Foraging Decisions and Populations Dynamics: Ungulates under a Warmer Climate

John Ossanna: Welcome from US Fish and Wildlife Service's National Conservation Training Center in Shepherdstown, West Virginia. My name is John Ossanna. I'd like to welcome you to our webinar series held in partnership with the US Geological Survey's National Climate Change and Wildlife Science Center.

Today's webinar is titled "Foraging Decisions and Populations Dynamics -- Ungulates under a Warmer Climate." We're excited to have James Cain and Jay Gedir with us today.

Janet Cushing: Hi, everyone. This is Janet Cushing. I think Shawn is indisposed at the moment, so I will be happy to introduce our speakers. Just so everyone knows, my name's Janet Cushing. I am the acting chief of the National Climate Change and Wildlife Science Center in Reston, Virginia.

It is my honor today to introduce our two speakers. James Cain is the assistant unit leader of the USGS New Mexico Cooperative Fish and Wildlife Research Unit and an Adjunct Associate Professor in the Department of Fish, Wildlife, and Conservation Ecology at New Mexico State University.

He has a BS from Colorado State University, an MS from California State University, Sacramento, and a PhD from the University of Arizona. James's research program focuses on habitat selection and foraging ecology of large ungulates with an emphasis on species inhabiting arid and semi-arid ecosystems.

Previous research projects include studies on desert big horn sheep, mule deer, American pronghorns, elk, and feral burros in North America, and zebra, cape buffalo, impala, puku, lechwe, and sable antelope in southern Africa. Quite a huge portfolio.

Jay Gadir is a research scientist in the Department of Fish, Wildlife, and Conservation Ecology at New Mexico State University. Jay has a BS from the University of Guelph, Ontario, a master's degree from the University of Reading in the UK, and a PhD from the University of Alberta. He has conducted post-doctoral research on a variety of taxa in the UK, Africa, New Zealand, Canada, and USA.

Research interests include vertebrate population dynamics, large mammal ecology, behavior and management, reintroduction and conservation ecology, and Bayesian statistics. He's a member of the IUCN Reintroduction and Deer Specialist Group. Thank you to both of you. I will turn it over now.

James Cain: Thanks for the introduction, and I'd like to thank everybody for taking time out of their day to come listen to some of the work that Jay and I've been doing for the last couple of years. This is a large project focusing on a couple species.

Jay and I decided to do tag-team on the presentation here and split it up between some of our foraging work with desert sheep and some of our population dynamics work with American pronghorn. I'm going to go ahead and give some of our foraging dynamics work with desert sheep in relation to water balance and nutrient intake in water-stressed environments.

The environmental context in which ungulates inhabit largely determines the forage conditions that they have to deal with and also the water availability in terms of drinking water. There's a lot of spatial and temporal variability, both within and across systems. This ranges from temperate systems all the way through semi-arid to arid environments.

Regardless of which type of environment an herbivore occupies, in large part, it's its foraging decisions that determine whether or not they're able to meet their seasonal water or daily water and nutrient requirements based on the foraging resources available to them and also the constraints of their environment.

Most ungulates, especially small to medium size ungulates, are restricted by gut capacity and rumination time. This is going to influence the type of forages that they're able to select in order to best meet their nutritional requirements. Ungulates in arid environments have an added limitation that they're often in water-limited environments, so there's not a lot of drinking water available.

They frequently select forages based on moisture content in order to help them meet their water requirements. When there's lots of forbs available in the environment during wet seasons, they can forage in a manner that allows them to meet their nutrient requirements because forbs are high in nutritional content, as well as they're relatively high in moisture content.

They can meet both needs by foraging on the same types of forages. During dry periods, typically it's the cactus and the succulents that are highest in water content, but they're notoriously low in nutrition, particularly protein. This sets up a trade-off in the dry season.

If they're going to be selecting forages based on moisture content, they're actually going to be trading off some nutrient content in terms of their protein intake or their nitrogen intake. For ungulates in arid climates, it's water scarcity related to variable precipitation that are going to be really important for driving survival and reproduction.

This, of course, is going to be directly influencing population dynamics and long-term population persistence. Unlike temperate areas, which are seasonal and driven often by snow melt during the spring, precipitation is what largely determines surface water availability as well as forage abundance and nutritional quality of that forage in these arid systems.

