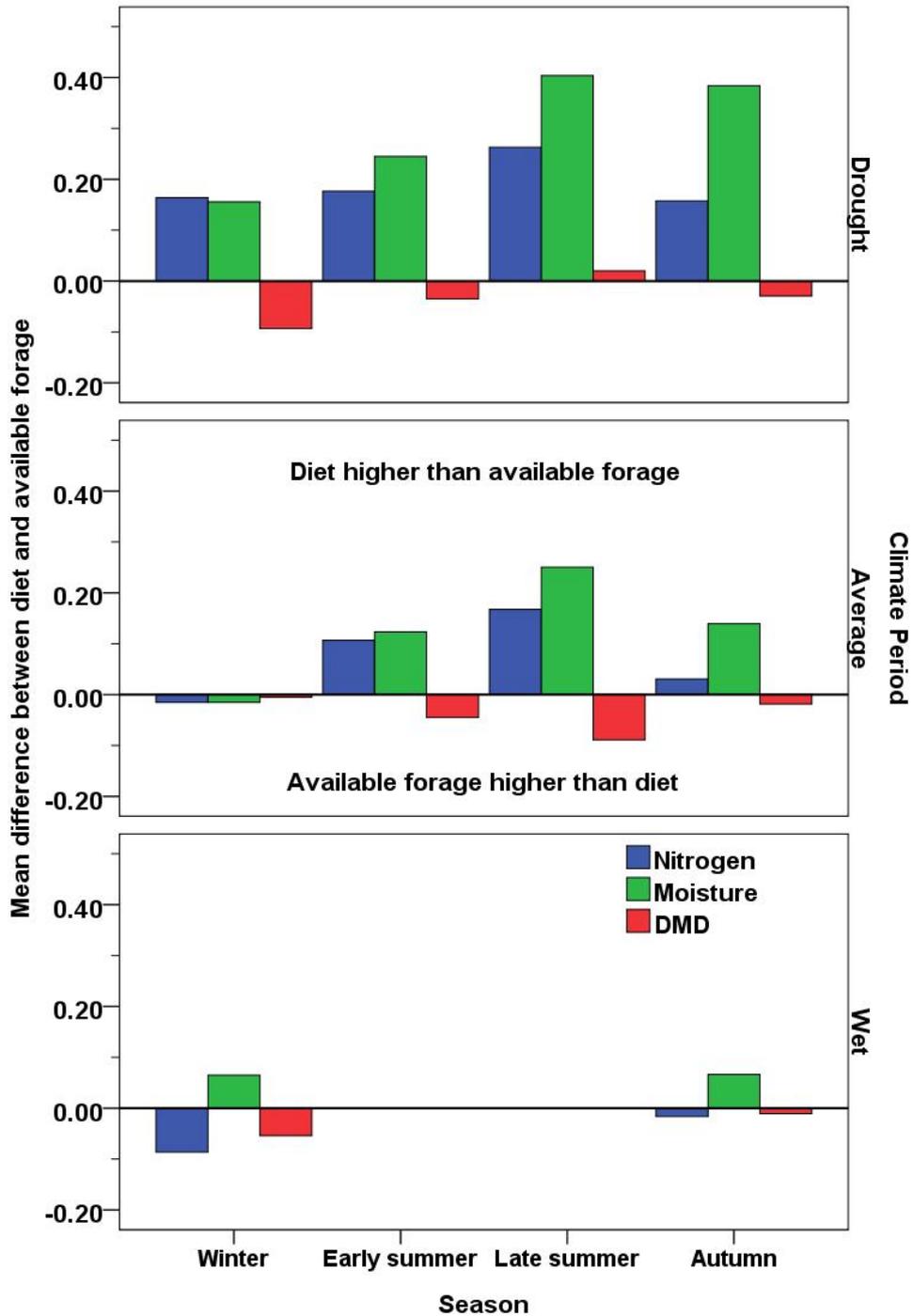


Figure 1.3. Seasonal differences (weighted means) for nitrogen, moisture and dry matter digestibility (DMD) of adult female desert bighorn sheep diets and available forage in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), during drought, average, and wet conditions. Values >0 indicate nutritional metrics were higher in diet selected by desert bighorn sheep than in available forage; values <0 indicate that nutritional metrics were higher for available forage than selected diet. There are no bars for early and late summer under wet conditions because during the study wet conditions did not occur during any summer seasons.

than the next two highest ranking models, respectively. Forage selection by female desert bighorn sheep increased with increasing forage N and moisture content; however, after accounting for the effects of N and moisture, forage selection was negatively associated with DMD (Table 1.5; Fig. 1.4a,b). Sheep forage selection had a quadratic relationship with moisture content, and model-averaged parameter estimates indicated that selection was strongest at intermediate levels (Table 1.5; Fig. 1.4c). Models with interactions between precipitation period and nutritional metrics had less support than those including precipitation period as an additive term (Table 1.4) indicating that the influence of each nutritional metric on sheep forage selection was independent of climate periods (e.g., selection for N did not depend on climate period).

Desert bighorn sheep diet breadth across seasons depended on precipitation (precipitation period \times season; $F_{4,340} = 22.04$, $p < 0.001$), and was generally lowest during drought and increased with rainfall (Fig. 1.5). Diet breadth was similar among seasons during drought, whereas under average and wet conditions sheep diet breadth exhibited high variability among seasons, but generally increased across precipitation periods (Fig. 1.5).

Table 1.4. Highest ranking a priori models with a $\Delta AIC_c \leq 10$ assessing the relationship between forage selection by adult female desert bighorn sheep (Cabeza Prieta National Wildlife Refuge, Arizona, USA, 2002–2005) and nutritional quality and precipitation period. Number of parameters (K), Akaike’s information criterion adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike weights (w_i) are given.

Model	K	AIC_c	ΔAIC_c	w_i
N + DMD + Precipitation	5	426.6	0	0.643
N + DMD + Moisture + Precipitation	5	428.7	2.1	0.225
DMD + Precipitation	4	431.32	4.72	0.061
DMD + Moisture + Precipitation	5	433.73	6.73	0.018
Moisture + Moisture ² + Precipitation	5	434.64	7.13	0.012
N + DMD + Precipitation + N \times Precipitation + DMD \times Precipitation	9	435.26	8.04	0.008
N + Moisture + Moisture ² + Precipitation	6	435.55	8.66	0.007

Table 1.5. Model-averaged coefficient estimates, standard errors (SE), and 95% confidence limits for variables in the top models testing the relationship between forage selection by adult female desert bighorn sheep in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), and forage nutritional content and precipitation period.

Variable	Model-averaged parameter estimate		95% Confidence limits	
	Estimate	SE	Lower CL	Upper CL
N	19.26	7.52	4.51	34.01
DMD	-2.23	0.52	-3.24	-1.23
Moisture	1.91	0.13	0.94	1.45
Moisture ²	-3.73	0.94	-5.57	-1.89
Precipitation (drought)	-0.03	0.46	-0.94	0.87
Precipitation (average)	0.1	0.43	-0.75	0.95

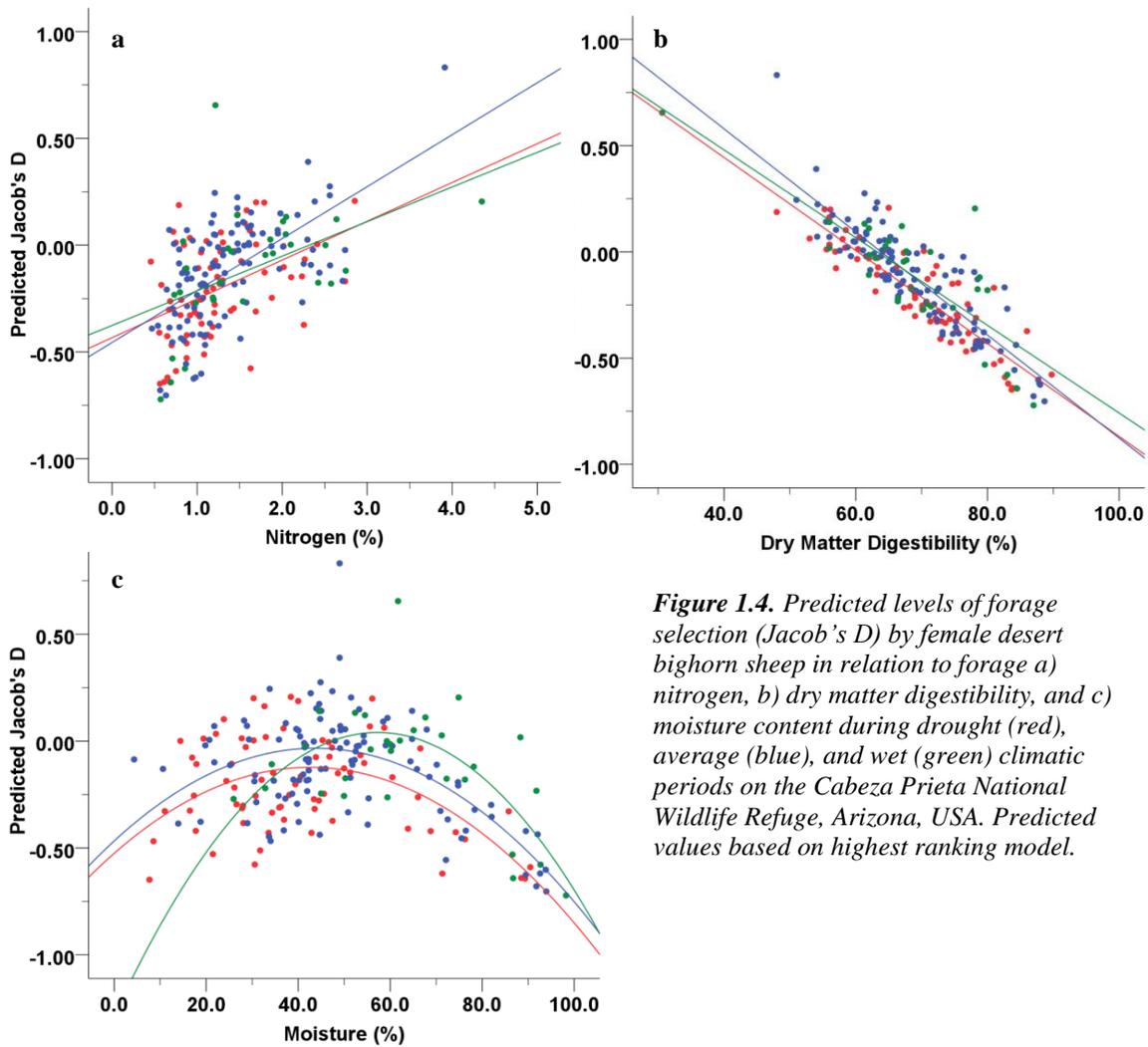


Figure 1.4. Predicted levels of forage selection (Jacob's D) by female desert bighorn sheep in relation to forage a) nitrogen, b) dry matter digestibility, and c) moisture content during drought (red), average (blue), and wet (green) climatic periods on the Cabeza Prieta National Wildlife Refuge, Arizona, USA. Predicted values based on highest ranking model.

