Snow Dynamics and Mountain Fox (*Vulpes vulpes macroura*) in Yellowstone: Incorporating Climate in Species-Habitat Models

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Abstract

Snow pattern dynamics in northern temperate regions exert a critical regulatory role on a multitude of ecosystem processes. Snow cover onset and ablation, snow-water equivalent (SWE) patterning, snow-pack penetrance (over-snow travel; access to prey in the sub-nivean space), and timing of major snow events are all important to terrestrial animals. As climate patterns shift, changes in patterning of snow dynamics may exert important adaptational influences on animal ecology and energetic budgets. Snow data are available from remotely sensed, in situ measurements, and modeled estimates, but a consistent set of approaches for assessing the ecological impacts of changing snow metrics has not yet been realized. Access to standardized low/no-cost snow covariates for animal-habitat models remains an important goal that has ramifications for both management and research. We investigated the winter use patterns of mountain red fox (*Vulpes vulpes macroura*) on the northern range of Yellowstone National Park (YNP) and evaluated snow cover and SWE alongside more traditional habitat attributes. We found that SWE is an important determinant of habitat use by red fox on the northern range of YNP. Based on SNOTEL and observational data, we suggest that snow-hardening events may also play a key role for mountain fox foraging success in YNP and contribute to a mechanistic explanation for why SWE is important.

Introduction

Snow in northern temperate regions (such as Yellowstone National Park, YNP) governs many organismic processes, including herbivory, across-snow travel and migration, and predation in the sub-nivean space. Snow can be thought of as a highly dynamic landcover type with the potential to exert strong effects on animal space use patterns. Snow cover occurs in Yellowstone from November to June and mean daily minimum temperatures average below freezing for eight months of the year (Newman and Watson 2009). Snow cover's effects on what constitutes available habitat and prey are as yet only generally characterized in the heterogeneous winter environment of YNP.

Red fox are an important medium-sized carnivore in YNP and are one of the three species of canid (along with wolves, *Canis lupus*, and coyotes, *Canis latrans*). During the 1880s numerous fox with a variety of coat colorations were seen in YNP (Norris 1881), so it is known that fox were present when the Park was created. Prior to the 1950s, red fox were rare to absent from the lower elevations of Montana, and it appears that fox ranges were originally restricted to the mountainous, western, and southern parts of the state (Fuhrmann 2002). The indigenous Yellowstone fox appears to be the montane form, and is generally nocturnal and shy. It is common in forested habitats containing adequate densities of essential small mammal prey in and around the Yellowstone region. These fox can be seen mousing along ecotones, foraging at carcasses, especially during winter, and traveling the forest edge, particularly at dawn and dusk periods.

Red fox have been well studied in YNP (Crabtree 1993, 1997; Fuhrmann 1998, 2002; Van Etten 2006; Van Etten et al. 2007). Habitat use is well-characterized at a fine scale (Van Etten et al. 2007) and the relationships