In these arid climates, precipitation is notorious for being both temporally and spatially unpredictable in terms of distribution and also in terms of the amount. There could be periods of time when animals have to rely solely on preformed water in their forage to meet the daily water requirements if they don't have other sources of drinking water available to them.

There are a lot of species that have been widely documented as being able to survive extended periods without drinking water. You'll notice most of the species that I have here on the screen are African or Middle Eastern species.

That's simply because that's where most of the physiological work in terms of water balance and thermo-regulation have been done -- with African or Middle Eastern species -- with relatively little research being done on species that inhabit North American deserts, which is rather unfortunate.

All these species that are able to go prolonged periods without drinking water share a suite of physiological and behavioral adaptations. I'm not going to go into them here, but they're all listed. They all have some of these features and are able to do some of these things in order to help them survive longer periods without ingesting preformed water.

For many of the wildlife management agencies in the western US, as well as other parts of the world, they often have a water provisioning program for wildlife designed to provide them with supplemental sources of drinking water or perennial sources of drinking water in environments where water is scarce or seasonally unreliable.

It's typically geared towards either species that are game species or species of conservation concern. The idea is to increase productivity and range carrying capacity, or to manipulate or expand population distributions.

This whole program can be costly, and can be time-consuming. That's just even if you ignore all the political considerations of building these water sources or maintaining existing water sources in wilderness areas, which is where most of the target species live. Desert bighorn sheep are a primary beneficiary of some of these water development programs, particularly in the Southwestern US.

The reason for this is it's widely known that the distribution of desert sheep is often tied in close proximity to areas around drinking water during the driest periods of the year. This leads water to be considered an essential habitat component for the species. There are some populations of desert sheep that occupy areas with no known sources of perennial water.

There's the femoral sources of water after the rains, but they don't last for extended periods of time. This leads to the question -- If you have these populations that inhabit areas without perennial water, is this water provisioning program for desert sheep, is it beneficial or even necessary?

Our objectives were to look at whether or not the removal of supplemental surface water affected diet selection of desert sheep. We wanted to estimate seasonal water and nutrient intake. We wanted to determine if they could meet their water and nutrient requirements from their forage alone.

If not, based on the forage characteristics and the forage availabilities in the environment, are there decisions that they could have made in terms of selection of forage that would allow them to meet their water and nutrient requirements, solely based on forage?

We conducted this study in the Sierra Pinta National Wildlife Refuge in Southwestern Arizona along the Arizona-Mexico border. There are seven sources of perennial water. These are man-made water sources. There are three in the Sierra Pinta and four in the Cabeza Prieta. There are no other known sources of perennial water.

This gives you an idea for those of you unfamiliar with the environment. This is what it looks like. This is a typical desert bighorn sheep habitat in Western and Southwestern Arizona -- isolated, rugged, desert mountain ranges. This is typical of the habitat.

We divided our data seasonally and our data collection seasonally based on long-term climatic data. You can see, based on the mean precipitation, it's very arid out here, about four inches of rainfall, on average, per year. It has a bimodal distribution with peaks in the winter and light summer, but there's a lot of variability between years. It's almost 60 percent for the coefficient variation.

Then it's hot, as you would expect, with hot summers and mild to warm winters. We captured 37 adult female desert bighorn sheep. We fitted them with GPS collars. These data were transmitted via satellite every couple days. We used them to locate foraging locations for the desert sheep.

Our overall study design was a BACI study design with a two-year pretreatment period where we maintained all the water catchments. Then that was followed by a two-year posttreatment period or treatment period where we drained the water catchments in the Sierra Pinta Mountain Range. We visited all these foraging locations in both mountain ranges seasonally.

We used line intercept methods to look at forage availability. I'm just going to go through the methods quickly. If anyone has any questions, you can ask later. We collected forage samples from important forage species and looked at nutritional quality and moisture content as well as a couple other nutritional metrics that we needed.

We collected fecal pellet groups from adult desert bighorn sheep, bighorn females, for micro histological analysis to determine diet. Then, based on that availability data and the diet composition data, we used the Jacobs modified electivity index to calculate our index of selection with values.

Negative values being forage species that are avoided and positive values being species that are preferred. We then took data on desert bighorn sheep body mass and dry matter intake from similar adjacent populations in order to calculate some of our nutrient and water balance requirements.

