“Can Camouflage Keep up With Climate Change? White Hares on Brown Snowless Backgrounds as a Model to Study Adaptation to Climate Stress”

Webinar Transcript

Speakers:
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Christy Coghlan: Good afternoon from the U.S. Fish and Wildlife Service’s National Conservation Training Center in Shepherdstown, West Virginia. My name is Christy Coghlan, and I'd like to welcome you to today's broadcast of the NCCWSC Climate Change Science and Management Webinar Series. This series is held in partnership with the U.S. Geological Survey’s National Climate Change and Wildlife Science Center. Today's webinar will focus on "Can camouflage keep up with climate change? White hares on brown snowless backgrounds as a model to study adaptation to climate stress”. Our speaker today is Dr. L. Scott Mills.

Everybody, please join me in welcoming Shawn Carter, Senior Scientist at the USGS National Climate Change and Wildlife Science Center in Reston, Virginia.

Shawn, would you please introduce our speaker?

Shawn Carter: Sure, happy to Christy, thank you. Thank you everyone for joining us today. Today, Scott Mills is going to be joining us and giving a presentation. He recently is, I think he's still in the process, actually, of transitioning to a new faculty position in Fisheries Wildlife and Conservation Biology at NC State. Prior to that, Scott was a professor or Wildlife Biology at the University of Montana, where his interests were in the area of Applied Population Ecology.

At this new job, he's going to be addressing questions on global environmental change, working with the NC State faculty and also our USGS Southeast Climate Science Center and the North Carolina Museum of Sciences.

He's also going to continue studying hares and color coat change and also expanding work to consider snowshoe hares across North America and look at other color coat changing species around the world.

He's also hoping to embark on new projects relevant to global environmental change in the Southeast. But, he's not quite sure what the focal species might be, ranging from salamanders, alligators, flying squirrels, or maybe something completely different.

A broad portfolio, some interesting work. Today, we're going to hear about his work where he was at Montana. With that, I'll turn it over to today's presenter, Scott Mills.

Scott Mills: Great, thank you Shawn. Thanks to everybody out there. I will say I'm a newbie. This is my first time doing a webinar. I'm used to faces out there so that I can glare at them if anybody falls asleep but I have been told I have a little attention meter here. It's an exclamation point. I'm told that I can keep track of whether anybody is dozing off out there in the ether. Anyway, it's great to be here. The movers are carrying my stuff out of my lab and office and house as we speak so it's good to get a little break from the moving to give this presentation.

I would like to begin by stepping back a bit and just talking a little bit about the genesis that brought me to this place. I have [pause].

There we go. I've been studying snowshoe hares pretty much continuously since 1998. The studies all along have been focused on addressing population dynamics of the snowshoe hare and particularly addressing the role that predation has on individual and population level dynamics.

This particular slide shows the radio collar and the remains of a snowshoe hare. It doesn't take long to realize that when you are in this business of studying hare population dynamics,you're really in the business of studying how many different ways hares can die, and also, getting an appreciation for the role that predation has in shaping population dynamics and individual behavior.

I won't go into a lot of detail. Just to point to a couple of the big, broad brush places wherewe and others have thought about the role of predation in shaping hare population dynamics and behavior.

Of course, we're all familiar with the classic 10 year cycles of hares and lynx. But some work that we did about 10 years or so ago, we explored the role that heterogeneity across the forested landscape creates differences in predation rates in closed and open forests and in so doing, actually is strong enough to dampen the population dynamics.

In this case, there's a population level effect where predation across a heterogeneous landscape is sufficient to take away the cycles that are so classic in the north.

Just jumping to an example of an individual way that individual behavior is shaped by predation, we looked at hares at times of full moons which are shown by the white dots here and at times of non-full moons when there was snow on the ground and when there was no snow on the ground.

The big thing that jumps out here is that when there's snow on the ground and the moon is full, so the hares are illuminated on the bright, white background, they seem to behave as if they're perceiving predation risk. They move a lot less. They hunker down a lot more at those times.

Alas, it doesn't do them any good. They still die more, even when doing that. Here, you can see that when there's snow on the ground and the moon is full is the time when hares die the most.

All of these things have been bouncing around in my mind as I thought about population and individual level manifestations, or implications, of predation. With that in mind, I became struck, over time, thinking about this, which is that at the heart of a snowshoe hare's life history strategies, its camouflage is really its best defense from predation.

They are remarkably well camouflaged, and they are a species that actually changes its camouflage in order to track changing weather conditions. Hares, in the fall, they change from brown, they start gaining white. By late fall, early winter, they're completely white. Then, when the days begin to get longer again, in the spring, they have another color moult back to being brown again.