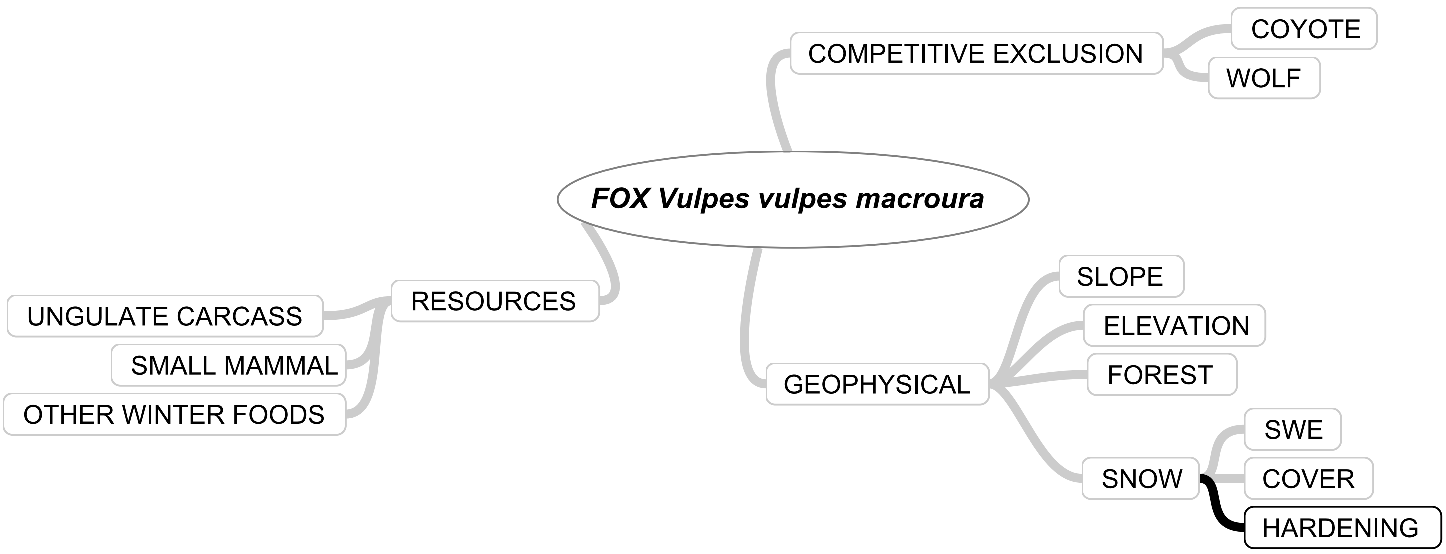

Figure 1. Fox-habitat relationships.

with prey and competitors have been characterized (Crabtree and Sheldon 1999; Gese et al. 1996).

This highly specialized boreal forest carnivore exists at all elevations throughout YNP, with a continuous distribution through the adjacent wilderness regions of the Beartooth Plateau, and it occurs at elevations up to 10,000 feet during the winter months. From a general ecological perspective it is useful to examine the potential structuring effects of snow on fox spatial use patterns. Furthermore, in snow-dominated alpine and subalpine landscapes, the YNP fox can be seen as a sentinel species for climate change, providing insight into snow ecology in the severe winter environments, within the context of the larger system of predator, prey, and geophysical constraints in this severe winter environment.

We followed the systems approach of Kausrud et al. (2008) who examined meso-carnivore and snow dynamics in Norway. These authors investigated the larger context of an integrated community of predators and prey strongly influenced by snowpack dynamics. They found warm periods during late winter are increasing in their system. At the same time, the cyclicity of small mammal populations has dampened, which in turn appears to be linked to declines in the predator populations. Thus links between global climate shifts and regional to local snow dynamics and concomitant effects on predator-prey dynamics are suggested. In YNP we are interested in beginning to work out characterization of snowpack dynamics with respect to the fox/small mammal populations.

Methods

In working with complex geophysical covariates such as snow, where mechanisms potentially exerting effects on organismic space use or habitat selection are not yet understood, we find it helpful to visualize the fox-habitat system, framed in terms of testable covariate relationships (see Figure 1). We think about the influences on fox habitat use in three general categories: 1) geophysical constraints—these are the classic habitat or landscape metrics used in most animal-habitat models and include slope, elevation, and snow metrics; 2) energetic covariates, or food; and 3) dominant competitors or hazards—in the fox context this includes coyotes, which we know from previous research in YNP and elsewhere can strongly condition where fox spend their time. We then draw the actual model from this idealized universe of possible space-use determinants and define the list of covariates that we actually have on or have the capacity to create (Figure 2).

We evaluated the relative effects of snow cover and SWE within the context of a conventional habitat model for red fox, based on from ground-telemetry data from the Lamar Valley on the northern range of Yellowstone. Data from a single representative winter season (2003–2004) were used, a time period during which eight fox were radio-collared in the Lamar Valley. We used the following covariates (explanatory variables) in the statistical model:

- Elevation (from Digital Elevation Model)
- Slope

Soda Butte Creek and Abiathar Park, located in the northeast portion of Yellowstone National Park.