We split these up by male and female. They had different dry matter intake seasonally. Also, we had non-reproductive females and then reproductive females where we had separate dry matter intake rates. Also, for reproductive females, we had early and late breeding females.

This is because desert bighorn sheep are notorious for having a really long and protracted lambing season that could last, anywhere from four to five months. Depending on when those lambs are born and when those adult females are in late gestation, they could be under different nutritional constraints during different periods of the year.

Then, we used some standard equations for calculating water intake as the sum of preformed and metabolic water. For the metabolic water, we assume that 50 percent of that was not utilizable because some water would be lost through excretion -- through urination and defecation -- as well as through pulmonary and cutaneous evaporation.

Then some seminal work done by Paul Turner in Southern California reported daily water requirements of male and non-reproductive female bighorn sheep as being three to four percent of their body weight per day. This changed the amount that actually depended on which season we were talking about.

When you're looking at reproductive females, their water requirements are about 11 percent higher during late gestation and 30 percent higher during lactation. We accounted for that added water stress on the reproductive females.

For the nitrogen requirements for males and non-reproductive females, we assume that 0.89 percent of the dry matter intake was the minimum nitrogen requirements. Then, of course, that increased to 1.5 percent during late gestation and 1.8 percent for lactation for the reproductive females.

This is a standardized precipitation index during our study period. Negative values are drought periods. Values around zero were average, and then values above zero are wet periods. We started our period during...it was still the worst drought on record for this area, so it was extreme drought. Then we went through a period of average rainfall, and then ended during a wet period.

This whole sequence during our study basically spans range and variability in precipitation that you see in this Sonoran Desert system. We were fortunate in that we actually captured all that variation in precipitation.

Just to give you an idea what that looks like, this is what it looked like during a drought period, and then these are the same valleys during that wet period. It basically looks like somebody went out and planted alfalfa out in these desert valleys.

In terms of our analyses, we used generalized linear models to test for impacts of water removal on desert bighorn sheep diet. Before, we just saw a larger transformation, but then all of our data that I'm going to present were back transformed to the original scale for presentation.

There were 24 species in the diet. We had 16 of those that we had collected and analyzed. Those 16 species composed anywhere from 78 to over 95 percent of the seasonal diet. We got most of the most important species in the diet we have nutritional content data on. In terms of water content, grasses tended to be lowest.

Grasses were lowest in moisture content. Then forbs, shrubs, and trees are intermediate and, as expected, succulents had the highest moisture content. In terms of nitrogen content, grasses were similarly low in nitrogen content, especially compared to shrubs, trees, and forbs here. Also, as I mentioned earlier, succulents were also really low in nitrogen content.

They have a lot of water, but they're really poor in terms of providing a source of protein for ungulates. What we found overall was that we found that the water content of the diet differed by range and by season. I'll walk you through these graphs here. In all these subsequent graphs, the symbol shape corresponds to a different season.

The open symbols are the treatment range and the closed symbols are the control range. This over here is the pretreatment period, so water was removed here. This is the post-treatment period. What we were looking for is if there is a shift in diet due to the removal of water.

You would expect the treatment and the control range, the difference between those two to change from pretreatment to the posttreatment period. Overall, we found some differences between ranges, particularly during the pretreatment period with lower values here for the treatment range.

Then, overall, most of our differences in diet water content really had to do with an increase in moisture content during that treatment period that was associated with the increase in rainfall. In terms of mean nitrogen content in the diet, we saw similar patterns with some lower values for the treatment range during the pretreatment period.

Overall, the main pattern that we see in the data is just an increase in nitrogen content in the forage from the pre- to the posttreatment period, corresponding to that increased rainfall during the wet period. In terms of diet composition and selection, these are basically similar graphs. We have the proportion of the diet here, which corresponds to the solid and light symbols here.

We've got the Jacobs D index in X axis here, so it's a mean Jacobs D. It corresponds to the axis over here. Then pretreatment, post-treatment open circles again are the treatment and the control. Again, we're looking for a change in the difference between the treatment and control range. In terms of shrubs, they varied anywhere from 15 to 35 percent of the seasonal diet.