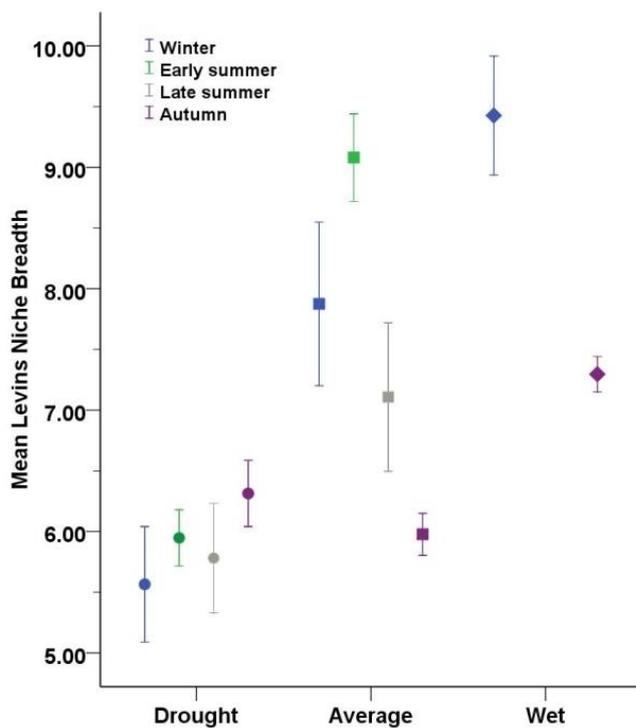


Figure 1.5. Mean seasonal Levins Niche Breadth of adult female desert bighorn sheep diets in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), during drought (circles), average (squares) and wet (diamonds) conditions. Blue symbols are winter (Jan – Mar), green are early summer (Apr – Jun), grey are late summer (Jul – Sep), and purple are autumn (Oct – Dec).

Water and nutrient balance

We estimated desert bighorn sheep water and nutrient balances on SP (treatment range) during the treatment period, when water catchments were maintained empty. Early and late summer were the only seasons where we predicted that both sexes would have a negative daily water balance (Table 1.6). In all seasons, sexes and reproductive states (early and late breeders), there was a surplus of daily N intake, with the exception of early summer, when we estimated that late breeding females (during early lactation) would have a slightly negative N balance (Table 1.6). The diet of non-reproductive and early breeding female desert bighorn sheep in early summer would have to include 23% higher moisture species for them to be able to attain a positive water balance, while still maintaining a positive N balance; this equates to a shift in their diet of 10% (Fig. 1.6a). Males would need to shift their diet by 33%, to 46% higher moisture species consumed to meet their water and N requirements in early summer (Fig. 1.6c). To overcome the larger water deficit facing desert bighorn sheep in late summer, diets of all females would have to include 47% higher moisture forages (31% diet shift; Fig. 1.6d) and male diets would have to include 71% higher moisture species (55% diet shift; Fig. 1.6e).

Table 1.6. Estimated seasonal daily water and nitrogen (N) balance of desert bighorn sheep non-reproductive females, reproductive females (early and late breeders) and males on Sierra Pinta Mountains (treatment range) during the treatment period in Cabeza Prieta National Wildlife Refuge, Arizona. Intakes are calculated from dry matter intakes reported in Mazaika et al. (1992), and forage moisture and N content measured in this study.

Season	Water maintenance (ml)				N maintenance (g)			
	Female	Reproductive female		Male	Female	Reproductive female		Male
		Early	Late			Early	Late	
Early summer								
Intake – average precipitation ^a	1970	1970	2305	2666	41.4	41.4	48.4	56.0
Requirement ^b	2080	2080	2704	3120	25.5	25.5	50.2	34.4
Balance	-110	-110	-399	-454	15.9	15.9	-1.8	21.6
Late summer								
Intake – drought ^c	1310	1310	1310	1778	29.4	29.4	29.4	39.9
Requirement	1560	1560	1560	2340	17.4	17.4	17.4	23.7
Balance	-250	-250	-250	-562	12.0	12.0	12.0	16.2
Autumn								
Intake – high precipitation ^d	1760	1760	1760	2383	36.1	36.1	36.1	48.8
Intake – drought ^e	1501	1501	1501	2031	36.4	36.4	36.4	49.3
Requirement	1560	1732	1560	2340	19.1	32.3	19.1	25.9
Balance – high precipitation ^d	200	28	200	43	17.0	3.8	17.0	22.9
Balance – drought ^e	-59	-231	-59	-309	17.3	4.1	17.3	23.4
Winter								
Intake – high precipitation ^d	2519	2947	2519	3409	52.9	61.9	52.9	71.6
Intake – drought ^e	2044	2391	2044	2766	42.3	49.5	42.3	57.2
Requirement	1560	2028	1732	2340	27.9	55.1	47.1	37.8
Balance – high precipitation ^d	959	919	787	1069	25.0	6.8	5.8	33.8
Balance – drought ^e	484	363	312	426	14.4	-5.6	-4.8	19.4

^a Calculated from forage N, moisture content and desert bighorn sheep diet under average precipitation during treatment.

^b Water requirements based on Degen (1977); N requirements based on Hebert (1973) and DeYoung et al. (2000).

^c Calculated from forage N, moisture content and desert bighorn sheep diet under drought conditions during treatment.

^d Calculated from forage N, moisture content and desert bighorn sheep diet under above average precipitation during treatment.

^e Calculated from forage N and moisture content under drought conditions during pretreatment, and desert bighorn sheep diet during above average precipitation during treatment.

We estimated a deficit in daily water and N intake for late breeding female desert bighorn sheep in early summer in the absence of surface water (Table 1.6). We examined whether a female nursing a lamb during this season could meet her water and N requirements through shifts in forage consumption. In this case, if the female shifted her diet, not only from low to higher moisture forages, but concurrently a portion from low to higher N forages, she could potentially meet her daily water and N requirements with a diet shift of 44% (Fig. 1.6b).

In autumn under drought conditions, we predicted that female and male desert bighorn sheep would be able to meet their daily N requirements, but unable to meet their daily water requirements through forage alone (Table 1.6). By shifting part of their diets from low to high moisture forage species, we estimated that non-reproductive and late breeding females could achieve a positive water balance in autumn if their diets included 23% higher moisture forages (8% diet shift; Fig. 1.6f). Male and early breeding female desert bighorn sheep diets in autumn would need to include 59% higher moisture species to meet their daily water requirements (44% diet shift; Fig. 1.6g,h). During winter under drought conditions, we predicted that reproductive female desert bighorn sheep (i.e., early and late breeders) would be able to obtain enough water from their forage to meet their daily requirements; however, we estimate that they would have a N deficit (Table 1.6). To overcome this negative balance, early and late breeding female diets would have to include 18% and 7% higher N forages, respectively (early breeders – 17% diet shift, Fig. 1.6i; late breeders – 6% diet shift; Fig. 1.6j).

Conclusions and Recommendations:

Unpredictable precipitation patterns present challenges to ungulates inhabiting arid climates. Desert ungulates cope with their xeric and often nutrient-stressed environment through physiological adaptations and behavioural modifications. Given the availability of quality forage (i.e., suitable moisture and protein content), ungulates on arid lands can make foraging decisions that allow them to survive during the hottest and driest seasons. The DBS serves as an excellent example of how an ungulate can adapt to survive in an arid environment. This study revealed that, based on observed diets, DBS would not be able to meet their daily water requirements in some seasons and under some climatic conditions in the absence of surface water. However, our results demonstrate that resourceful foraging decisions could potentially allow DBS to overcome seasonal nutrient deficits, and concurrently gain a positive water balance solely from the forage they consume. Our findings raise questions about the efficacy, or in fact necessity, of the management practice of providing supplemental water to DBS during water-stressed periods (at least under the climatic conditions observed during our study). Indeed, projected temperature increases and decreasing precipitation over the coming century will undoubtedly alter DBS water requirements and forage moisture and nutrient content, and thus, could further compromise DBS ability to subsist solely on forage. This study only addressed water and nutrient requirements for adult survival, and it is unknown whether these conditions can facilitate population growth. Therefore, future research should investigate how water provision may also affect other demographic rates that ultimately lead to population growth.

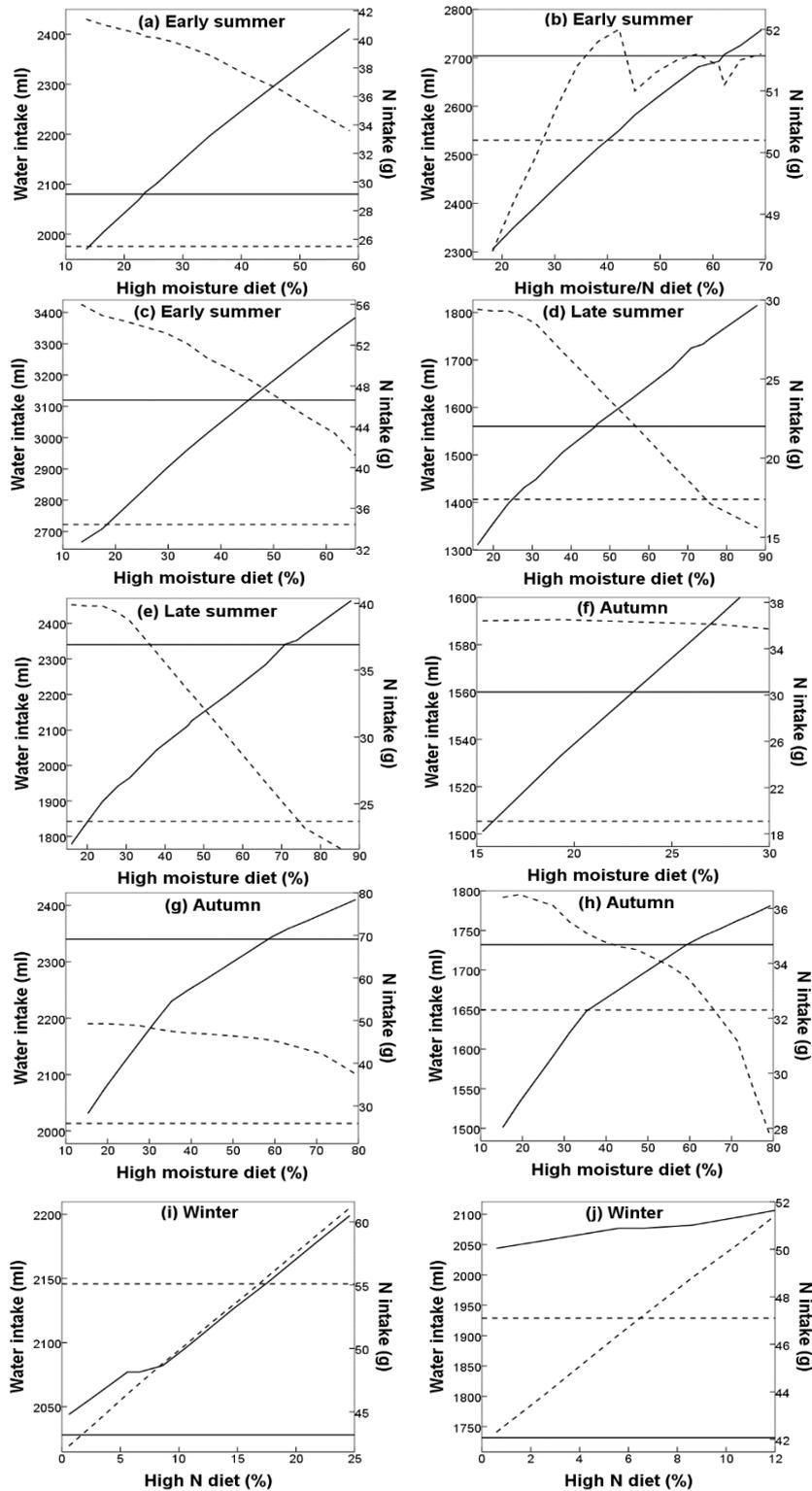


Figure 1.6. Seasonal water (ml; solid line) and nitrogen (N; g; dashed line) intake of desert bighorn sheep (DBS) under average precipitation for a) non-reproductive and early breeding females, b) late breeding females and c) males, and under drought conditions for d) non-reproductive and reproductive females, e) males, f) early breeding females, g) non-reproductive and late breeding females, h) males, i) early breeding females and j) late breeding females in response to shifts in diet in Cabeza Prieta National Wildlife Refuge, Arizona, USA. Panels f to j are calculated from forage moisture and N content in pretreatment under drought conditions, and DBS diet in treatment under above average precipitation. The start of lines at the left represent observed diet proportions (i.e., without shifts). Horizontal lines represent DBS daily maintenance requirements for water (solid) and N (dashed), and thus intakes above these lines represent a positive balance.