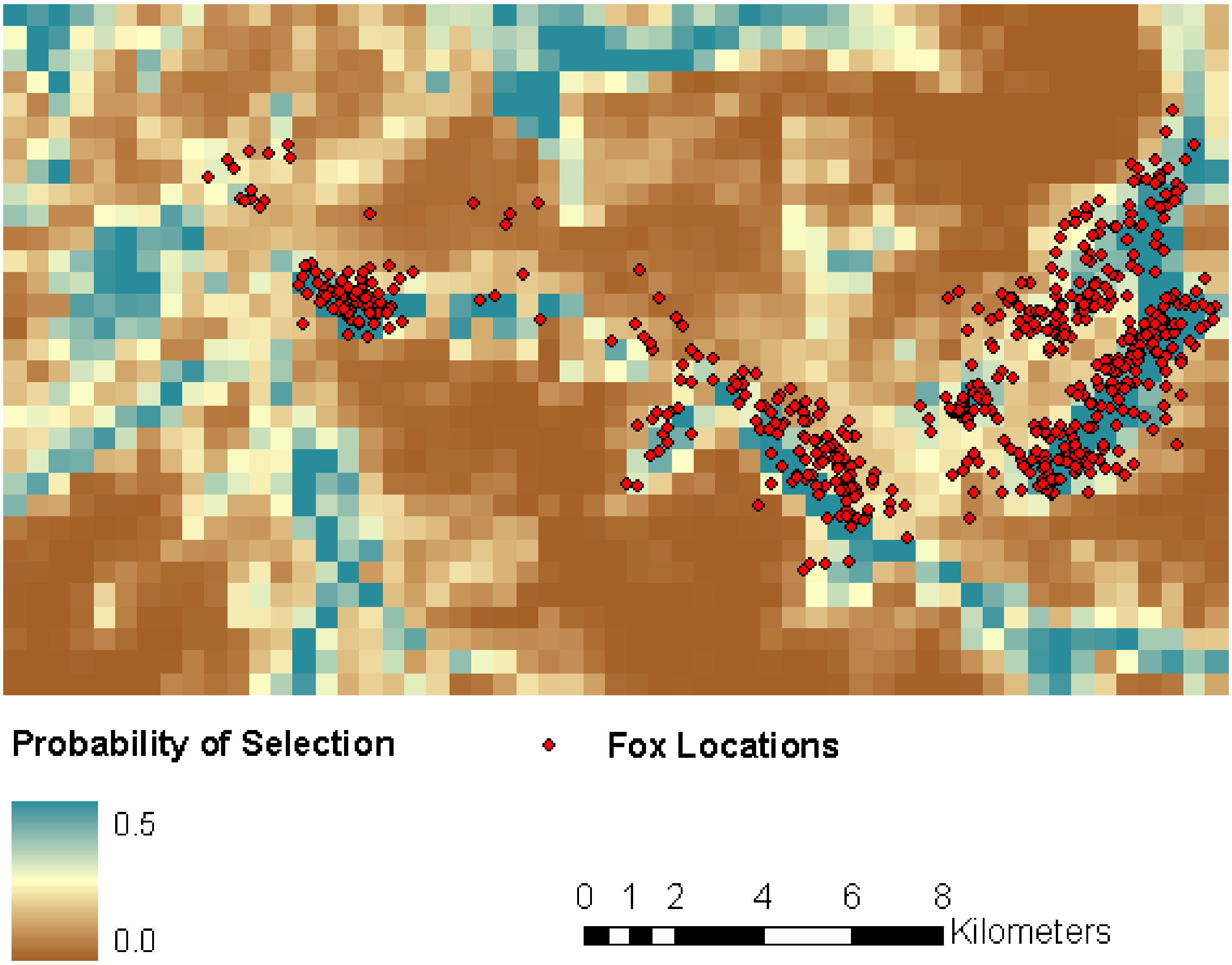

Figure 2. Red fox locations (ground telemetry, winter 2003-4) are shown as red points, superimposed over the the fox Resource Selection fit surface (tan/blue color ramp). The resource selection model was run in 'R' code, within an ArcGIS platform. Probability values indicate the likelihood of fox use, according to the model.