There were no real differences between seasons and ranges. There were differences between seasons. Overall, they tended to be avoided, largely because of their high availability. Most of the vegetation biomass in the system was shrubs. Grasses represented a really low proportion of the diet. They increased here in the late summer season during the pretreatment period in both ranges.

They had really negative Jacobs D indexes, so they were selected against. Forbs were selected for in almost all seasons and the proportion in their diet increased corresponding with that increase in rainfall. Trees made up the bulk of the diet and were selected for during most seasons. There was really no shift in selection or in composition following the removal of those water sources.

Succulents made up a moderate amount of the diet, but they were always highly selected for. This is our water and nitrogen balance ledger. Here we have the water maintenance requirements for females, reproductive females, and males. Then the similar for the nitrogen balance. Then here we've got each season, and then depending on if we had droughts or not during that particular season.

Some of these have different levels of calculations beneath them than others. What we found was that, in the absence of freestanding water, all sexes and reproductive classes wouldn't be able to meet their water requirements based on the forage moisture content alone during drought periods. Then late reproducing females had a nitrogen deficit during early summer.

Then both early and late reproducing females had a nitrogen deficit during winter, when there was a drought period during winter. What we did was we then conducted some hypothetical diet shifts to see, if they were based on the forage characteristics that were available to them, were there decisions they could have made that would allow them to alleviate these deficits?

We basically just tested these hypothetical diet shifts. What we did was we took the percentage of the diet with the lowest moisture content or the lowest nitrogen content and we removed two percent of that and replaced that two percent with the highest species that was in the diet and available at that time.

We just did this repeatedly until a proportion of that species in the diet fell less than one percent. Then we moved on to the next lowest nitrogen and moisture content species until water and nitrogen balance became positive.

What we have is that this is the observed diet right here. The horizontal solid line is the minimum water requirement. The horizontal dashed line is the minimum nitrogen requirement. The observed diet here on the right for non-reproductive and early breeding females. In the observed diet during early summer they were at a water deficit, but they were positive in terms of nitrogen balance.

In order to get to a positive water balance, they had to shift their diet by 10 percent to include 23 percent of the higher moisture content species in their diet. Late breeding females had to shift their diet by 44 percent in order to get above this threshold for minimum water requirements.

During the early summer, males had to shift their diet by 33 percent and include 46 percent of the higher moisture content species in their diet. During late summer, females had to shift their diet by 31 percent and males had to shift theirs by 55 percent in order to meet their daily water requirements.

During autumn, non-breeding females and late-breeding females had to shift their diet by about eight percent and males had to shift their diet by 44 percent. Early breeding females had to shift their diet by 44 percent in autumn to meet their water requirements.

Then, for early-breeding and late-breeding females during winter, the early-breeding females actually had to shift their diet by 17 percent from lower nitrogen content species to higher nitrogen content forage species in order to meet their nitrogen requirements. The late-breeding females only had to shift theirs by about six percent.

Overall, we found that the diet quality was similar between ranges across seasons and that the supplemental water removal had little effect on diet selection. Forbs consumption increased, but their preference for forbs was pretty high across the entire study period.

The increase in forb was basically due to an increase in its availability associated with the increasing rainfall during the later part of the study. During the drought period, all the animals had a water deficit if they didn't have surface water available. This is for both sexes during all seasons except for winter.

Then, the early-breeding and late-breeding females had nitrogen deficits during the winter and early summer during drought periods. Based on the characteristics of the available forage, there were forages available that would have allowed them to shift their diets in order to meet their water and nutrient requirements.

Similar diet shifts have been demonstrated in several other species, particularly in African and Middle Eastern species where they've been documented to shift their diet in response to temporally changing nutritional constraints.

In terms of early and late breeding, ungulates typically synchronize their reproduction so that their young are born when their resource demands are highest during a period with peak forage abundance, or highest nutritional quality, or maybe they'll have their young right before that peak and forage abundance.

We wanted to look at whether or not breeding timing had an advantage for water and nitrogen balance. What we found overall was there relatively little difference in the shift in the diet or the proportion in the diet required between early- and late-breeding females when they're in water deficit.

In terms of nitrogen deficit, the early-breeding females had to shift their diet by twice as much as the late-breeding females. The late-breeding females probably have a little bit of an advantage in that they're lambing coincides with periods of higher nitrogen levels.