Thinking about predation as a shaping force for hares, and thinking about how the hare's coat color is critical to its camouflage, and thinking about how the coat color changes seasonally, all began to really strike me as I started seeing this more and more out in the forest, as we were doing our field work.

This is what I call a light bulb, hopping around in a brown forest. It's one of our radio collar hares.

I should say that all the pictures in the slide show today are from our research photos. None of them are re-touched, or none of them involve moving hares around. There was somebody that asked me, one time, "I don't believe that is actually a hare in its natural habitat. I think you got that hare and took it somewhere and placed it there."

None of these hares have been moved, or touched, or anything.

Anyway, seeing these white hares more and more over time was striking. It was especially striking as I reflected on the fact that the single biggest signal of climate change in temperate regions around the world is a reduction in number of days with snow on the ground.

Here, we're looking at this for the Northwest. The red means that the snow water equivalent has increased over the half century. The blue means it's decreased. Obviously, very few blue dots out there and lots of red dots, some of which are quite large, showing a reduction in snow water equivalent.

Here we're looking at it in a slightly different way, for a slightly different geographic region. This pattern is shown, really, around the world, Europe, Asia, northeastern North America, that the snowpack is staying for a shorter period of time in temperate regions. This is largely driven by increased rain on snow events in the fall, and especially in the spring.

Seeing these light bulbs hopping around the forest increasingly, these hares and realizing that the snowpack was getting shorter, it obviously got me wondering what would be the implication of that. The implications of a light bulb hopping around in the forest.

What comes to mind is probably this. This is actually a picture that was sent to me by acolleague in Colorado, Jake Ivans, who is studying hares down there. This is sort of the intuition that comes to mind when you see that white hare. You figure, "This must be what's happening to hares." Of course, there are other options.

Really, the question has become, over the last few years with our research group, to what extent are hares becoming increasingly mismatched, and what are the implications of that mismatch in terms of changing vital rates, birth and death rates, survival rates, in particular, and then what might the implications of that be for the future, for hares.

We actually know quite a lot about how wild animals will respond to global stressors: climate change, or, really, any other human-caused stressor. That can be captured in this graphic for climate change. In the case of climate change, the stressor that's an anthropogenically-driven stressor, is changes in the physical environment. That affects plants and the physical environment. That in turn leads to animals having, really, three options. It all boils down to these three options.

These are: animals successfully move to stay within a physical environment envelope that's appropriate to them, or, they locally adapt without moving. These can be happening together. If they're not able to do these two things, then the species will be expected to decline. Of course, how these things play out is going to ultimately change the ecosystem structure.

I'm sure in this audience I don't need to focus very much on moving as a strategy. There's ample evidence for animals changing geographic range and changing movement patterns. This has been widely described across a wide range of species. I believe that we spend a lot less time considering the scope and potential of the second option, that is the possibility to successfully adapt, in place, to climate change stressors without necessarily moving and without necessarily declining or dying.

One of the ways that plants and animals have been shown to adapt in place to climate change is through changes in the timing of their life history events, phenologic changes. Often times, phenologic changes that are described, such as hibernation emergence or changes in migration, are pretty complicated, multi-trophic level phenologic changes. An animal's migration time becomes disconnected from the optimal phenologic time of their food source and that creates mismatch.

The challenge with those kinds of examples is that number one, they go across multiple trophic levels. Number two, it's hard to attribute them necessarily to climate change, because other things are going on, in many cases land use changes, that can change migration times or food emergence.

Here, in this case, with this case we're talking about today, it's a very straight-forward example, in a sense that either it's a climate change-driven effect that manifests itself either as a presence or absence of snow. We feel like it's a very nice model system to ask this question of: what is the potential for animals that have a very strong, fitness-related, trait that's affected by this climate-related driver, what's the potential for these animals to locally adapt to a decrease in snowpack?

As I talk more through the talk, what I mean by, when I talk about “adapt”, I'm using it in a bit of a broad sense to say, either dealing with it locally through plasticity and the coat color change, changing the timing or the rate of the coat color change, or plasticity in behavior, or actually evolving changes that lead to adaptation through natural selection. I'll touch on each of these.

Of course, snowshoe hares are not the only players. This is not necessarily a snowshoe hare story strictly. Many of us are familiar that Arctic fox undergoes seasonal coat color changes. Several species of weasels undergo seasonal coat color changes. Lemmings go from brown to white. One or two species of hamsters go from brown to white.

We can map them out and see that a large part of the world is covered by these seasonal coat coloring species. The genus that has the most coverage of seasonal coat color change is Lepus. Snowshoe hare here. This is mountain hare, Lepus timidus in Europe and Asia, and the arctic hare, and also, white tailed jack rabbit.