SUBPROJECT 2.

Impact of Drought on Southwestern Pronghorn Population Trends and Predicted Trajectories in the Southwest in the Face of Climate Change.

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Purpose and Objectives:

Many pronghorn populations across the Southwest appear to be declining. In response, managers are applying various techniques in attempts to increase pronghorn numbers often without a clear understanding of the causes of these declines. Some population declines have been associated with drought conditions resulting in reduced forage quality and quantity impacting survival of adults and fawns. Various climate change models predict warmer and drier conditions, which is likely to exacerbate future drought-related population declines, forcing managers to make some difficult decisions regarding the long-term viability of their management practices and the persistence of some pronghorn populations in the Southwest. Our objectives were to: 1) determine the extent of pronghorn decline in the Southwest; 2) identify climatic factors which best predict these declines; and 3) use downscaled climate forecast data to project how climate change may effect pronghorn population dynamics to the end the of the century.

Organization and Approach:

Objectives 1-3. Long-term data from annual aerial surveys of 18 pronghorn populations from Arizona, New Mexico, Utah and Texas were analyzed (Table 2.1). Annual rate of population growth (λ) was calculated as the response variable. When population-specific harvest and translocation data were available, population estimates for calculating λ were adjusted according to the following equation:

$$\lambda_t = \frac{N_t}{N_{t-1} - h - r + a} \quad (1)$$

where λ_t is population change from time $t-1$ to t , N_t and N_{t-1} are population estimates from current and previous surveys, respectively, h is number of pronghorn harvested, and r and a are number of individuals removed from and released into the population, respectively, through translocations. With the exception of south-central New Mexico, population-specific harvest and translocation data were not available, and thus, were unaccounted for in these models.

Climate Data

Mean monthly climate data (precipitation [mm/day] and mean temperature [°C]) were derived from historical and future simulations from the World Climate Research Programme's Coupled Model Intercomparison Project phase 5 (CMIP5) Global Climate Models (GCM) subset from the National Center for Atmospheric Research Community Climate System Model version 4 (Maurer et al. 2014). Comparisons of GCM historical simulations with observations often show biases, which may vary by location and/or season. A monthly bias-correction and spatial disaggregation (BCSD) statistical downscaling technique was used to correct for such biases (Wood et al. 2004; Maurer 2007). Model evaluations demonstrated that results from downscaling algorithms were in good agreement with observations, with precipitation and average surface temperature biases of ± 0.04 mm/day and $\pm 0.05^\circ\text{C}$, respectively, for all values for all time steps and grid cells (Brekke et al. 2013). The aim was to compare two realistic future global climate situations; an optimistic lower atmospheric CO₂ concentration (ACDC) scenario and a pessimistic high ACDC

scenario. Therefore, our climate projections were modeled with data derived from the BCSD CMIP5 Representative Concentrations Pathways

Table 2.1. Modeled pronghorn populations in the southwestern United States.

Population	Survey Period ^a	Population Range	Area (km ²)	Population Change (%) ^b
Utah				
Northwest	1977-2011	64-584	779	-68
West	1978-2013	130-2034	5,425	58
East	1977-2013	133-929	1,884	-28
Southeast	1977-2013	49-197	420	-44
South-central	1977-2013	512-2232	911	-12
Arizona				
Northwest	1976-2013	74-619	3,816	-34
Central	1961-2013	1,663-5,802	22,355	-55
East-central	1961-2013	391-2,808	13,714	-27
Southeast - N10	1961-2013	29-314	1,365	-69
Southeast - S10	1961-2013	13-420	1,044	-50
New Mexico				
Northeast	1992-2008	1,327-2,828	797	-27
East	1985-2009	64-239	816	99
East-central	1980-2005	90-423	384	-38
West-central	1993-2011	210-576	802	-15
South-central	1994-2014	49-506	1,469	-80
Southwest	1990-2011	86-240	469	-33
Texas				
Trans-Pecos	1977-2013	2,751-17,226	21,780	-79
Panhandle	1977-2013	2,568-12,809	45,334	324

^a Population surveys conducted in summer in Arizona and Texas, in spring in New Mexico, and in winter in Utah. New Mexico switched to summer composition surveys in 2010. Utah switched to spring surveys in 2009.

^b Period from early 1990s to start of population projections.

(RCP) 4.5 and 8.5 (Moss et al. 2010; van Vuuren et al. 2011). These scenarios attempt to account for external factors that have affected climate in the past, since GCMs calculate their own internal patterns of natural variability. The RCP 8.5 pathway represents a comparatively high ACDC scenario of continued global dependency on fossil fuels, whereby ACDC approaches 2.5 times current levels by 2100 (Riahi et al. 2011). The RCP 4.5 pathway represents a lower ACDC scenario, whereby there is an increase of about 60% in ACDC by mid-century, followed by a decline to near 1990 levels by 2100 (Thomson et al. 2011).

A drought index was also tested as an additional measure of precipitation for predicting pronghorn population dynamics; Standardized Precipitation Index (SPI; Guttman 1999). The SPI represents the number of standard deviations that observed cumulative precipitation deviates from the long-term climatological average. SPI for 3-, 6-, 12-, and 24-month periods were calculated from all available monthly precipitation data in the BCSD CMIP5 climate dataset using program SPI SL 6 (National Drought Mitigation Center 2014).

Monthly mean temperature, total precipitation, and mean SPI (3-, 6-, and 12-month periods) were summarized by important periods in an adult female's annual reproductive cycle relative to peak fawning (i.e., early, mid-, and late gestation [3 months each] and lactation [4 months]). Peak pronghorn fawning is usually over three weeks during the early growing season, with the majority of births occurring within a ten day period (Autenrieth and Fichter 1975). In our study area, fawning peaks in mid-April in southern Arizona, in mid-May in northern Arizona and Texas Trans-Pecos, and in late May in Utah, New Mexico, and Texas Panhandle (Buechner 1950; Larsen 1964; Canon 1993; Ticer et al. 2000; Miller and Drake 2006; J. Weaver pers. comm., A. Aoude pers. comm.). Mean temperature and total precipitation were also calculated for 12 and 24 months preceding each population survey. Climate data were summarized over several time periods (overall and in relation to reproductive seasons) to increase the likelihood of using climate covariates with the highest predictive power when projecting populations (see next section). All data were scaled prior to analysis by subtracting the mean and dividing by standard deviation (Gelman and Hill 2007).

Population Models

Bayesian inference was used to estimate parameters from regressions using a Markov-Chain Monte Carlo (MCMC) technique by creating models in R 3.0.2 (R Core Team 2013) and running them in OpenBUGS 3.2.3 (Lunn et al. 2009) using R2OpenBUGS (Sturtz et al. 2005). An information-theoretic approach was used, whereby competing models were ranked by their deviance information criterion (DIC, Spiegelhalter et al. 2002). All models included a covariate for density effect (i.e., population in the previous year). Precipitation and temperature model comparison sets were run separately, and each model set included a null model. These top individual precipitation and temperature covariates were then combined in models (i.e., one precipitation and temperature covariate per model), and these combined models were run including a term for the interaction between precipitation and temperature (Eqn. 2). Competitive models (with precipitation and temperature alone or in combination) had $\Delta DIC \leq 2$ from the model with lowest ΔDIC .

$$\ln(\lambda_t) = \beta_0 + \beta_1 X_{N[t-1]} + \beta_2 X_{prec} + \beta_3 X_{temp} + \beta_4 X_{prec*temp} \quad (2)$$

In an effort to maximize predictive power when making pronghorn population projections, the combined model (or in some cases, single climate covariate model) with the lowest DIC was selected to embed in the projection model. The selected model was then run with the corresponding projected climate data derived from the BCSO CMIP5 RCP4.5 and RCP8.5 datasets to predict λ_t . Annual pronghorn population sizes to the year 2090 were then projected with λ_t using an integrated modeling approach (Schaub and Abadi 2011), whereby population projections were generated concurrently with climate parameter estimates and λ_t , such that uncertainties from these estimates were propagated into the projections. Population projections were made in the absence of any management intervention (e.g., harvest or translocation) and assume that pronghorn peak fawning periods will not significantly shift in response to climate change.

Project Results, Analysis and Findings:

Sixteen populations demonstrated a significant relationship between precipitation and λ , and in 13 of these, temperature was also significant. Precipitation predictors of λ were highly seasonal, with lactation being the most important period, followed by early and late gestation (Table 2.2). The influence of temperature on λ was less seasonal than precipitation, and lacked a clear temporal pattern.

The climatic projections indicated that all of these pronghorn populations would experience increased temperatures, while the direction and magnitude of precipitation had high population-specific variation. Models predicted that nine populations would be extirpated or approaching extirpation by 2090. Results were consistent across both atmospheric CO₂ concentration scenarios, indicating robustness of trends irrespective of climatic severity (Figure 2.1).

Table 2.2. Climate predictor regression equations used to project pronghorn populations, derived from historic climate data and pronghorn population surveys.

Population	<i>n</i> ^a	Regression equations for projections ^b
Utah		
Northwest	19	$\ln(\lambda_t) = 0.04 - 0.18X_{N[t-1]} + 0.14X_{SPI03EG} - 0.06X_{TempLG}$
West	22	$\ln(\lambda_t) = 0.07 - 0.06X_{N[t-1]} + 0.09X_{SPI03MG} - 0.13X_{TempMG}$
East	23	$\ln(\lambda_t) = 0.16 - 0.09X_{N[t-1]} + 0.06X_{SPI12Lac} - 0.10X_{TempAnn12}$
Southeast	36	$\ln(\lambda_t) = -0.04 - 0.19X_{N[t-1]} + 0.11X_{PrecLac} - 0.07X_{TempAnn12}$
South-central	33	$\ln(\lambda_t) = 0.29 - 0.12X_{N[t-1]} + 0.06X_{SPI12Lac}$
Arizona		
Northwest	37	$\ln(\lambda_t) = 0.04 - 0.08X_{N[t-1]} - 0.08X_{SPI03Lac} + 0.06X_{TempAnn12}$
Central	53	$\ln(\lambda_t) = 0.13 - 0.09X_{N[t-1]} + 0.03X_{PrecLG} + 0.04X_{TempMG}$
East-central	52	$\ln(\lambda_t) = 0.19 - 0.13X_{N[t-1]} + 0.02X_{SPI03Lac} - 0.04X_{TempAnn24}$
Southeast - N10	48	$\ln(\lambda_t) = 0.06 - 0.09X_{N[t-1]} + 0.07X_{SPI06Lac} - 0.05X_{TempLG}$
Southeast - S10	48	$\ln(\lambda_t) = 0.06 - 0.11X_{N[t-1]} + 0.14X_{SPI06Lac} + 0.10X_{TempEG}$
New Mexico		
Northeast	17	$\ln(\lambda_t) = -0.02 - 0.07X_{N[t-1]} + 0.08X_{PrecLG} + 0.09X_{TempEG}$
East	17	not significant
East-central	17	$\ln(\lambda_t) = -0.04 - 0.51X_{N[t-1]} + 0.21X_{SPI03EG}$
West-central	14	not significant
South-central	19	$\ln(\lambda_t) = -0.12 - 0.28X_{N[t-1]} + 0.17X_{SPI06Lac} - 0.27X_{TempEG}$
Southwest	18	$\ln(\lambda_t) = -0.01 - 0.18X_{N[t-1]} + 0.14X_{PrecLG}$
Texas		
Trans-Pecos	36	$\ln(\lambda_t) = 0.02 - 0.14X_{N[t-1]} + 2.8X_{PrecLac} + 0.14X_{TempAnn24} - 2.8X_{PrecLac*TempAnn24}$
Panhandle	36	$\ln(\lambda_t) = 0.09 - 0.01X_{N[t-1]} + 0.14X_{SPI12EG} + 0.08X_{TempLac}$

^aNumber of years modeled.