The lambs are going to be able to capitalize on that increased autumn forage quality earlier in development than the earlier born lambs. Desert bighorn sheep are widely known to have a highly variable diet. Not only within a population, across seasons, or across time, but also across their range and across populations.

They're really adaptable in terms of the diet that they eat. One unique feature of desert sheep is that, because of their distribution in these isolated desert mountain ranges, they really have to make do with the forages that are in their available range.

Unlike pronghorn and mule deer, which can adapt to nomadic or even a migratory movement pattern in response to changes in precipitation and forage conditions, these desert sheep are largely stuck where they are. There is some inter-mountain range movements, but there's not wholesale migration or nomadic movements like you would see in other species.

This ability to have this diverse diet and to be able to adapt seasonally, depending on current conditions, is going to serve them well and allow them to cope with periods of water and nitrogen stress.

Now, succulents are obviously a superior source in dietary water, and they're widely documented in previous work. They make up a large proportion of the diet for desert sheep, particularly during dry periods. They do have high levels of oxalic acid and they have been shown to cause renal toxicity, at least in domestic ungulates.

Based on previous work, desert bighorn sheep may have a physiological capacity to deal with this because the levels that have been reported in desert bighorn sheep diets are similar to levels that are being reported to cause toxicity in domestic species.

Here's just a couple of examples. This is a barrel cactus here that desert sheep were eating. Here's some saguaro cactus that they've been chewing on. Then some agave stalks, so when they start to flower the desert sheep will come and eat the agave stalk.

We tested the most extreme water stress scenario -- we assumed that there would be no drinking water available -- and found that, if they were to make some of these resourceful foraging decisions, they could potentially survive, based on the forage conditions that we observed during our study.

Which makes sense, given that they evolved to live in this desert, and they have a lot of physiological adaptations to deal with water deprivation. They have a lot of water in their rumen, and they tap that water first when they're going through dehydration. That allows them to maintain water in their blood and body tissues.

They can also decrease body water loss by decreasing metabolic rate, which has the added benefit of reducing energy requirements during periods with poor forage conditions. They can increase the extraction of water from their feces, and they can concentrate their urine.

Also, when it does rain and there are potholes or ephemeral sources of water available, they can consume almost over 20 percent of their body weight in a single drinking bout. We need to couch these results in terms of this is the current climate and the current forage conditions that we observed.

If you get decreases in precipitation or shifts in precipitation patterns, that is obviously going to have an effect. They could cause further deficits in terms of nitrogen and water balance with a changing climate. These are some of the folks that contributed to the study. I'll turn it over to Jay now and be happy to answer any of your questions once Jay's done.

John: All right, Jay, you're on the floor.

Jay Gedir: Thanks, John. Thanks to everyone for tuning in and bearing with us for the second half of this. Jimmy was telling us about climate effects on a desert ungulate at more of an individual level. Now we're going to look at the effects of climate change at a population level.

This study was done in collaboration with the Fish and Wildlife Service. We were investigating how pronghorn populations in the southwestern US might respond to predicted changes in climate over the coming century. First, a little bit about the species. Pronghorn are endemic to North America. They range in the west.

You can find them from southern Canada all the way down to northern Mexico. They are the fastest terrestrial animal in the western hemisphere, capable of bursts of speeds up to 100 kilometers an hour. Globally, they're second only to the cheetah. Unlike the cheetah, they can sustain speeds up to 50 kilometers an hour over long distances.

Also, unlike many other ungulates, they're poor jumpers, so their movements can possibly be restricted by things like fences and highways. Pronghorn habitat primarily consists of short, mixed grassland, mixed grass shrub, and, to a lesser extent, desert, and usually at elevations of 1,000 to 2,500 meters.

Pronghorn have a very long gestation -- more than eight months -- because they have the highest reproductive investment of any ungulate in North America, and that's the fawn to maternal mass ratio. In part, this is because they typically bear twins.

Pronghorn populations have experienced massive decline over the past few hundred years, from numbering in the tens of millions in the early 19th century to only 13,000 a hundred years later. This is primarily due to the European settlers. As they moved westward, there was some widespread over-hunting of pronghorn and extensive conversion of native grassland to crops.

Almost daily, we have new statistics thrown at us about the world's climate changing. Basically, the Earth is warming at an accelerated rate. This rate is predicted to increase this century, and this increase will be even more significant in the southwest US. Recently, there have been frequent droughts.