Lots of species undergo seasonal coat coloring change. What do we know about the drivers of it? The best we know, from studies of other circannual processes, in some studies of coat color change is that it's triggered by day-length. This is important because it means that it's not like a chameleon, animals aren't changing from brown to white whether or not there's snow on the ground. They're changing based on a shortening of day-length or lengthening day-length.

Essentially, it's a process of hormones being triggered by photo periods. Here's a schematic developed for weasels. We see that as brown animals in the summer confront decreased day-length, shorter days, then that initiates the hormonal cascade that ultimately leads to the production of white fur. In the spring, as the days get longer, again, a hormonal cascade that leads to, again, production of a brown coat.

We have this species confronting reduced snowpacks with a presumed mechanism of triggering of the coat color change daily.

The way we've attacked this question over the last few years is to radio a bunch of snowshoe hares, intensively follow them every week, go out, as best we can and get pictures of every single hare so we can quantify the phenology, get pictures and observations of the ground around the hare so we could quantify the presence throughout the snow and quantify a contrast or mismatch.

We've done this at two different study areas, one near Seeley Lake, Montana, western Montana, and one near Yellowstone, just outside of Yellowstone Park, at quite a bit higher elevation.

I should note now that much of what I'll be talking about today has been done with my master's student, Marketa Zimova. We also had an amazing bunch of undergraduates. If anybody's interested in the more gossipy side of this research project, you can go to our blog, our "snowshoe hare chronicle blog", which the students run. It's entertaining. Also, there's publications and stuff on there too.

The first publication on this work came out a couple of months ago. What I'll talk about in the next few slides came from this paper.

This picture tells a lot of the story. Let me walk you through this. What this basically describes is the phenology of the coat color change here and the snowpack here. I'll start with here. This just shows that we go across the year, from fall to late fall. The right side panels are the spring, and the late spring.

Looking first at the middle panels, you can see, we've got three different years going on here,. Each year is a different color. For example, here in 2009, big drop of snow. The snow melted. The snow came again. Melted, and then eventually, by late November, early December, it was constant.

Different years, different amounts of snowpack, and that was shown across years, or even more so in the spring. We can see that the spring of 2011 was a very big snowpack. Snow stayed around a lot longer.

The bottom panels are temperature measures, which show also that the temperatures differed across with year. We kept track of temperature because we were trying to explore that as a covariant for the coat color phenology.

Here's the bunny story. Here's the hare story. Up here for the three different years, the vertical lines show the initiation dates or the completion dates of the color molt. The brown hares began to change to white, they initiated the molt right around the second week of October. You can see the confidence intervals overlap, which tells us that there's no plasticity in the initiation of the coat color change. Across all three years, the initiation was on about the same date.

Also, in the fall, the rate of coat color change across the different years didn't change. We can see that by, again, overlapping confidence intervals. That tells us that the rate of change from brown to white was constant across all three years.

In the spring, we again see overlapping confidence intervals for the initiation date. It's early April. But there is some plasticity in the rate of change. There's no plasticity in initiation but some plasticity in the rate of change. You can see, especially here, that in that 2011 big snow year, the hares were able to put on the brakes somewhat and slow down the rate of change once it's initiated.

To get more support for that, just coming at it from another angle, the ideal way to look at plasticity would be to look at the same animals that survive multiple years and see how much they change from year to year according to environmental conditions -- in this case, according to snowpack. The problem is that hares are lunchmeat for everything in the forest, so they don't usually survive more than a year. It's hard for us to get animals that survive in the same location for multiple seasons.

Here, we're looking in the fall at nine hares that survived at least one fall -- in this case, survived two falls, shown by the solid and dotted line. You can see that the fall phenology shows very little plasticity, just like we talked about. All of them are shown over here piled on top of each other,

In the spring, we actually only had one hare that survived two years, but that one hare again does support what we found with the analysis I just talked about. That one hare did show plasticity in the two years that we were able to monitor, 2011 and 2010, so there is plasticity in the rate of the spring molt.

The other question that we addressed in the PNAS paper was...We've shown that there's not plasticity, but now what we should do is to turn to some climate downscaling, look at snow models developed specifically for our study site, downscale to the level of our study site, andask how much would we expect the snowpack to change in the future, and then how much would that lead to increased mismatch without adaptive changes.

What we ended up using was local weather stations, a whole bunch of them interpolated across the northwest for the present conditions, and then we turned to multiple global circulation models with two different CO2 forcings to look into the future.

What we found is the pattern that's been talked a lot about in the climate literature, which is that compared to the recent past, we expect in the future, depending on which CO2 forcing we use, we expect to see a reduction in number of days of snow on the ground, and even more so as we go further into the future to late century.

[pauses] Sorry. I just was distracted because my phone beeped, but I think it's all OK. Also, the moving van arrived outside. Ah, what a day.