^bCovariates used in population projection models: $N[t-1]$ = population estimate in previous year (density effect); $SPI03EG$ = Standardized Precipitation Index (SPI) over 3 months for early gestation; $TempLG$ = mean temperature during late gestation; $SPI03MG$ = SPI over 3 months for mid-gestation; $TempMG$ = mean temperature during mid-gestation; $SPI12Lac$ = SPI over 12 months for lactation; $TempAnn12$ = mean temperature over 12 months prior to population survey; $PrecLac$ = total precipitation during lactation; $SPI03Lac$ = SPI over 3 months for lactation; $PrecLG$ = total precipitation during late gestation; $TempAnn24$ = mean temperature over 24 months prior to population survey; $SPI06Lac$ = SPI over 6 months for lactation; $TempEG$ = mean temperature during early gestation; $SPI12EG$ = SPI over 12 months for early gestation; $TempLac$ = mean temperature during lactation.

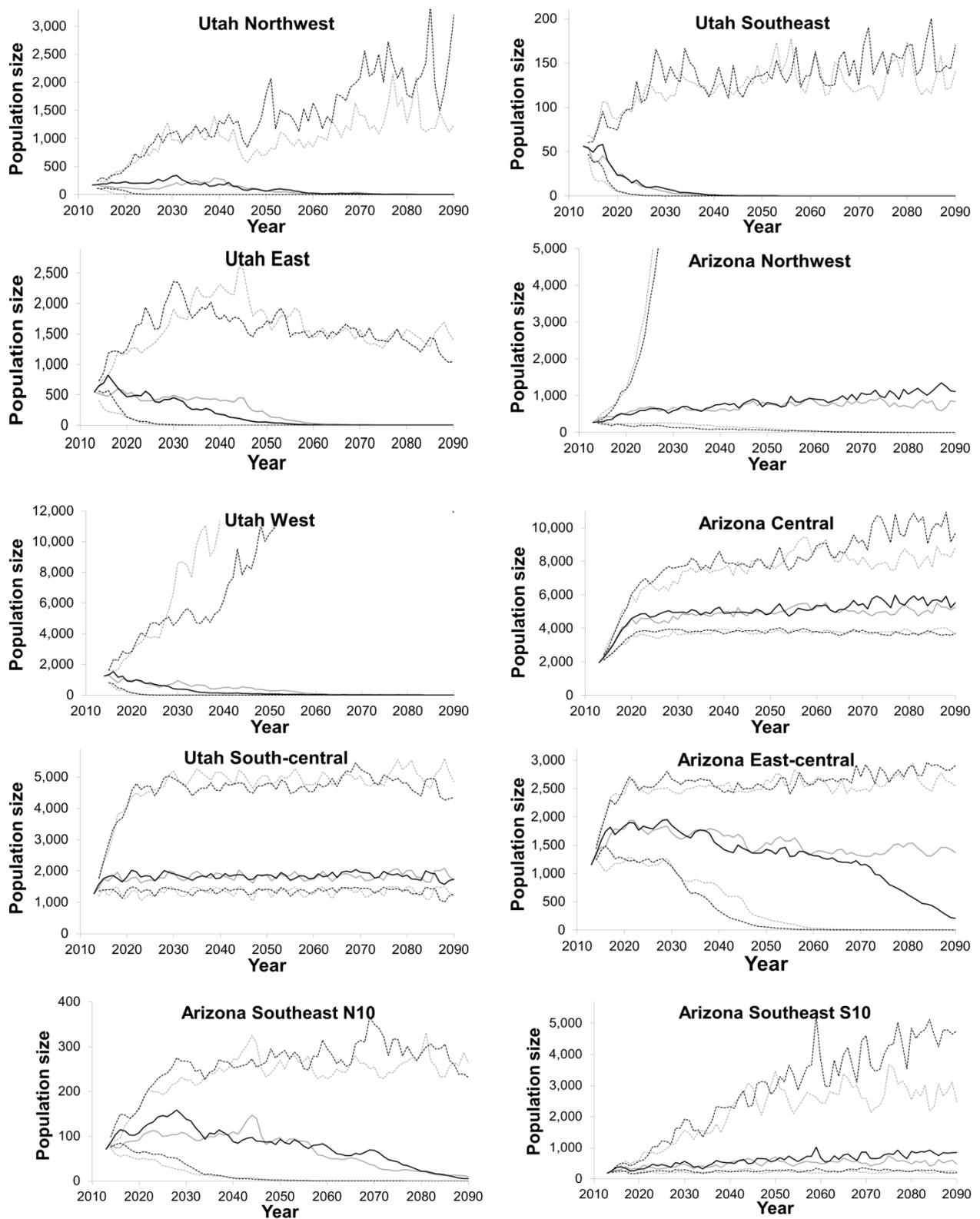


Figure 2.1. Pronghorn population projections to 2090 under high (RCP8.5; black lines) and lower (RCP4.5; grey lines) atmospheric CO₂ concentration scenarios for 16 pronghorn populations in the southwestern United States. Solid lines represent estimated median populations and dashed lines represent 2.5% and 97.5% credible intervals. See Table 2.2 for regression equations used in these models to project populations.

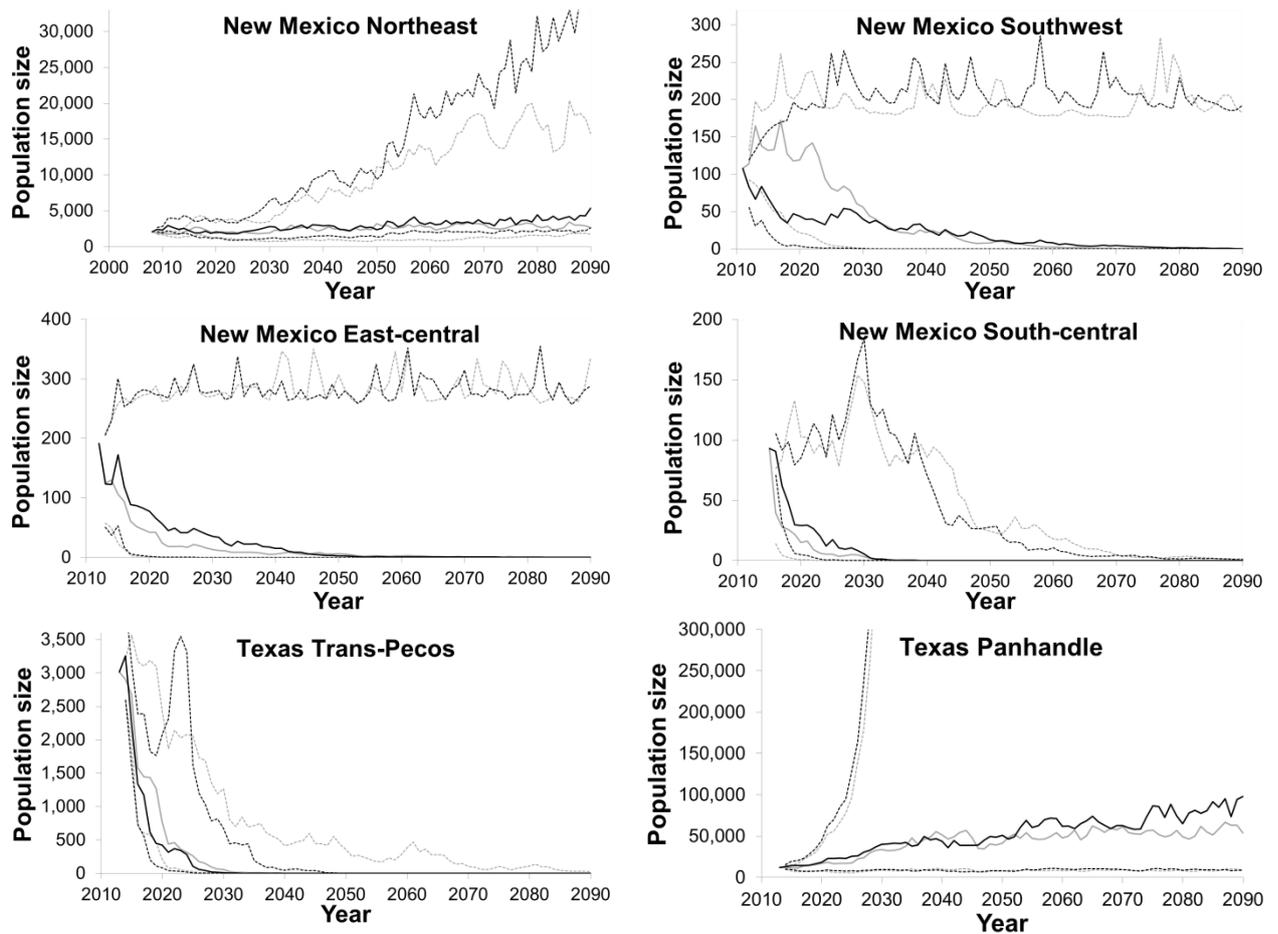


Figure 2.1 (continued). Pronghorn population projections to 2090 under high (RCP8.5; black lines) and lower (RCP4.5; grey lines) atmospheric CO₂ concentration scenarios for 16 pronghorn populations in the southwestern United States. Solid lines represent estimated median populations and dashed lines represent 2.5% and 97.5% credible intervals. See Table 2.2 for regression equations used in these models to project populations.

Conclusions and Recommendations:

Managing animal populations under the uncertainty of changing climates poses a daunting challenge to wildlife managers (Prato 2009). In pronghorn, the development of management plans spanning multiple populations and differing habitat conditions have mostly used inferences from single populations. Yet evidence from our work and other studies suggests that significant variation exists among the factors explaining the demography of local populations (Hoffman et al. 2010).

By examining 18 pronghorn populations across the Southwest, and using region-specific downscaled climate data aligned with the actual pronghorn ranges examined, we offered a high resolution and extensive overview that portrays and explains pronghorn population trajectories across this region. We found that while precipitation metrics formed the best predictors of population growth, temperature had the greatest influence on the future trajectory of the populations. Half of the populations were projected to decline and become extirpated around mid-century. The climatic effects we measured are regional in scale, and experienced by the other pronghorn populations excluded from this modeling exercise. It seems reasonable then, that the relationships we uncovered between climate and λ would also apply to these populations. Hence, for many pronghorn populations, any management actions applied to avert population declines may be unsustainable over time, as climatic shifts and the habitat changes wrought counteract human intervention. Indeed, for some of the increasing populations (e.g., in Utah, New Mexico, and Texas), growth appears to result more from unintended actions like supplemental feeding from agricultural fields that are generally considered economically costly and problematic.