Table 1. Model output from fox-snow habitat resource selection.

Parameter Estimates	Coefficent	SE (coeff)	t-value	p-value	vif
Intercept	-2.431	4.56	-0.53	0.590	NA
Elevation	-0.511	0.40	-1.28	0.201	4.1
Forest	0.292	0.25	1.18	0.239	1.3
Prey biomass	-0.196	0.08	-2.43	0.016	1.3
Slope	-0.269	0.15	-1.82	0.070	1.3
SWE	-1.857	0.27	-6.86	0.000	2
Snow cover	-0.154	0.08	-1.9	0.058	1.1

- Forest (percent forest cover)
- Sagebrush cover (percent)
- Small mammal prey (a modeled estimate from the preceding summer)
- Snow cover (MODIS snow cover product)
- Snow water equivalent (SWE)

We used resource selection probability function analysis (Lele and Keim 2006) to assess the contributions of these covariates to the patterning of fox space use.

Results and Interpretation

We found that snow, in the form of SWE (snow water equivalent; the amount of water present in a column of snow) was an important influence on where fox spent their time (see Table 1). The quadratic form of the response shows that fox do not select for areas of very low or very high SWE, preferring areas of intermediate SWE. We found that snow cover was marginally important. Elevation, which often dominates species-habitat models, was not an important predictor of where fox spent their time. This makes sense ecologically, since fox distribution is continuous from the lowest elevations in YNP (and below) up to the alpine environment on the Beartooth Plateau. Fox selected for habitat characterized by higher biomass of prey, but only up to a point, thereafter avoiding areas of highest prey density that may be associated with higher exposure risk to coyotes. This patterning may also be confounded by competitive avoidance strategy or possibly with SWE effects. Forest was not an important determinant of habitat selection at the 500 meter (m) spatial resolution of the original model; however, when the forest term was run at a 30 m (much finer grain) resolution, it became important, confirming the results from Van Etten et al. (2007) where fox show great finesse with respect to their use of forest and forest-edge habitats.

Finally, outside of the resource selection analysis, we investigated preliminary approaches for modeling snow-transformation (snow-hardening) by looking at data from the adjacent northeast entrance SNOTEL site and matching that snow data record to empirically observed fox captures, which typically are associated with periods of food stress (Figure 3). We speculate that an observed snow hardening event (rain-on-snow, accompanied by a warming then freezing temperature oscillation) during late February resulted in a surge in captures due to fox "shut-out" from access to prey in the sub-nivean space, demonstrating empirically the contribution of snow-hardening events to fox food availability, and pointing toward avenues for further investigation.

Conclusions

Changes in snow-pack dynamics and their effects on ecosystem function and biodiversity may exert strong effects on trophic interactions. Ungulate winter herbivory patterns, as well as prey access by terrestrial carnivores