This century they predict changing precipitation patterns, declines in water balances, and an increase in extreme weather events. Not only are we interested in examining pronghorn as a species that could become at risk through the effects of climate change, but pronghorn also can serve an ideal ecological model for examining the impacts of climate change on ungulates in general.

They inhabit diverse and extreme environments. Their populations exhibit large fluctuations, mostly depending on the severity of droughts in winters. Physiologically, pronghorn have a very small reticulorumen, and so they require a high-quality diet. This makes them sensitive to subtle changes in forage conditions. This can be exacerbated by the effects of climate change.

Pronghorn also have a very high reproductive capacity. Typically, they have pregnancy rates of 80 to 90 percent and twinning rates of 90 percent are not uncommon. Their mortality rates can often be high, especially with fawns in their first 30 days. When conditions are good, they have the capacity to rebound from severe population declines.

The two primary objectives of our study was to, first, identify and quantify relationships between past trends in pronghorn populations and climate at a local scale. We wanted to determine climatic factors that predict annual population growth rates in pronghorn.

Secondly, we wanted to couple these models of pronghorn growth with downscale projections of the explanatory climate covariance to forecast the long-term population trends for each of the populations over the coming century.

The study area encompassed about 1.1 million square kilometers of woods, about 300,000 square kilometers is pronghorn range. The gray shading in this map is pronghorn distribution and habitat. The climate in the study area ran from semi-arid to arid, and we identified 18 populations to model from Utah, Arizona, New Mexico, and Texas.

We compiled our population data from annual aerial surveys usually conducted in spring or summer. For the modeling, our dependent variable we used was the annual rate of population change, lambda. It serves as a really good metric because it summarizes both survival and recruitment.

Where impossible in our calculations of lambda, we also accounted for harvest and translocation when this information was available. Here's an overview of the 18 populations that we modeled. You can see that they encompass a wide range of population sizes and areas, as well as the time periods for which we had survey data.

We got our climate data from the global climate model data set listed at the top, there. These models were calibrated to historic, observed climate data to correct for biases. You can see that both precipitation and temperature estimates are very precise. This climate data also has high spatial resolution 14 by 14 kilometer grids, and the grids are specific to pronghorn range within each population.

We wanted to compare two realistic future global climate situations. More pessimistic, high atmospheric carbon dioxide concentration scenario -- Representative of Concentration's Pathway 8.5 -- where we continue our dependency on fossil fuels, and by the end of the century, CO2 levels in the atmosphere has reached two-and-a-half times current levels.

We also wanted to look at the more optimistic, lower CO2 concentration scenario, RCP 4.5, where levels increase by about 60 percent by mid-century, but, at that point, we basically clean up our act. By the end of the century, levels decline to near 1990 levels.

Our climate metrics were mean temperature, total precipitation, and Standardized Precipitation Index, which is the number of standard deviations observed, and the amount of precipitation deviates from the long-term average.

We also summarized climate data by 12- and 24-month periods preceding each population survey, by important female reproductive phases -- currently, mid-late gestation and lactation. Here's an overview of what the global climate models predict for temperatures through the century.

You can see that the temperatures are predicted to rise across the entire southwest, with an overall mean increase of 2.5 degrees Celsius for the lower atmospheric CO2 scenario and 5 degrees Celsius for the high scenario.

The projected precipitation trends. Overall mean total precipitation is not predicted to significantly change during the century under both of the climate scenarios, but this is highly variable among populations, with some populations being drier and some populations wetter.

For the modeling, we adopted an information of theoretic approach, and we did all of our modeling in a Bayesian framework. We hid the Deviant Information Criteria -- DIC -- to evaluate model performance. DIC is, essentially, the Bayesian equivalent of AIC, Akaike's Information Criterion.

Our first step was, for each population, we wanted to determine the best climate metrics to predict lambda. Note that in all models we included a covariant for density effect, which was simply the population in the previous year.

Next, we wanted to estimate future lambdas for each year using our projected climate data, calculate median population sizes up to year 2090 using an integrated modeling approach whereby the population projections are generated concurrently with both the climate parameter estimates and the lambdas, so that the estimation of uncertainty is propagated into our projections.