We see this reduction in number of days with snow on the ground. What we next did was, we said, "Let's take the snow duration, the number of days we expect to see snow on the ground,and superimpose that on the average phenology measured from our hares in the field."

The black line here is the average phenology across years and across hares. Hares are goingfrom brown to white and then back to brown. The vertical lines are the snow-on and snow-off dates from the recent past and then from the future with the two different CO2 forcings.

The gray area is what we call mismatch. For this exercise, we call it a hare mismatch if it was at least 60 percent white hare on a brown, snowless background. Given that definition...You can adjust that. We've done that, and the story still stays the same.

The gray shows the mismatch, the duration of mismatched hares. You can see that going into the future, that increases such that as we see a decrease in number of days of snow on the ground going into the future, we would expect to see a three- to eight-fold increase of mismatched white hares on brown, snowless backgrounds.

That is striking, but it still doesn't tell the whole story because we still have to answer the critical question. What happens to these mismatched hares in terms of, do they die more, and how might they be able to adapt, either through plasticity or through adaptive changes through natural selection, which could happen in a myriad number of ways.

The question of increased mortality during times of mismatch, or increased mortality for mismatched hares, goes way back to that study I talked about in the beginning when I was talking about the source-sink dynamics that we described. One thing we found there that was quite interesting and actually served as a genesis, really, as a catalyst for all this work that's happened since, was we were a bit surprised.

We were looking at hares in closed and open forest patches because we were interested in source-sink dynamics. We found that in the winter and summer, hares had higher survival. The higher survival during the summer, when there would be presumably less predators, and during the winter, when it's bitter cold. Survival was actually higher than it is in the fall and the spring. Survival is lowest up on these open stands in the fall and spring.

This is an interesting coincidence, but it's certainly not compelling with respect to coat color change, because lots of other things are happening in the fall and the spring besides coat color change. Animals are switching their diet. Deciduous leaves are coming on. Predator communities are shifting. So this itself was tantalizing, but it wasn't compelling.

But we have over the last few years been working on the really compelling analysis. I cannot yet tell you details, but the details will be coming out soon. It's quite a complex analysis. We've used our radio-collared hares. It's a complex analysis because of the changing phenology of the hares and accounting for the changing seasons and other forms of mortality, missing observations.

But there are some complications. Marketa, my student, will talk some about the results more in detail at the Conservation Biology meeting later this month. We're working on a paper. I will say that we do find a signal indicating non-trivial costs to being mismatched. We do find a cost to hares in terms of survival of being mismatched.

If we have mismatched hares, and they are more vulnerable to being killed when they are mismatched, then the next critical question...I think this has not been well considered for many cases in terms of climate change. The really critical question is, what do we expect to happen?

As I said, a lot of times, we tend to think, "Oh my gosh. Let's figure out how to move them or let them move." Or we say, "They can't move. That means they're doomed." But there is, of course, this third option, this potential ability for hares to adapt. They can adapt through either plasticity or through natural selection.

We have begun to consider plasticity. I've already told you that they have very little plasticity in terms of the coat color change itself. The initiation date in the fall and the spring are fixed, there's a little bit of plasticity to slow down or speed up the rate of change in the spring, but if there's no snow before they initiate, they're going to be mismatched.

Can they adapt through behavioral plasticity? Well, so far, we don't see a signal of this. We've looked at the obvious things that hares might do to be able to adapt to mismatch. We find that they do not conceal themselves in vegetation more when they're mismatched. Of course, this assumes that a hare looks down at itself like an emperor with no clothes and then decides that it better do something about it and gets behind some bushes or behind a tree. We don't find a signal of that.

We don't find that hares flee at further distances with increasing mismatch. Instead, their flight distance seems a lot more tightly linked to their concealment, not to mismatch per se.

We find that hares don't look around, at least not at the local site level, and plop themselves down in a place that matches their coat color the best. As Marketa has said, they didn't get the memo for the dress code, and so did they look around for the site that best fits the dress code. Instead, if there's areas with snowy and non-snowy places, they tend to prefer the bare ground places.

This is not to say that there is no potential for plasticity of hare behavioral plasticity. There's lots of other ways to look at it and consider it. Just we haven't found it so far.

So, limited plasticity in the coat color change, limited plasticity in the behaviors. What about the ability to adapt through natural selection? This is the next big direction where we'll be taking this project, so I don't have a lot to tell you on this yet, but I will say...Actually, I guess I'll back up here and stay for a second.

At first, I think, this can strike people as crazy to even be thinking about natural selection, but it's only crazy if you think about natural selection as being all about fossils and speciation and thousands of years. Then it seems impossible to imagine that it's relevant.