Regardless, the climatic conditions underpinning the pronghorn populations in the southwestern United States are shifting beneath them, making the ecosystems increasingly inhospitable to pronghorn persistence. Alternative management actions to enhance pronghorn habitat, such as prescribed burning and rotational livestock grazing, combined with translocations, may serve to delay pronghorn declines. However, increasingly, managers will be attempting to mitigate long-term and region-wide ecosystem changes that will be difficult, and economically challenging to forestall. Presently, there appear to be few pronghorn populations in the southwest that will persist in a natural state (i.e. lacking management intervention).

Species that are most vulnerable to extinction are those with restricted ranges, fragmented distributions, small populations, and/or those suffering population declines or habitat loss (Price et al. 2000). Such criteria describe most of the pronghorn populations in the southwestern United States examined by this study. These populations already exist in peril, at risk of local extinction even without the complexities begot from climate change. We intend for the information provided by this study, describing the effects of climate change on southwestern pronghorn, to inform decision-making for conserving and managing pronghorn in North America and to trigger future efforts for other ungulates inhabiting arid regions and confronting similar circumstances elsewhere.

SUBPROJECT 3.

Drought Effects on Habitat and Stream Connectivity of Rio Grande Cutthroat Trout Conservation Populations.

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Purpose and Objectives:

Rio Grande cutthroat trout (*Oncorhynchus clarkii virginalis*, RGCT), the southernmost subspecies of cutthroat trout, is endemic to the Rio Grande, Canadian, and Pecos River basins of Colorado and New Mexico. The subspecies is currently restricted to 11% of its historic range with most populations occupying isolated high elevation headwater streams (Alves et al. 2008). In 2007, the USFWS (Service) entered into a status review of RGCT and found that the subspecies warranted listing as an endangered or threatened under the Endangered Species Act of 1973; however, listing was precluded by higher priority listing actions (U.S. Office of the Registrar 2008). To help resolve some of the uncertainty related to climate vulnerability of existing populations of RGCT, we initiated a series of research and monitoring projects in 2010 to characterize the impact that climate change was having throughout the subspecies current range. In 2011, the Southwest experienced one of the worst droughts on record lasting well over 16 months (<http://www.droughtmonitor.unl.edu/archive.html>).

Research from 2010 through 2013, demonstrated that low winter snowpack and reduced seasonal precipitation across the subspecies' range resulted in baseflows well below 1.0 cubic feet per second (cfs), with extended reaches of streams becoming dry (Zeigler and Todd, personal observations). The overall findings of the research highlighted that average annual air temperature had increased by 0.29°C per decade and that the timing of onset of snowmelt had shifted 10.6 days earlier in the year throughout the current and historical range of RGCT (2.3 d/decade; Zeigler et al. 2012). In addition, the research also documented a 5.3% decrease in April 1 snow water equivalent that was followed by lower summer base flows, and that the majority of the cutthroat populations in New Mexico and Colorado were experiencing flows less than 1.0 cubic feet per second (cfs), thereby increasing the risk to the effects of a drying and intermittency from a warming climate (Zeigler et al. 2013).

Organization and Approach:

Through the assistance of the U.S. Geological Survey National Climate Change and Wildlife Science Center, a monitoring program was initiated to characterize stream temperature and summer base flow of a subset of RGCT populations. Although the majority of populations occupy thermally stable habitat, a large portion of these populations occupy small streams with extremely low summer baseflow. As a result of this widespread stream intermittency, a Stream Temperature Intermittency and Conductivity logger (STIC) was developed to document the duration of stream intermittency in a subset of RGCT populations and a methods paper resulted (*see* Chapin et al. 2014). The STIC is a modified HOBO Pendant™ data logger (ONSET, Inc) that enables simultaneous collection of high-resolution water temperature and electrical resistance with the same instrument during extended deployments. Earlier field trials demonstrated when properly deployed, this single, multi-functional sensor can yield valuable data on the timing and quality (i.e., temperature) of stream systems.

In the spring of 2013, we selected 29 RGCT populations based on stream size (less than 3 m width), baseflows less than 0.5 cfs, and visual confirmation of intermittency (Zeigler and Todd, personal observations). Within these populations, we deployed 54 loggers from May 2013 to September 2014 (Table 3.1). We placed multiple STICs throughout individual streams to obtain potential longitudinal differences if streams dried. The STICs monitored water flow and temperature in shallow flow sensitive habitat (i.e., riffles) to document the moment and duration of

flow cessation. Fish populations can persist in intermittent streams if there is adequate still-water habitat remaining (i.e., pools or deep water). However, extended durations of hydrological isolation of disconnected still-water can be detrimental to the aquatic community through the reduction in available habitat, loss of connectivity, as well as the eventual degradation of water quality and food resources within the still-water pool.

Project Results, Analysis and Findings:

Performance of the STICs

The functionality of the STIC technology was deemed acceptable in assessing site-specific stream intermittency. As an example, the STIC in Figure 3.1 was deployed at the bed surface within the thalweg (main channel) of a RGCT stream (Sangre de Cristo Creek near Fort Garland, Colorado) observed to go dry seasonally. The data in Figure 3.1 demonstrates that while the STIC sensor was deployed within a flowing stream (approximately 6/23/13), the stream began to dry later that week. The STIC response dropped from ~60 to 0 reflecting the stream was dry by the end of that week on approximately 6/29/13.

Assessment of Intermittency within Rio Grande Cutthroat Trout Streams

Throughout the 16-month study, precipitation was at or above normal throughout the Southwest (Palmer Drought Index: accessioned 9/15/2015). As such, the instream flow conditions documented by the STICs likely do not represent the low flows that would be anticipated during drought conditions. However, in spite of the heavy rains and elevated baseflow conditions throughout the majority of the monitored streams, two streams displayed evidence of intermittent conditions. For example, within Cat Creek (Table 3.1), the longitudinal deployment of three STICs indicated the lower drainage remained wet while the uppermost drainage displayed intermittent flow. Similarly, in the North Fork of Carnero Creek (Table 3.1), the uppermost site indicated dry conditions for much of the summer.

Stream Habitat and Population Level Effects of Drought

In fall of 2014, several streams were assessed for the presence and absence of still-water habitat by measuring pool depth and frequency. Due to the low prevalence of stream intermittency, field observations are anecdotal but reveal that stream intermittency (in the absence of significant still-water refugia or pools) may influence re-establishment of a fishery. For example, in the uppermost segment of Cat Creek, where STIC data indicates highly intermittent conditions, no fish were captured during an electrofishing survey a few months after the logger recorded intermittency. In contrast, at an adjacent STIC downstream that recorded persistent flow throughout the summer, RGCT were captured throughout pools. At the lowest STIC site, in which water temperature data and field observations indicated intermittency, no fish were collected. While anecdotal, it appears that continued stream flow may allow RGCT to persist in contrast to areas above and below intermittent reaches that resulted in no fish migration or repopulation.

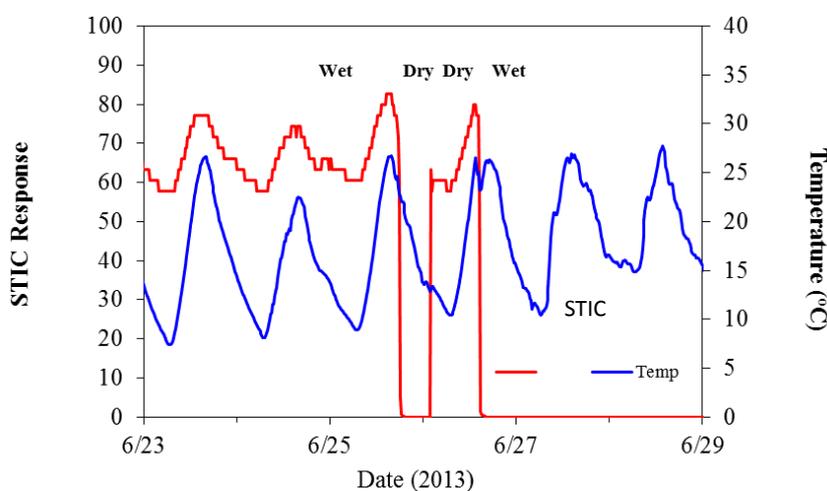


Figure 3.1. Stream temperature (°C) and wet/dry status (STIC Response) within a riffle habitat of Sangre de Cristo Creek (near Fort Garland, Colorado).

Table 3.1. Streams throughout New Mexico and Colorado with populations of Rio Grande cutthroat trout streams where 54 Stream Temperature, Intermittency and Conductivity logger (STICs) were deployed August 2013 and retrieved September 2014.

Stream Name	Population ID	Basin	Number of STICs	Evidence of Intermittency
McCrystal Creek	11080002cp001	Cimarron	3	N
Middle Ponil Creek	11080002cp003	Cimarron	1	N
E. F. Luna Creek	11080004cp001	Mora	2	N
Cat Creek	13010002cp002	Alamosa-Trinchera	3	Y
Jim Creek	13010002cp005	Alamosa-Trinchera	1	N
Torcido Creek	13010002cp009	Alamosa-Trinchera	1	N
Torcido Creek	13010002cp010	Alamosa-Trinchera	1	N
Deep Creek	13010002cp012	Alamosa-Trinchera	1	N
West Indian Creek	13010002cp015	Alamosa-Trinchera	1	N
Wagon Creek	13010002cp016	Alamosa-Trinchera	1	N
Sangre de Cristo Crk	13010002cp016	Alamosa-Trinchera	5	Y
East Pass Creek	13010004cp002	Saguache	1	N
Jacks Creek	13010004cp003	Saguache	1	N
Cross Creek	13010004cp003	Saguache	1	N
M. F. Carnero Creek	13010004cp007	Saguache	4	N
N. F. Carnero Creek	13010004cp008	Saguache	4	N
Prong Creek	13010004cp011	Saguache	1	N
Cave Creek	13010004cp012	Saguache	1	N
Tio Grande	13010005cp002	Conejos	1	N
Tanques Creek	13010005cp003	Conejos	1	N
Rio Nutrias	13010005cp004	Conejos	2	N
Powderhouse Creek	13020101cp004	Upper Rio Grande	3	N
La Queva Creek	13020101cp005	Upper Rio Grande	1	N
Grassy Creek	13020101cp006	Upper Rio Grande	1	N
Comanche Creek	13020101cp006	Upper Rio Grande	2	N
Vidal Creek	13020101cp006	Upper Rio Grande	1	N
Rito de las Palomas	13020202cp002	Jemez	3	N
Rito de los Pinos	13020204cp002	Rio Puerco	1	N
Osha Canyon	13020101cp024	Upper Rio Grande	3	N
Pinelodge Creek	13060005cp001	Arroyo del Macho	2	N

Conclusions and Recommendations:

Drought has affected RGCT, however, empirical data in which individuals and populations are affected by stream intermittency associated with drought remains unclear. Japhet et al. (2007) and Patten et al. (2007) documented several populations were extirpated by drought in 2002. The extent of the negative impact of the 2002 drought on the majority of RGCT populations, however, was unknown because only a small subset of the populations were visited to evaluate the impact following the 2002 drought. In light of the likelihood of increasing drought conditions in the Southwest, the need to identify the extent and duration of stream intermittency associated with drought is required to assess the long term persistence. This project attempted to examine the duration and extent of stream intermittency throughout RGCT populations identified at risk of drying (i.e., low flow <1.0 cfs; small wetted width <3 m) by authors of this report.