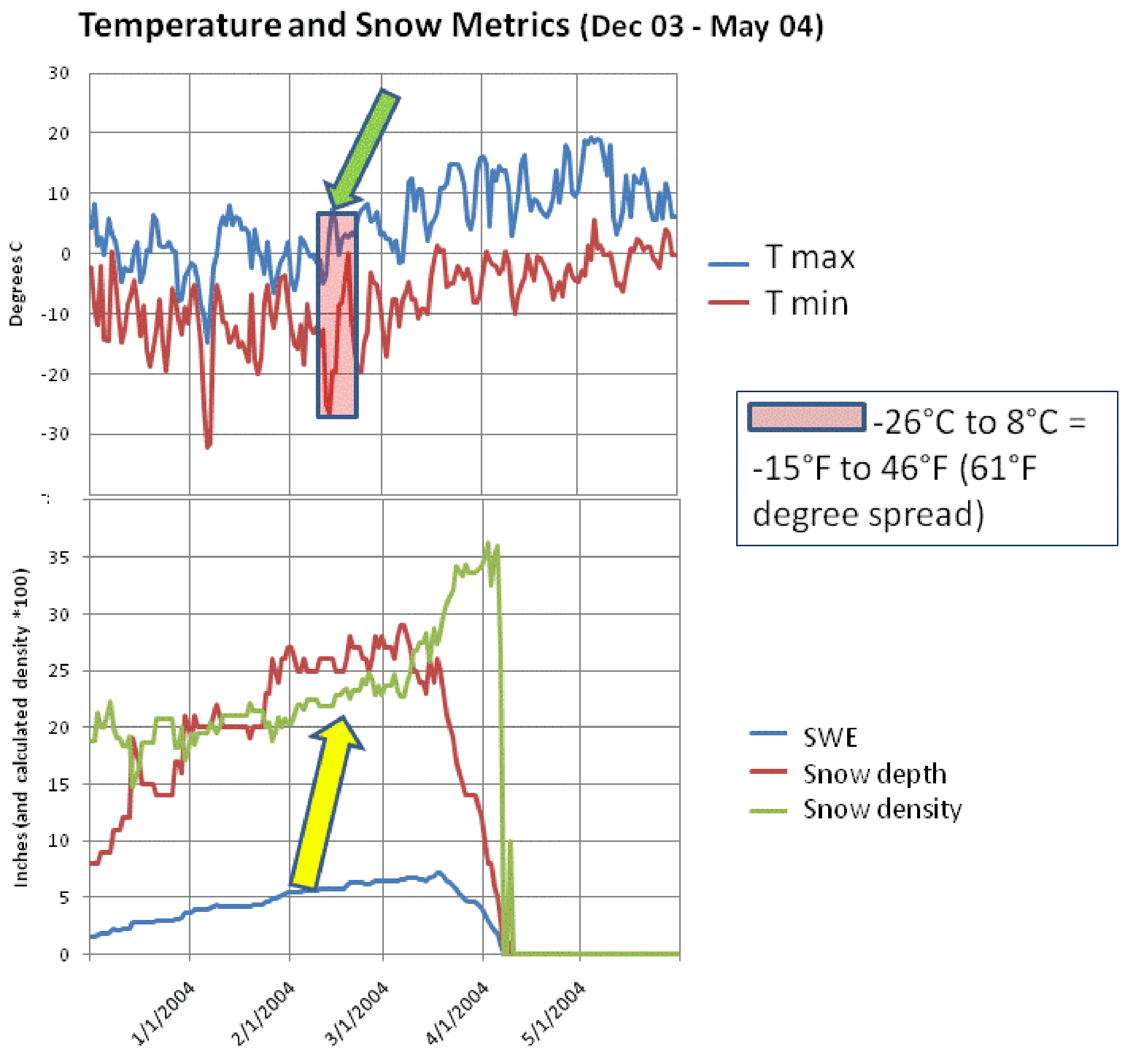

Figure 3. Snow water equivalent (SWE) and snow depth data taken from the northeast entrance SNOTEL site adjacent to the study area in Yellowstone National Park. Snow density was calculated as SWE divided by snow depth. Note the snow hardening events (increased snow density values) that occurred during February and March prior to snow ablation (final meltdown) in mid-April.

(both over snow and below snow) are affected. The mechanisms through which snow may influence the patterning of animal-habitat relationships is not yet well characterized, or supported by theory.

Climate-driven snow-attribute changes may be relevant to a more comprehensive set of ecosystem dynamics, including carnivore across-snow predation (e.g., the wolf-ungulate system) as well as more comprehensive food web interactions. These food web interactions include all predation in the sub-nivean space by other meso-carnivores, such as mustelids, as well as herbivory (winter access to forage) by ungulates.

Snow hardening events, particularly those accompanying springtime conditions, impact fox winter ecology by enhancing snow mobility. During this study, fox were observed making longer range movements during the brief periods that the snow surface "set up." If, as Kausrud et al. (2008) suggest, changing seasonal temperature and precipitation regimes exert effects on snow subsurface and surface attributes, then we may expect to see a continuing suite of impacts on fox prey access, mobility, and energetics in YNP.

Suggested Citation

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