But, actually, I would say that some of the most exciting developments in biology with respect to climate change in the last two decades has been the understanding that evolution actually can happen quite fast on ecological time, and it can lead to quite strong morphological, behavioral, biochemical changes.

Natural selection can be a relevant factor on ecological scales, especially if the Biology 101 attributes of natural selection are fulfilled. That is, if we have a trait that's variable, if it's under strong directional selection, that is, it affects fitness so it's under strong directional selection and it's heritable. We are interested in asking the extent to which this could be true for snowshoe hares.

What I'll tell you a little bit of what we thought about, and what we've done so far and then where we're going next.

Variable traits. This is a classic variable trait. This is a kind of trait that if you were natural selection, you would love to act on. This is a variable trait both within populations and among populations. Let's talk about each of those.

Within populations, different hares definitely change their coat color and there is plasticity in the rate of coat colors within populations. This is one of our study sites, one year, one day, and you could see that the full range of possibilities are available. Here's a white hare on whiteground. Here's a brown hare on brown ground. Remember, this is the same site, same day, and in fact, there because you can see the snow patches and the hares are different colors. Then youcould have white hares on brown ground, brown hares on white ground. There's definitely variability to act, for selection to act on.

This is looking at the same thing. For one population, one year. Each green dot is an observation of a hare on a given day. Again, this is going across the calendar and from hares that are all brown to all white. Yeah. We're looking, here, in the spring, they're all white. Then they start to change to brown. See, there's lots of variation so that, for example, on April 25th, you have hares that are everything from nearly completely white, they've begun to change, but they're still at 95 percent white, all the way down to close to about 5 percent white.

You see the full range. This is what natural selection could operate on.

Also, we know there's variability in the traits by looking at the species across this range. From most of the snowshoe hare range, they change from brown to white seasonally. But along the coastal region, for example, Olympic Peninsula, southwest British Columbia, there are hares that do not undergo the white molt in the wintertime. They stay brown all winter.

There are, even, some very interesting populations that we're very excited about studying in the Cascade Mountains of Washington and Oregon, where in the same populations there are white hares and brown hares in the winter in the same population.

Similar sorts of cross population variability plays out for the Lepus timidus, the mountain hare, which is in Europe and Asia. In particular, so far, we know of at least one population in Ireland of Lepus timidus that stays brown during the winter, doesn't undergo coat color molt.

This is definitely a variable trait. That's what natural selection likes to have in order to operate on, be able to change phenotypes quickly. It’s a variable trait within populations and among populations.

Does the trait affect fitness? We're pretty confident, and becoming more confident almost on a daily basis, at this point, that it does indeed affect fitness. We see limited plasticity either through the coat color change timing or through behaviors. As I say, our analysis, it's still preliminarily at this point, pointing towards a fitness cost of mismatch.

The next question is, is it heritable? What would be the mechanism by which natural selection could operate? What would be the genetic basis by which natural selection could operate to change this trait, and how fast could it change with potentially the timing or rate of the coat color change?

To go down this path, we will be linking our field data. We'll keep doing our field data, and we'll link that with the marvelous world of genomics, transcriptomics and genomic approaches that will, hopefully, ultimately take us down the path towards understanding candidate genes for the coat color change.

This is something we've just begun working with colleagues here at University of Montana, Jeff Good, and our colleagues Paulo Alves and Zef Ferreira at the University of Porto.

We've just begin this, but I'll show you some more, really, hot off the press results. This is just from the last month or so. I guess, this header didn't show up very well, but it says, "The initial transcriptome sequence analysis." This is our very, way initial beginning of our genomic analysis. What we focused on, the sort of low hanging fruits of this, is the focus on that polymorphic population that I mentioned in the Cascade Mountains.

We've sampled it several times. We haven't yet collected field data there. We've sampled quite a few individuals from there so this analysis is based on 10 snowshoe hares, all of which were collected in January. Six were brown, four were white.

In the world of genomics, it's just amazing that 46,000 genetic markers that we've been able to analyze so far in this very preliminary run. In general, the differentiation between the six brown and the four white individuals, F_{ST} as a measure of genetic differentiation, in this case, between these two color groups is quite small. It's quite small F_{ST} and that's not surprising.

You wouldn't expect to see a huge differentiation between brown and white hares found in exactly the same spot. But interestingly, we do so far have almost 2,000 outliers as genetic markers. These could include markers that with more work may become candidate genes that help us understand the genetic basis of the seasonal coat color change.

No silver bullet yet. I can't announce to you that we've found the white gene, or the brown gene, or the coat color gene or anything like that. This will be, most likely, a long process. It will include some captive breeding. In fact my new job, amazingly, at North Carolina, they're building me what they laughingly call the "Hare Chiller" on the campus at North Carolina State. So I'm out there, I'll actually have a subzero temperature controlled chamber.