During the study period, a recent 12-month finding to list the RGCT was deemed unwarranted because the subspecies was not in immediate danger of extinction, however, it listed drought from a warming climate as a major threat to future persistence (U.S. Federal Register

2014). Although long term forecasting (population viability models) indicated that a large portion of the populations would persist through to 2023 and 2080 (USFWS 2014), the models did not include data describing the effects of drought and stream intermittency on vital rates (growth, recruitment, survival).

To summarize, while few RGCT populations experienced stream intermittency because of the serendipitous wet cycle from 2013 to 2014, the STICs provided water temperature data deemed comparable to the ProV2 temperature loggers. Thus, STICs offer a low-cost and long-duration (battery can be replaced) solution that not only provides unambiguous and continuous water temperature, but also provides continuous stream intermittency information of stream flow. An important caveat of this research is that while RGCT populations may not experience stream intermittency during average to above average precipitation years, very little is known of their vulnerability during below average precipitation years. Additional research is needed that describes the effects stream intermittency may have on vital rates of RGCT populations if they are to persist into the future.

SUBPROJECT 4

Effects of Climate on Scaled Quail Reproduction and Survival.

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Purpose and Objectives: Over the past half century scaled quail have exhibited long-term declines in both range and population size (Campbell 1968, Church et al 1993, Saiwana et al 1998, Peterson and Perez 2000, Guthery et al 2004). The factors thought to be contributing to this decline include shrub encroachment on grasslands, habitat loss/degradation, and long-term changes in temperature and precipitation across their range (Campbell 1968, McNew et al 2014). A long-term trend in warmer, drier conditions and reduced monsoonal rainfall across their range is one factor hypothesized as a primary cause of this decline, through reduced nest success due to temperature and humidity levels above a critical threshold for egg and chick survival. While habitat loss cannot be discounted as a possible driver, population declines in areas managed specifically for scaled quail in western Texas have been observed across the same time frame indicating that these reductions are independent of habitat-related factors (Rollins 2000). Coupled with climate models forecasting shifts in the arrival of summer monsoon rains away from the critical reproductive periods of June and July (Cook and Seager 2013), the long-term forecast for scaled quail response to decreased rainfall and higher temperatures is bleak. Scaled quail are considered to be a key indicator species of the health of the habitats they occupy across the southwest and are frequently used to assess the success of restoration projects undertaken by federal and state agencies (Coffman 2012). Our objective was to determine the effect of temperature, humidity, precipitation, and habitat characteristics on the survival of nest, brood, and adult scaled quail.

Organization and Approach:

We captured scaled quail between February and May in 2014 and 2015 using standard walk-in funnel traps baited with chicken scratch. All captured quail were classified by sex and age, and fitted with aluminum leg bands with a unique number and necklace-style VHF transmitters. We tracked collared quail 1-3 times per week and monitored them for survival from their date of capture until early November each year.

Adult Survival

Seasonal survival of adult scaled quail was estimated using the known-fate model in program MARK (White and Burnham 1999). Encounter histories for adult survival were coded using weekly time periods with a total of 36 encounter occasions. We included group metrics of sex and season (year). The group metric of age was excluded due to small sample size and uneven distribution. A ΔAIC_c value < 2.0 and/or combined AIC_c weights was used to determine the most parsimonious model(s).

Nest Survival

Hens relocated on multiple occasions in the same area were considered to be nesting and were flushed off the nest in order to obtain clutch size. Once located, the nest was marked by GPS using Universal Transverse Mercator, a nest identification number was assigned, and clutch counts and nesting vegetation characteristics were measured. All nests were monitored until termination (i.e., hatched, abandoned, or depredated). A nest was considered successful if ≥ 1 egg hatched.

Once nests hatched, were abandoned, or were depredated, we collect data on the habitat characteristics at the nest site and the surrounding area. Two perpendicular, 8-m transects were centered on the nest bowl in north-south and east-west orientations. The dominant plant at the nest bowl was identified and percent canopy cover was estimated for shrubs, forbs, grasses, and bare ground using a 60 x 60 cm Daubenmire frame (Daubenmire 1959) at the nest bowl. The distance and height of the nearest shrub, forb, and grass was measured from the center of the nest bowl. Visual obstruction readings (VOR) were recorded using a Robel pole at the nest bowl in each cardinal direction from a distance of 4 m; sighting height was 1 m (Robel et al. 1970).

Daily survival was estimated using the nest survival model in program MARK (White and Burnham 1999). We included the group metric of season and covariates of precipitation, weekly minimum temperature, weekly maximum temperature, VOR, grass density, percent bare ground, shrub density, and shrub height. Temperature and precipitation data were obtained from the PRISM Climate Group (Oregon State University, Corvallis, Oregon).

Brood Survival

Hens with successful nests were tracked via homing in order to locate surviving broods. When a hen was located, she was observed for brooding behavior and, if possible, to record the number of chicks. Each hen was tracked via homing until no evidence of a brood remained or the hen and brood joined with a covey and broods could no longer be distinguished. All brood locations were recorded using a handheld GPS unit.

Vegetation and cover characteristics of locations where broods were observed were surveyed. The brood site was defined as the exact location of the chicks, and the brood area as incorporating the brood site and all measurements within four meters of the brood location. Two perpendicular, eight meter transects were centered on the brood site location in north-south and east-west orientations. Percent canopy cover was estimated for shrubs, forbs, grasses, and bare ground using a 60 x 60 cm Daubenmire frame (Daubenmire 1959) at the brood site and at four-meter intervals along each transect. A Robel pole was used to estimate visual obstruction readings (VOR) from 4 m away from the brood site at a sighting height of 1 m. A point-centered-quarter survey was performed at brood locations and at four-meters from the brood site in all four cardinal directions. Each brood location was paired with a random point located along a randomly selected compass bearing between a randomly selected distance between 30 and 500 m from the brood location; similar vegetation sampling was repeated at each random location.

Weekly survival of broods was estimated using the known fate model in program MARK (White and Burnham, 1999). We included the group metric of season (year) and covariates of precipitation, weekly minimum temperature, and weekly maximum temperature.

Project Results, Analysis and Findings:

A total of 118 birds were captured in 2014 and 2015 (51 males, 65 females, and 2 of unknown sex). A majority of this sample were juvenile birds, 101, with four individual birds from the 2014 sample being recaptured as adults in the 2015 sample.

Adult Survival

All 118 birds captured and tracked were included in the adult survival analysis. In total, 24 mortalities occurred in 2014 ($n = 10$) and 2015 ($n = 14$). Mortalities caused by avian predators ($n = 15$), mammalian predators ($n = 4$), humans ($n = 1$), and other ($n = 4$).

Model selection of 4 *a priori* models were used to assess breeding season survival of the 118 scaled quail. All four models were plausible based on their AIC_c values and weights (Table 4.1). These top models included the variables year, sex, year×sex, and a constant model, and parameter estimates were model averaged to account for model selection uncertainty (Table 4.2). The model averaged results estimated derived seasonal survival of male scaled quail to be 34.7% (SE = 0.11) in 2014 and 44.4% (SE = 0.09) in 2015. Results for female scaled quail were 36.6% (SE = 0.09) in 2014 and 44.1% (SE = 0.09) in 2015.

Nest Survival

A total of 58 nests were located during the 2014 ($n = 19$) and 2015 ($n = 38$) breeding seasons. Of the 2014 nests, 1 failed due to hen mortality, 3 were abandoned, and 1 was depredated by an unknown predator. Nest mortality events in the 2015 field season included 16 depredations and 5 hen mortalities.

Model selection of 16 *a priori* models was used to assess survival of scaled quail nests (Table 4.3). These models included average weekly minimum temperature, average weekly

maximum temperature, and average weekly precipitation. Vegetation variables included percent bare ground, visual obstruction, shrub density, shrub height, and grass density. Eight of the 16 *a priori* models had some support, and therefore were model-averaged to account for model selection uncertainty (Table 4.3). These top eight models included average maximum and minimum temperature, percent bare ground, and grass density. Model averaged estimate of the daily nest survival was 97.3% (SE = 0.007; 95% CI 0.95 – 0.99) with average nest survival estimated to be 39.4%. Nest survival model averaging suggested positive relationships between survival and maximum nest temperature and density of grass, and had a negative relationship with increasing minimum temperature and percent of bare ground.

Table 4.1. Model selection output from 4 *a priori* models used to assess the breeding season survival of adult scaled quail in the West Potrillo Mountains, New Mexico, 2014-2015.

Model	AIC _c	ΔAIC _c	AIC _c Weight	Model Likelihood	K	Deviance
Global	320.90	0.00	0.39	1.00	1.00	115.06
Year	320.97	0.07	0.38	0.96	2.00	113.13
Sex	322.90	2.01	0.14	0.37	2.00	115.06
Sex×Year	323.80	2.90	0.09	0.23	4.00	111.94

Year – Survival is a function of year (2014, 2015)

Sex – Survival is a function of sex (male, female)

Table 4.2. Model-averaged breeding season survival estimates for adult scaled quail in the West Potrillo Mountains, New Mexico, 2014-2015.

Year	Sex	Estimate	SE	95% CI	
				Lower	Upper
2014	Male	0.35	0.11	0.16	0.59
2014	Female	0.37	0.09	0.21	0.56
2015	Male	0.44	0.09	0.28	0.63
2015	Female	0.44	0.09	0.28	0.61

Table 4.3. Model selection results assessing scaled quail nest survival in relation to climatic and vegetation characteristics in the West Potrillo Mountains, New Mexico, 2014-2015.

Model	AIC _c	ΔAIC _c	AIC _c Weight	Model Likelihood	K	Deviance
Maximum Temperature	83.15	0	0.35	1	2	79.12
Minimum Temperature + Maximum Temperature	84.31	1.17	0.2	0.56	3	78.26
% Bare Ground + Maximum Temperature	84.82	1.67	0.15	0.43	3	78.76
% Bare Ground + Maximum Temperature + Minimum Temperature	86.27	3.12	0.07	0.21	4	78.18
% Bare Ground + Minimum Temperature	87.54	4.39	0.04	0.11	3	81.49
Grass Density	87.76	4.62	0.03	0.1	2	83.74
Global Model	87.9	4.75	0.03	0.09	1	85.89
Minimum Temperature	87.9	4.75	0.03	0.09	1	85.89
VOR ^a	89.12	5.97	0.02	0.05	2	85.09
Shrub Density	89.64	6.49	0.01	0.04	2	85.61
Shrub Height	89.78	6.63	0.01	0.04	2	85.75
% Bare Ground + Grass Density	89.78	6.64	0.01	0.04	3	83.73
Precipitation	89.9	6.76	0.01	0.03	2	85.88
% Bare Ground	89.91	6.76	0.01	0.03	2	85.88
% Bare Ground + VOR	91.11	7.97	0	0.02	3	85.06
% Bare Ground + Precipitation	91.93	8.78	0	0.01	3	85.87

^aVOR – Survival is a function of average visual obstruction reading

Brood Survival

Model selection of 6 *a priori* models was used to estimate the survival of scaled quail broods (Table 4.4). These models included climate variables of average weekly minimum temperature, average weekly maximum temperature, and average weekly precipitation. Due to model uncertainty, these 6 *a priori* models were model averaged. Weekly survival of scaled quail broods was estimated at 86.7% (SE = 0.03, 95% CI 0.79 – 0.92). Overall brood success was estimated at 49.0%. Brood survival was inversely related to maximum temperature, minimum temperature, and amount of precipitation.

Table 4.4. Model selection results from 6 *a priori* models assessing brood survival of scaled quail in the West Potrillo Mountains, New Mexico, 2014-2015.