We have a look at the climate predictors that we derived from each population. You can see that 16 of the 18 pronghorn populations' climate factors are good predictors of annual population growth. In all of these 16 models, seasonal precipitation most strongly influenced lambda, most importantly during lactation, but also in some during early gestation and late gestation.

For temperature, in 13 of the 16 models where climatic factors were important for population growth, temperature was also a good predictor of lambda, but this was more variable in both the direction of the relationship and the periods that were important.

Let's briefly look at what these changes in temperature and precipitation mean to the pronghorn populations in the Southwest. In all of these graphs, the X axis is year, the Y axis is projected population size.

The solid lines here represent the projected median population estimates, with the red being the more optimistic scenario and black being the more pessimistic scenario. The dashed lines are the 2.5 percent and 97.5 percent credible intervals, which are essentially Bayesian equivalent to confidence intervals, although credible intervals actually estimate the true uncertainty in a model.

You can see in Utah that four of the five populations are predicted to become extirpated by the end of the century. In Arizona, three populations are predicted to persist, but the East Central population, under the pessimistic climate scenario, and the Southeast North 10 population, under both scenarios, it looks like, at the beginning of next century, they will be approaching extirpation.

In New Mexico, three out of four populations are predicted to become extirpated by the end of the century, and two populations in Texas. Firstly, the panhandle population. We've predicted unrealistic growth for this population, but you can see the credible intervals are crazy. the credible intervals for the panhandle population are so wide that we probably can't put any credibility into these predictions.

For the Trans-Pecos population, unfortunately it's predicted to continue the crash it started in the late '80s when pronghorn numbers plummeted from 17,000 to about 3,000 at the start of projections. It looks like this population could become extirpated in the next 20 years.

To summarize the population models, looking at the historic population trends, 82 percent of the pronghorn populations have declined since the '90s, and we can see that some of them have declined quite considerably. Projection models predict that more than half of the populations will become extirpated or approaching extirpation by the end of this century. I wanted to also mention that there was a similar response under both climate scenarios. For the populations that are predicted to disappear, the mean time with a probability of extirpation, it seems a likelihood of persisting, so it becomes more unlikely that they are going to disappear.

The time was 54 years for the lower scenario and 48 years for the high emissions scenario. Late gestation and lactation are most energetically-demanding periods for female ungulates, and our models indicate that precipitation during these periods are important in three-quarters of the populations. Obviously, increased precipitation leads to more abundant and higher-quality forage.

If this occurs in late gestation, it'll help the mothers meet the high-energy requirements of their last trimester of pregnancy, and they can birth healthy fawns. If it occurs during lactation, mothers can respond by producing more milk, which can help them meet the demands of their rapidly growing fawns, thereby increasing fawn survival.

As well, adult females in better condition should also have higher survival. The benefits of higher forage availability actually go beyond the importance of just individual nutritional status. Increased vegetation can provide important cover as protection from predation, especially coyotes with pronghorn.

Pronghorn mothers use a hiding strategy to protect fawns from predators, and this is particularly important in their first four or five days, before they're able to outrun a predator. Having greater coverage during this important time of year can help reduce fawn mortality. Similarly, greater forage abundance can also benefit adults in the same way.

Ungulates, during a drought, ultimately trade-off between safety and forage abundance. In a study in Arizona, they found during drying conditions, pronghorn moved from open, flat terrain to alluvial plains at the base of mountains, biotas. Here, the water runoff from the mountains created a higher diversity of vegetation. It was taller, denser vegetation.

When pronghorn were using these areas, causative mortality shifted from primarily malnutrition to nearly all of the deaths being attributed to predation. Our models also suggest that when temperature is also important to the population, it exerts a strong influence. Populations with a negative relationship between temperature and lambda failed.

That includes all of the populations in Utah where precipitation is predicted to increase up to 39 percent. In a contrast, populations with temperatures hotter than we associate with lambda were predicted to persist. That includes, for example, central Arizona, where a reduction in precipitation of 36 percent is predicted.

If these higher temperatures occur in autumn, early-gestation, can extend the growing season. If it occurs in winter, mid-gestation, it can increase nutritious winter forage and, ultimately, lead to earlier spring green-up, but, if these higher temperatures occur during summer, during lactation, it can lead to dry conditions and earlier senescence of the vegetation.