As far as I know, there's nothing like that in use anywhere for looking at seasonal coat color change. We'll be able to look at that mechanism to coat color change and things like that to the genomics.

The engineers love the challenge of coming up with a subzero temperature chamber in Raleigh, North Carolina summertime.

This shows us the big picture. The grand vision or hope that I have for this project. Really, in order to answer this question, can any trait, but in this case we think camouflage is a nice trait, can camouflage keep up with climate change? To do that, we have been and will continue to quantify the extent of mismatch, the adaptive cost of being mismatched. Continue to work on the snow downscaling, that I talked about that we did in the PNAS paper, so that we can get realistic models for snowpack that are relevant to the animals themselves, and understand the drivers of the coat color change and of the mortality.

If we can do that, then we, actually, can understand the rate at which the animals might be able to adapt by either plasticity or through evolutionary changes. Then from that, we hope to again link that to what we've been doing since 1998 in terms of studying population dynamics. We can understand the consequences of mismatch on survival rates then we can put that into population projection models that we've been working on all these years to understand hare population dynamics. And get to the sort of end point, the very exciting, I think, important endpoint of to what extent will climate change be likely to actually change the population dynamics of this particular species that is important by its own right, and also very important as a strong ecosystem interactor?

That is where we're heading, and it's complex and exciting. More complex than this. This was an interview, an article that came out. Notice the date. This was one month after I got the funding from USGS Climate Science Center to begin this research so I hadn't even ordered the first radio collar. Hadn't even ordered...We had done nothing, actually, on this project, but it was announced in the title that this is a disappearing rabbit, that they're vanishing.

Of course, many of you will know there's two errors in this title. One is that these are hares, they're not rabbits. And the other is that we don't, really, know anything at this point about them disappearing, but we do hope to get to that point.

With that, I'd just like to end by thanking a lot of people, a remarkable group of graduate students and undergraduate students. Both field assistants, we have 10 of them out in the field right now, four of them working on senior thesis projects. It's been a labor of love for lots of folks.

As I mentioned, the genetic work is being done in collaboration both here at Montana and at University of Porto where the rabbit genome is sequenced so there's this historical reason to do that. Paul Lucaks has helped us a lot with a lot of the, really, complicated Bayesian modeling that we have to turn to with this kind of analysis here.

Obviously, the funding and administrative support. This, really, goes all the way back to 1998, but has been just terrific across lots of different federal and state agencies.

So with that, let me see, I'm going to check my attention meter and see...Oh. [laughs] We've got some sleepers, we've got some people texting, but nevertheless, I'm happy to answer questions. Wake up everyone.

Christy: OK. We'll now be open to questions. OK. Our first question is from Kevin McCarty. Go ahead and unmute your phone, please?

Kevin McCarty: Yes, this is Kevin McCarty.

Scott: Hi, Kevin.

Kevin: Hey, how's it going?

Scott: Good.

Kevin: Yes. My first question...Actually, I have two if you don't mind. My first question is with the phenomenon that you found in the Olympic Peninsula area, the ones that did not change color. Was there a recording towards what the elevation was that these hares were found at?

Scott: Yeah. I haven't particularly done any work on hares in the Olympic. This is based on what is really well known in terms of natural history of the Olympic Peninsula. As you know,the Olympic Mountains go really quickly out to sea level so the hares tend to be at what we, here in Montana, would consider to be quite low elevation. They're not found in the boreal area. They're at relatively low elevation, and of course, it's maritime climate at the Olympic. No, I can't speak to any specifics of elevation, but just to say that, in general, the hares are found in relatively low elevation. They end up with many times not having winter long snowpack.

Kevin: OK. Then to the second part. I want to ask you if there was any research or any side research that looked towards the predators that are, actually, feeding upon the hares, if they are having any kind of effect with the climate change, as well, if that could be any kind of contributing factor?

Scott: Yeah. This is a really good question. It's obviously a lot harder to get a handle on predator's dynamic, tracking something like this. But John Sidle, here at the Rocky Mountain Research Station and his research group, have been studying Canada Lynx in exactly these study areas since, basically, the same year I started studying hares. John and his group have been studying Lynx. We haven't formally connected that, but there's lots and lots of years of Lynx telemetry data and we are working together. I guess, the short answer that question is not so much, but definitely interesting and important.

Kevin: OK. Thank you very much.

Scott: Thank you.

Christy: Our next question is from Erik Beever. Can you, please, unmute your phone, star six, please?

Erik Beever: Hey, Scott. Congratulations on the new position, the PNAS paper and the "Hare Chiller." I'm wondering if that might be a treatment for baldness, as well, that "Hair Chiller?"

Scott: [laughs] Thanks, Erik. I'll look into that.