Model	AIC _c	ΔAIC _c	AIC _c Weight	Model Likelihood	K	Deviance
Minimum Temperature	99.85	0	0.38	1	2	95.76
Global Model	101.15	1.29	0.2	0.52	1	99.12
Precipitation + Minimum Temperature	101.45	1.59	0.17	0.45	3	95.25
Precipitation	102.07	2.21	0.13	0.33	2	97.97
Maximum Temperature	103.09	3.23	0.08	0.2	2	98.99
Precipitation + Maximum Temperature	104.04	4.19	0.05	0.12	3	97.84

Conclusions and Recommendations:

In 2014 and 2015, males and females did not show a significant difference in survival between sexes. However, survival of adult scaled quail did differ between 2014 and 2015; male and female survival were estimated at 34.6% and 36.5% respectively in 2014, while male and female survival in 2015 was approximately 44%. These estimates are in line with one previous study on scaled quail survival (Pleasant et al. 2006), but were much lower survival estimates reported in other previous studies (Lerich et al. 2002, Rollins 2000, Buntyn 2004).

Interestingly, maximum temperature was a strong predictor of nest survival during the 2014 and 2015 breeding seasons. Specifically, the variables in the model represented the extremes of temperature our nests experienced during the breeding season. Although scaled quail hens show a strong ability to buffer ambient temperature shifts, as evidenced by ibutton data from nests (K. Zummo unpubl. data), extremely high temperatures may cause higher nest failure especially when nests are laid in areas with high bare ground and low grass cover (Guttery et al 2013)

Indirectly related to the effects of temperature, ground cover, such as the percentage of bare ground or density of grass surrounding a nest were also found to influence nest survival. Thus it follows that nests with less bare ground and increasing densities of grass around nests appear to protect them to some degree from climatic extremes such as the high temperatures we observed during our study (Pleasant et al 2006).

Similar to nest survival, minimum temperature and precipitation were strong predictors of scaled quail brood survival. Extreme temperatures, especially cold, coupled with precipitation events may diminish a chick’s ability to regulate body temperature (Guttery et al 2013). It was interesting that in our study, high temperatures influenced nest survival and low temperatures influenced brood survival.

Outreach and Products:

We have developed or plan to develop several products from this project. There have been four publications as a result from this project and one manuscript is in preparation.

- Cain, J.W., III, J.V. Gedir, P.R. Krausman, and J.R. Morgart. In prep. Shifting habitat selection by desert bighorn sheep to cope with extreme climatic variability. To be submitted to Ecology.
- Cain, J.W., III, J.V. Gedir, P.R. Krausman, J.P. Marshal, J.D. Allen, G.C. Duff, B.D. Jansen and J.R. Morgart. 2017. Extreme precipitation variability, forage quality and large herbivore diet selection in arid environments. *Oikos* 126:1459–1471.
- Chapmin, T.P., et al. 2014. Robust, low-cost data loggers for stream temperature, flow intermittency and relative conductivity monitoring. *Water Resource Research* 50:6542-6548.
- Gedir, J.V., J.W. Cain III, G. Harris, and T.T. Turnbull. 2015. Effects of climate change on long-term population growth of pronghorn in an arid environment. *Ecosphere* 6: art 189.
- Gedir, J.V., J.W. Cain III, P.R. Krausman, J.D. Allen, G.C. Duff, and J.R. Morgart. 2016. Potential foraging decisions by a desert ungulate to balance water and nutrient intake in a water-stressed environment. *PLoS ONE* 11(2):e0148795.doi:10.1371/journal.pone.0148795
- Todd, A.S., B.N. McGee, M.P. Zeigler, and C.A. Caldwell. 2016. Water and air temperature throughout the range of Rio Grande cutthroat trout in Colorado and New Mexico; 2010-2015: U.S. Geological Survey data release: ScienceBase: <http://dx.doi.org/10.5066/F73R0QZC>.

We have presented our work at several professional society meetings and webinars:

- Cain, J.W., III, and J.V. Gedir. 2018. Foraging decisions and populations dynamics: ungulates under a warmer climate. National Climate Change and Wildlife Science Center webinar. 22 February 2018
- Gedir, J.V., J.W. Cain III, P.R. Krausman, J.D. Allen, G.C. Duff, and J.R. Morgart. 2017. Potential foraging decisions by desert bighorn sheep to balance water and nutrient intake. 2017 Biennial Meeting of the Desert Bighorn Council, St. George, Utah, USA.
- Gedir, J.V., J.W. Cain III, P.R. Krausman, J.D. Allen, G.C. Duff, and J.R. Morgart. 2016. Potential foraging decisions by desert bighorn sheep to balance water and nutrient intake in a water-stressed environment. 23rd Annual Conference of the Wildlife Society, Raleigh, North Carolina, USA.
- Gedir, J.V., J.W. Cain III, G. Harris, and T.T. Turnbull. 2016. Predicting long-term pronghorn population dynamics in the Southwest in response to climate change. 27th Biennial Western States and Provinces Pronghorn Workshop, Anaconda, Montana, USA.
- Gedir, J.V., J.W. Cain III, G. Harris, and T.T. Turnbull. 2015. Predicting long-term population dynamics of an ungulate in an arid environment in response to climate change. 5th International Wildlife Management Congress, Sapporo, Japan.
- Cain, J.W., III, J. V. Gedir, P.R. Krausman, J.D. Allen, and G.C. Duff. 2015. Extreme precipitation variability, forage quality and large herbivore diet selection in arid environments. 5th International Wildlife Management Congress, Sapporo, Japan.
- Gedir, J.V., J.W. Cain III, G. Harris, and T.T. Turnbull. 2015. Predicting long-term pronghorn population dynamics in the southwest U.S.A. in response to climate change. 48th Joint Annual Meeting of the Arizona/New Mexico Chapters of The Wildlife Society, Las Cruces, New Mexico, USA.
- Cain, J.W., III, J. V. Gedir, P.R. Krausman, J.D. Allen, and G.C. Duff. 2014. Forage nutritional content and diet selection by desert bighorn sheep across widely varying climatic conditions. 21st Annual Conference of The Wildlife Society, Pittsburgh, Pennsylvania, USA.
- Caldwell, C.A., M.P. Zeigler, and A. Todd. 2013. Utility of stream temperature and hydrology: Implications of climate related vulnerabilities and persistence of Rio Grande cutthroat trout. New Mexico Academy of Sciences/New Mexico EPSCoR Annual Meeting. Albuquerque, New Mexico.

Zeigler, M.P., A.S. Todd, and C.A. Caldwell. 2013. Threat of climate change to the persistence of Rio Grande cutthroat trout. Rio Grande Cutthroat Trout Range-wide Meeting. Alamosa, Colorado.

Zeigler, M.P., C.A. Caldwell, and A.S. Todd. 2013. Utility of stream temperature and hydrology measurements in evaluating climate related vulnerabilities of Rio Grande cutthroat trout populations, with applicability to other native southwestern salmonids. 46th Joint Annual Meeting Arizona and New Mexico Chapters of the Wildlife Society and Arizona/New Mexico Chapter of the American Fisheries Society. Albuquerque, New Mexico.

Zeigler, M.P., C.A. Caldwell, and A.S. Todd. 2013. Utility of stream temperature and hydrology measurements in evaluating climate related vulnerabilities of Rio Grande cutthroat trout populations. 4th Annual Native Trout Conference. Phoenix, Arizona.

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Appendix 1

Table A1. *A priori* models for predicting forage selection by adult female desert bighorn sheep in Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), as a function of forage nitrogen content (N), moisture content (Moist), and dry matter digestibility (DMD), and Precipitation (drought, average, and wet conditions).

Model	Model Structure
1	Null (intercept only)
2	N + Precipitation
3	Moist + Precipitation
4	DMD + Precipitation
5	Moist + Moist ² + Precipitation
6	N + Moist + Moist ² + Precipitation
7	N + Moist + Precipitation
8	N + DMD + Precipitation
9	DMD + Moist + Precipitation
10	DMD + N + Moist + Precipitation
11	N + Precipitation + N × Precipitation
12	Moist + Precipitation + Moist × Precipitation
13	Moist + Moist ² + Precipitation + Moist × Precipitation + Moist ² × Precipitation
14	DMD + Precipitation + DMD × Precipitation
15	N + DMD + Precipitation + N × Precipitation + DMD × Precipitation
16	N + DMD + Moist + Precipitation + N × Precipitation + DMD × Precipitation + Moist × Precipitation
17	DMD + Moist + Precipitation + Moist × Precipitation + DMD × Precipitation
18	N + Moist + Precipitation + N × Precipitation + Moist × Precipitation

Table A2. Mean percent forage availability and diet contribution (\pm SE) for adult female desert bighorn sheep by forage type, season, and precipitation period on the Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005). – = not available; during the study wet conditions did not occur during any summer seasons.

Season ^a	Forage	Drought				Average				Wet			
		Forage availability		Diet contribution		Forage availability		Diet contribution		Forage availability		Diet contribution	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ES	forb	0.6	0.3	1.1	0.18	6.6	1.6	8.0	0.52	–	–	–	–
	grass	1.5	1.0	6.1	0.50	2.2	0.5	1.1	0.22	–	–	–	–
	shrub	71.8	3.5	25.9	0.85	63.3	3.0	27.1	0.67	–	–	–	–
	succulent	1.6	0.8	19.9	0.71	2.7	0.9	13.3	0.66	–	–	–	–
	tree	24.5	3.3	44.3	0.93	25.2	2.6	33.3	0.90	–	–	–	–
LS	forb	1.9	0.6	2.9	0.67	4.2	0.9	7.2	0.67	–	–	–	–
	grass	2.4	0.8	7.9	0.47	1.1	0.5	4.5	0.38	–	–	–	–
	shrub	59.9	3.5	12.2	0.68	71.7	3.6	12.2	0.62	–	–	–	–
	succulent	2.4	0.6	20.2	0.79	1.6	0.5	18.4	0.61	–	–	–	–
	tree	33.3	3.6	41.7	1.15	21.2	3.4	39.9	1.00	–	–	–	–
A	forb	8.9	2.7	6.3	0.64	3.0	1.1	3.9	0.51	4.9	2.2	17.1	1.50
	grass	1.5	0.6	1.6	0.16	2.2	0.9	1.7	0.41	1.2	0.6	2.5	1.32
	shrub	58.2	4.9	27.6	1.07	58.6	5.7	27.4	1.29	58.2	4.8	16.9	3.35
	succulent	1.5	0.5	16.5	0.78	1.2	0.7	16.3	1.04	4.2	1.8	9.5	3.15
	tree	29.9	5.5	40.8	0.75	35.1	5.9	42.1	1.30	31.5	5.0	42.1	1.91
W	forb	4.8	1.7	4.6	0.77	6.9	1.9	15.3	1.56	22.3	4.9	13.9	1.02
	grass	1.2	0.6	0.8	0.27	4.5	2.5	2.1	0.54	2.4	0.6	2.4	0.47
	shrub	74.1	5.4	27.3	1.24	58.3	5.9	33.0	1.58	53.2	4.9	28.8	1.38
	succulent	2.9	1.3	18.1	1.82	2.4	1.1	6.5	1.66	1.4	0.5	11.7	0.89
	tree	16.4	5.1	43.2	1.43	27.9	6.6	19.2	3.07	20.4	4.0	19.1	0.93

^aSeason: ES = early summer, LS = late summer, A = autumn, W = winter.

Table A3. Mean percent forage availability (Avail.), diet contribution (Diet), neutral detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (ADL) of forage available to adult female desert bighorn sheep by forage type, season, and precipitation periods in the Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005). – = not available; during the study wet conditions did not occur during any summer seasons.