Temperature can really impact the pronghorn. In another way, too, in addition to exacerbating the negative effects of changing precipitation patterns, rising temperatures can also be a direct cause of mortality, particularly in areas that experience extreme temperatures and definitely an area like the Southwest.

Higher temperatures might require them to prioritize thermoregulation. They would start diverting foraging time to thermoregulating. A study on Australian sheep ewes showed that, as they were exposed to heat stress during their first 20 days of pregnancy, they had 100 percent embryo mortality.

A pronghorn study in southern Arizona found evidence suggesting that hyperthermia causes deaths in some four- to five-month-old pronghorn fawns. Also with the rising temperatures, densities of some of these species may change, given locations. Species distributions might shift poleward or to higher elevations as they try and move into areas that are more within their physiological tolerance.

In the Southwest US, pronghorn populations are approaching the southern extent of their species is range. Only 0.1 percent of the North American pronghorn population extends into Mexico, in small isolated populations.

Five of the six of our southernmost pronghorn populations are predicted to disappear by the end of the century. Other small pronghorn populations follow this same trend. It could equate to a northward shift of the southern limit of the species' range, but this might not mean range contraction.

With warmer temperatures in the north, they could also shift their northern limit to their range to the warmer areas of the north. Just briefly, I'll try and wrap this up. Our small populations, less than 200, were all predicted to fail, five out of six of them. The larger populations are all predicted to persist.

We know that smaller populations are probably more susceptible to both environmental stochasticity as well as demographic stochasticity. Just here, Price, et al, suggests that species most vulnerable to extinction are those with restricted or contracted ranges, fragmented distributions, smaller declining populations, and decreasing habitat.

This actually describes most of the pronghorn populations in our study, as well as many other ungulate populations in the arid Southwest. Just overall conclusions. Our approach in examining 18 pronghorn populations across the entire Southwest.

Using region-specific downscaled climate data, comparing that data with population specific pronghorn range has provided a high resolution extensive overview that portrays and explains pronghorn population trends across the region. The Bayesian approach and the integrated modeling approach give us utter confidence in our population estimates.

As a final take-home message from this study, without curbing the effects of climate change or without management intervention -- things like translocations, habitat enhancement, or reduced harvest -- it's looking like the future of many of the pronghorn populations in the Southwest appear to be in jeopardy.

Some people and organizations that helped make this study happen. With that, Jimmy and I will take questions.

John: Thank you both for the presentation. We do have one question right up now. I'll quick read that off. If other people have questions, feel free to throw them into the chat box. The first one comes from Bob Parmenter. This one is for James.

He's asking, "Have you seen any changes in predator-prey interaction -- for example, with cougar kills -- as big horn sheep move to different foraging habitats and impacts on reproduction success and survivorship?"

James: For the population that we worked with in southwestern Arizona, there really weren't a lot of resident cougars. If there were cougars, they had such a large home range that they didn't come through that mountain range very often.

We really didn't see any pattern in what cougar predation we did have. We didn't see any differences between the wet period and the dry period. Some work we've done in New Mexico suggests that there could be an interaction between predation of lambs and forage conditions.

During dry periods, when mothers may come further down the mountain to access forage into areas that are less rugged, if they're leaving their lambs for longer periods of time unattended or they are bringing their lambs with them further down the mountain, then they become more susceptible.

One lamb survival study that we did, we found that we had higher coyote mortality of lambs during the dry year, whereas during the wet year, it was exclusively mountain lion predation. There are big differences in where on the mountain the coyote mortalities occurred versus the lion predation. There could be some interaction, but we don't have a lot of data on that.

John: Thank you very much. I see somebody typing away. Tabatha's question, "Did you see shifts in locations that matched shifts in diet?"

James: No, we didn't. The forage characteristics in the forage species were fairly similar regardless of whether we were at the bottom of the mountain or at the top of some of those mountains. Some of the species composition changed when you got further away from the mountain into the valleys. Even during the drought period, the sheep didn't go there.

We did see a bit of a shift towards drainages during the dry period, but the diet composition remained the same because the species composition was similar between some of the washes and some of the more upslope areas. That could have been due to differences in forage quality rather than differences in forage species.

John: It doesn't look like we have any other questions. Once again, thank you, gentlemen, for your presentation. Thank you for participating.

James: Thanks.

Jay: Thanks.