Erik: [laughs] Good. In your slide about the projected mismatch of hares, you had snow-off as a one day phenomenon. I have a follow up question, but can you discuss that real quickly?

Scott: You mean the vertical line that was a snow-on, snow-off date?

Erik: Yeah. Snow-on is plausible, but I didn't understand how that could be a one day phenomenon for snow-off?

Scott: Yeah. Obviously, that's taken a semi-continuous phenomenon where I was showing our field data where I was showing the snow comes, it goes, it comes, it goes in the fall. In the spring, it goes, it comes, it goes. So it's taken a continuous event and making it dichotomous. Basically, we came up with the criteria for continuous snowpack from the climate modeling, and we used that as a threshold. One thing we did find, though, was those dates that came from the climate modeling corresponded really well to our field data where we were out there every week taking pictures of the snow around every hare. We had this nice field measure of when the snow came and when it went weekly. That corresponded really well to the models on off dates that came from the climate models.

Erik: OK. Great. Secondly, this is stepping back a touch. You talked towards the end about adaptability and the process either of through behavioral plasticity or through natural selection. Can you talk about, let's say, first within hares, which individuals might be most likely to be able to adapt? Would you come at that from a purely genetic perspective? Also, if you want, which species might be most likely able to adapt?

Scott: Yeah. That's a great question. It's obviously one that is a huge management relevance. It's a point that I expand on a lot more when I give talks like this or I give climate change talks to, for example, land manager groups. As far as I do think, it gives a ray of hopeand it gives an action item that land managers can do when they...Land managers can't necessarily do anything about carbon footprint, or carbon credits or CO2 output. They can do something, I think, to facilitate adaptation. That is, again, by the basic principles of natural selection, we expect the force of natural selection to operate the best when the population is large, because if the population gets small, genetic drifts can overwhelm selection. Maintain populations that are large enough to respond to selective forces, that have a moderate level of gene flow among populations. That is not so much gene flow that local adaptation might be swamped. Not so little gene flow that adaptive variance can't arrive in a population.

So those are two things, maintain relatively large populations, relatively well-connected populations and also, going along with those, minimizing the other stressors that are operating on here. I always think about this for any species, is being confronted by an anthropogenic stressor, the best possibility for it to adapt is to give it more latitude for adaptation through minimizing other stressors.

Not to say that any of those three things are easy, of course, but those are action items that people could do at a local level.

As to which species, of course, for other life history traits, obviously, things like rapid generation time, generalist life history habit, those would also lead to more rapid adaptations as a general rule of course, as a general theoretical rule.

Hares are pretty well suited for that. Hares aren't rabbits so they don't have the kind of intrinsic growth rate that rabbits do, but they still are pretty well suited for rapid...They have relatively fast generation times. They are, at least in some ways, relatively general.

Erik: Thanks. Excellent presentation.

Scott: Thank you.

Christy: We have another question from Sean Sultaire.

Scott: I don't take any questions from that guy. I'm just kidding. He was one of our field assistants.

Christy: [laughs] Sean, if you could press star six, unmute your phone?

Scott: I was just kidding, Sean.

Christy: [laughs] OK. While we're waiting for him to get on, let's go to our next question. It's Carol...

Sean Sultaire: Hey, Scott?

Christy: Oh. Are you on?

Sean: Did I make it on?

Christy: Yes, you did.

Sean: OK. I think I pushed pound six on that one. Great presentation, Scott. It seems like a lot has been going on since I left, definitely. I had a question about the scale of inference for predicting future snow cover and population dynamics, if that's going to be limited to the current study area or more broadly across Southern portion, like Southern hare populations.

Scott: Yeah, no, that's a good question. I mean, I think to the extent that we can unravel mechanisms, then obviously, that's going to increase the generality. I mean, if all we're doing is describing the phenomenon of increased mismatch and mortality for hares in this one area, then that's not very generalizable. Then we have to basically to, repeat that for everywhere in the world and every species. But to the extent that we can unravel mechanisms of the role that plasticity might play, mechanisms of the way in which natural selection might act to change the initiation date of the coat color change, then it seems that it would be very generalizable.

The goal, the wonderful thing, would be to get, essentially, a measure of, "OK, with this much mismatch, here's the force of selection, and here's the adaptive response that these species are capable of." Even that, once you understand the mechanisms, you could start asking that for other species with coat color change, or other species that have phenological mismatch.

Sean: Going along with that, just one more question, if you don't mind. I know you've done some landscape genetics in the past, across snowshoe hare range. You found for most southern populations there was not a lot of genetic divergence from the core Boreal population, consistent with the core-periphery hypothesis for range-boundary genetics. I wonder how you think that could play into this species' adaptive response to changing snow conditions.