Season ^a	Forage	Drought					Average					Wet				
		Avail. ^b	Diet ^c	NDF	ADF	ADL	Avail.	Diet	NDF	ADF	ADL	Avail.	Diet	NDF	ADF	ADL
ES	forb	0.6	1.1	55.9	39.3	7.3	6.6	8.0	50.0	45.2	15.6	–	–	–	–	–
	grass	1.5	6.1	65.8	39.8	15.9	2.2	1.1	64.3	42.3	14.9	–	–	–	–	–
	shrub	71.8	25.9	43.7	32.8	14.6	63.3	27.1	41.6	37.7	14.9	–	–	–	–	–
	succulent	1.6	19.9	38.9	18.11	8.79	2.7	13.3	36.2	26.9	10.3	–	–	–	–	–
	tree	24.5	44.3	48.3	35.1	14.9	25.2	33.3	43.7	36.2	15.0	–	–	–	–	–
	mean			50.5	33.0	12.3			47.2	37.7	14.1	–	–	–	–	–
LS	forb	1.9	2.9	55.6	41.1	8.7	4.2	7.2	40.6	46.9	17.0	–	–	–	–	–
	grass	2.4	7.9	63.4	42.3	15.7	1.1	4.5	62.7	39.6	9.4	–	–	–	–	–
	shrub	59.9	12.2	48.3	38.0	14.1	71.7	12.2	36.8	42.2	17.0	–	–	–	–	–
	succulent	2.4	20.2	43.1	28.4	10.1	1.6	18.4	28.5	29.7	12.5	–	–	–	–	–
	tree	33.3	41.7	48.3	35.0	11.7	21.2	39.9	29.4	39.6	14.9	–	–	–	–	–
	mean			51.7	37.0	12.1			39.6	39.6	14.2	–	–	–	–	–
A	forb	8.9	6.3	57.4	44.0	13.6	3.0	3.9	57.4	45.3	13.7	4.9	17.1	53.3	41.5	13.1
	grass	1.5	1.6	61.1	37.4	8.9	2.2	1.7	56.9	42.6	11.9	1.2	2.5	67.6	42.8	15.6
	shrub	58.2	27.6	46.1	35.5	15.4	58.6	27.4	46.5	38.5	14.7	58.2	16.9	46.6	37.1	14.4
	succulent	1.5	16.5	43.2	28.6	16.0	1.2	16.3	42.1	28.9	9.5	4.2	9.5	39.7	25.5	9.4
	tree	29.9	40.8	45.7	33.9	12.0	35.0	42.1	49.4	38.3	13.7	31.5	42.1	50.1	39.1	12.7
	mean			50.7	35.9	13.2			50.5	38.7	12.7			51.5	37.2	13.0
W	forb	4.8	4.6	60.2	44.1	12.7	6.9	15.3	50.9	35.4	9.7	22.3	13.9	32.9	32.0	10.9
	grass	1.2	0.8	63.1	39.4	8.2	4.5	2.1	57.9	36.8	8.2	2.4	2.4	70.3	51.0	38.1
	shrub	74.1	27.3	47.5	43.1	15.6	58.3	33.0	44.4	36.2	12.7	53.2	28.8	34.7	35.9	14.2
	succulent	2.9	18.1	45.2	28.1	11.4	2.4	6.5	38.6	24.6	10.5	1.4	11.7	25.7	30.8	13.7
	tree	16.4	43.2	39.8	38.1	11.9	27.9	19.2	44.6	30.9	10.8	20.4	19.1	28.9	38.9	16.4
	mean			38.6	12.0	20.0			47.3	32.8	10.4			38.5	37.7	18.7

^aSeason: ES = early summer, LS = late summer, A = autumn, W = winter.

^bAvail. = Percent forage availability.

^cDiet = Percent diet contribution.

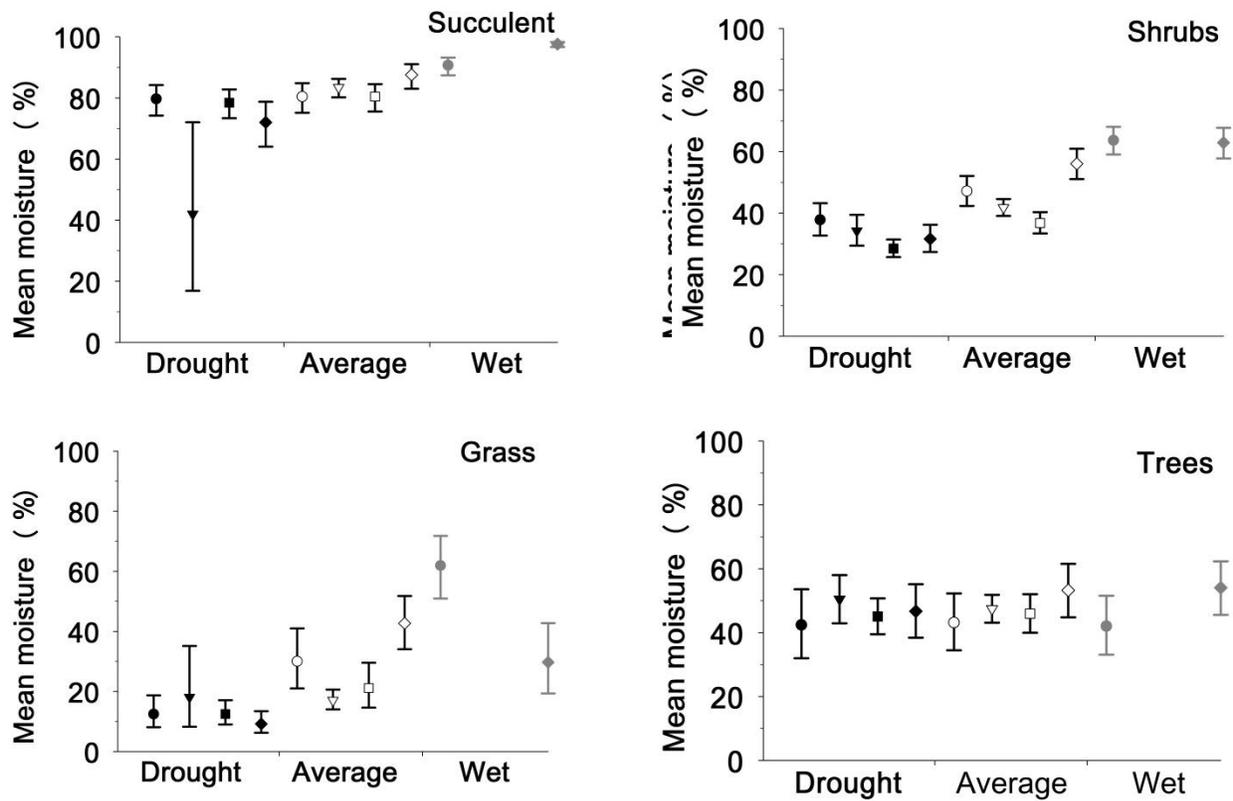


Figure A1. Mean seasonal moisture content of forage available to adult female desert bighorn sheep on the Cabeza Prieta National Wildlife Refuge, Arizona, USA (2002–2005), by plant type during drought (closed black symbols), average (open symbols), and wet (closed grey symbols) conditions. Circles are winter, triangles are early summer, squares are late summer, and diamonds are autumn. Means and error bars are back-transformed estimated marginal means and 95% confidence intervals.

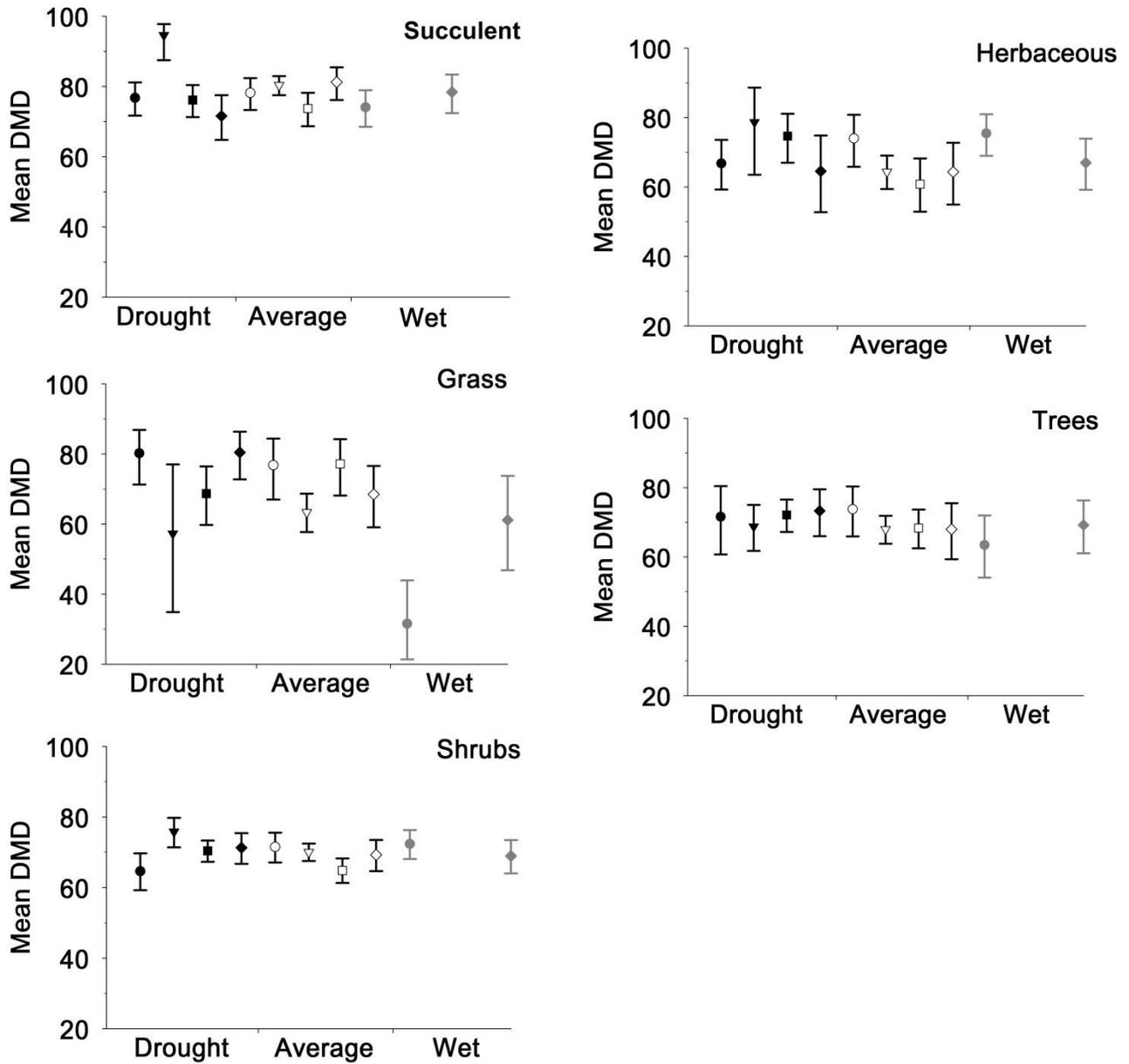


Figure A2. Mean seasonal dry matter digestibility (DMD) of forage available to adult female desert bighorn sheep on the Cabeza Prieta National Wildlife Refuge, Arizona (2002–2005), USA, by plant type during drought (closed black symbols), average (open symbols), and wet (closed grey symbols) conditions. Circles are winter, triangles are early summer, squares are late summer, and diamonds are autumn. Means and error bars are back-transformed estimated marginal means and 95% confidence interval.