Scott: Yeah, I think I kept in here, I put this as an extra slide in here. Can you guys see that? Can you see the new slide I have?

Sean: It's up there on mine.

Christy: Yes.

Scott: This is the landscape genetics project that Shawn is referring to that was done by my student Ellen Cheng. It was quite interesting. We found three distinct genetic groups -- the Boreal group across all of Canada and Alaska, a Southern group which, as Sean mentioned, does have lower heterozygocity, then what we call a Coastal group. This shows a few different things. One interesting thing that I hesitate to say much about, but I will anyway because, hey, there's nobody here. I'm just talking to the computer -- just kidding. The Coastal group includes the only hares that we know of that retain brown coats during the winter.

This is only in review right now, but we find that there's actually introgression into these snowshoe hares from black-tailed jackrabbits, which are the only Lepus species in North America that does not undergo seasonal coat color change.

Not to overplay it, or say that we found a silver bullet gene that black-tailed jackrabbits have given them the gene to stay brown, but it does imply that that might be a piece to understand the evolutionary history of hares, even with respect to coat color change of that grouping.

Sean: Very interesting.

Scott: Thanks.

Sean: Thanks, Scott.

Christy: OK, our next question is from Carol Mladinich.

Carol Mladinich: Pretty good. I am interested, when you talk about the changing snow conditions and what they're doing. You say they're snow downscaling. Can you talk a little bit about that? Is it because of the scale of the snowfall data that you're using?

Scott: What do I mean by snow downscaling? What I mean by that is, instead of trying to connect these phenologic changes of the hares to some really big snow prediction, like what you see in IPCC report. You know, where you see giant regions with changes in snow cover, or you see whole continents or whole countries? Those are kind of hard because there's so much variability within those regions. The snowpack over just several hundred kilometers can be really different. In fact, as we found in our two different study sites, the snowpack was really different, just because they were 1300 meters different in elevation. It's a really broad-brush trying to link biological changes to physical drivers or physical changers, if you only have this really broad-brush of regional or continental predictions of snow.

Carol: A higher resolution snow?

Scott: Exactly. With the climatologists here, we were able to come up with descriptions of the past and predictions of the future, that were relevant to these particular animals of these particular study sites.

Christy: We have our next question. It's from chat. It's from Rachel Muir. She asks, "Do snowshoes interbreed with any closely related species? Are hybrids viable? I have seen reference to a Brier Island, Canada subspecies. Their phenology might be instructive".

Scott: First, was the second one, what island?

Christy: Brier. That's B-R-I-E-R.

Scott: I've never heard of that. Yeah, I would love to hear about that. I've never heard of Brier Island. Yeah, definitely, I would love to hear more about that. As for the first question, it goes back to what I mentioned in answer to Sean's question, that we do see a signal of hybridization from black-tailed jackrabbits, ancient hybridization. I mean, this would be tens of thousands of years ago, or more.

Some black-tailed jackrabbits, we don't see that currently. That is an interesting question. What were the conditions which led to that. Does that happen now? We don't see that hybridization in other parts of the hare range that are sympatric with snowshoe hares.

I guess the short answer is that we don't have any reason to see, right now, that there's hybridization from any of the congeneric species with the snowshoe hare. But, we do see a signal that it has occurred at least once in the past with the black-tailed jackrabbit.

Christy: Our next question is from Kerry Holcomb. Kerry, could you please unmute your phone?

Kerry Holcomb: My question is about your genetic analysis. I know you're just getting started down this road, but do you anticipate that the difference in coloration is going to be led mainly by a genomic difference, or just purely an expressional difference? Like an embryological difference.

Scott: You're exactly right. That is very complicated. Yeah, definitely, that lies in the question that I'm sometimes asked, "Are you going to find the coat color genes?" Because, yeah, as you say, not only is it likely a suite of genes are involved, but also there's all these regulatory, there's lots of regulatory changes that cascade in and make it much more complicated. I'm guessing, just based on what's known from the genetic basis of coat color which, of course, for mammal coat colar has been really well studied in mice and dogs and horses. The coat color, the genetic basis, the complex genetic basis for coat color, or non-seasonal, just background coat color is pretty well understood. But, it's also known to be pretty complex.

I'm imagining that seasonal coat color will have all the complexities of the mammalian coat color plus all the additional complexities of being a circannual process.

Kerry: Yeah. There could be some really deep methylation patterns or all kinds of different fun stuff going on.

Scott: Yeah, right. I bet it won't be easy.

Kerry: Well, good luck. Great job.

Scott: Thank you.

Christy: OK. I'm just looking here at the participant list and I don't see any more questions. Do we have more questions before we close out the presentation? OK. All right. I'd like to thank Scott for a great presentation.

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