Climate change and food webs: jackrabbits, pronghorn, and coyotes in southern Greater Yellowstone

2011 Annual Report

by

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Summary

My research focused on two main objectives: identifying effects of snow depth on white-tailed jackrabbit density, and identifying the effect of jackrabbits on pronghorn fawn survival. For the first objective I measured an index of jackrabbit density using scat plots in three sites along a snowdepth gradient in the Upper Green River Basin. In addition to snowdepth, I measured vegetation and ungulate density in each of the three areas. Jackrabbit density was similar in the sites with highest and lowest snowdepth, but density was lower in the site with intermediate snowdepth. Sagebrush canopy cover and ungulate (specifically elk and deer/pronghorn) density varied along the gradient, but I found no associations between jackrabbit density and either ungulates or vegetation. Data to be collected in 2012 and 2013 will allow a more detailed investigation of the effect of snow on jackrabbits.

For the second objective I measured pronghorn fawn survival in three areas with jackrabbits (the Gros Ventre Drainage and two sites in the Upper Green River Basin) and two areas without jackrabbits (Antelope Flats and Elk Ranch in Grand Teton National Park). I used fawn:doe ratios in late July and early August as an estimate of fawn survivorship, and used pellet counts in scat plots as an index of jackrabbit density. At each site I also conducted scat counts along trails as an index of coyote use. Preliminary data suggest that, as expected, fawn survival decreases with increasing coyote use. More intriguingly, my data also suggested a trend of increasing fawn survivorship as jackrabbit density increased. If this pattern holds over subsequent years of data collection, these data suggest that pronghorn fawn survival in Grand Teton National Park may be adversely affected by the functional extirpation of white-tailed jackrabbits at the site.

Background

White-tailed jackrabbits (*Lepus townsendii*) disappeared from Grand Teton National Park (GRTE) sometime between the 1970s and 1990s for unknown reasons despite persisting in the nearby Gros Ventre Drainage and Upper Green River Basin. National Park Service (NPS) policy is to reintroduce extirpated species when (1) ecological conditions are favorable, (2) the species does not pose a risk to park resources, (3) populations with similar genetic history are available as source populations, and (4) humans played a role in the species' extirpation (NPS 2006). Current lack of knowledge concerning all four of these criteria prevents an evaluation of white-tailed jackrabbit reintroduction to GRTE as a management option. My PhD dissertation aims to provide specific information on three of the four criteria listed above. I am specifically evaluating **(1)** the suitability of ecological conditions within GRTE (particularly snow), **(2)** what effect white-tailed jackrabbits may have on GRTE resources (pronghorn), and **(3)** what factors are associated with white-tailed jackrabbit extirpations in GRTE and elsewhere.

In 2011 I collected data on the first two of these objectives. To complete the third objective I will compare environmental factors at numerous sites across the western United States where white-tailed jackrabbits either persist or have been extirpated; that work has not yet begun and will not be discussed any further in this report. Instead my 2011 work focused on **(1)** white-tailed jackrabbit density along a snowdepth gradient in the Upper Green River Basin, and **(2)** the effect of white-tailed jackrabbits on predator-prey relations between pronghorn (*Antilocapra americana*) and coyotes (*Canis latrans*). 2011 was my first of three planned field seasons.

Objective 1: Effects of snow on white-tailed jackrabbit density

Background

White-tailed jackrabbit abundance may be strongly affected by snow, and deep snow in GRTE has been hypothesized to have played a role in the species' disappearance from the park (Berger *et al.* 2006). However, the effect of snow on white-tailed jackrabbit abundance is almost entirely conjectural.

White-tailed jackrabbits' seasonal coat-color change reflects an evolutionary history of adaptation to snow. Snowdepth in early winter affects survival of snowshoe hares (*Lepus americanus*), which are closely related to white-tailed jackrabbits. Too little snowpack decreases cover for hiding and thermal regulation and leads to a decline in snowshoe hare survivorship; conversely too deep snow limits hares' access to food and also reduces survivorship. Snowshoe hare survival is therefore highest at intermediate snow depths (Kielland *et al.* 2010). Severe mortality in response to the interactive effects of deep snow, extreme cold, and high wind has been reported in black-tailed jackrabbits (*Lepus californicus*; Stoddart 1985). Extreme cold and high wind also has a pronounced effect on white-tailed jackrabbit metabolic rate (Rogowitz and Gessaman 1990), but how snow affects this jackrabbit remains unknown beyond the anecdotal observation that they appear to avoid areas of deep snow (Flux and Angermann 1990).

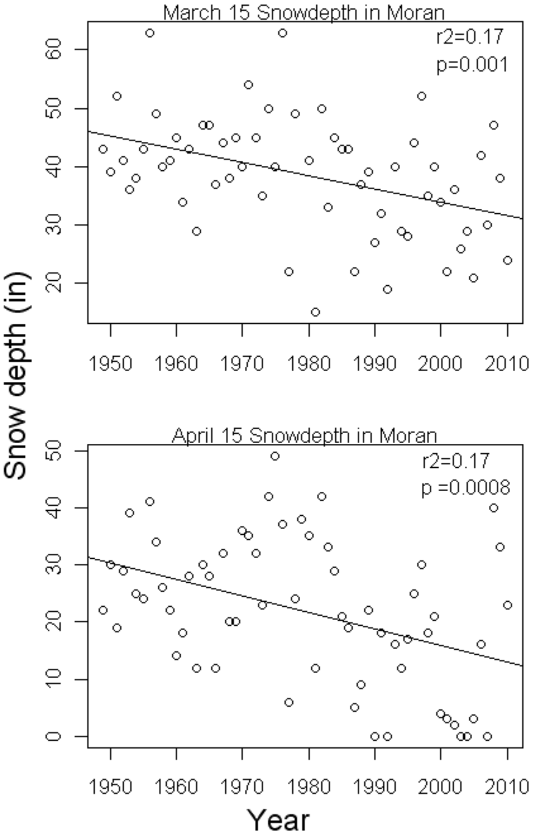


Figure 1 Late-winter snowdepth in Moran, Grand Teton National Park, from 1949 to 2010 (US Historical Climatology Network 2011).

Snowpack in southern GYE and other high elevation temperate regions is strongly affected by climate change, as warmer temperatures delay snow accumulation in the fall and accelerate snow melt in the spring. Winter temperatures in the GYE have been steadily rising over the last 100 years, with concomitant declines in snowpack (Wilmers and Getz 2005; Cheesbrough *et al.* 2009). In central GRTE, late-winter snowdepth has been declining over the last 60 years at a rate of approximately 2.5 inches per decade (Figure 1; US Historical Climatology Network 2011). My study aims to understand how white-tailed jackrabbit density is affected by snow, including the long-term prognosis for a potential population in GRTE.

To investigate how snow affects white-tailed jackrabbit distribution and abundance, I am investigating relative densities of white-tailed jackrabbits across a localized snowpack gradient in the Upper Green River Basin where winter snowdepth declines by half over a 50-mile span (Figure 2).

Study design

In the Upper Green River Basin, snowdepth declines along a north-south gradient in response to elevation change and localized wind and weather patterns. **I am capitalizing on this snowpack gradient to serve as a proxy for climate-induced temporal declines in snowpack**.

I can estimate associations between snowdepth and white-tailed jackrabbit density by measuring both – and other putatively important variables that affect jackrabbit density – across the gradient and analyzing them in a multivariate statistical framework.

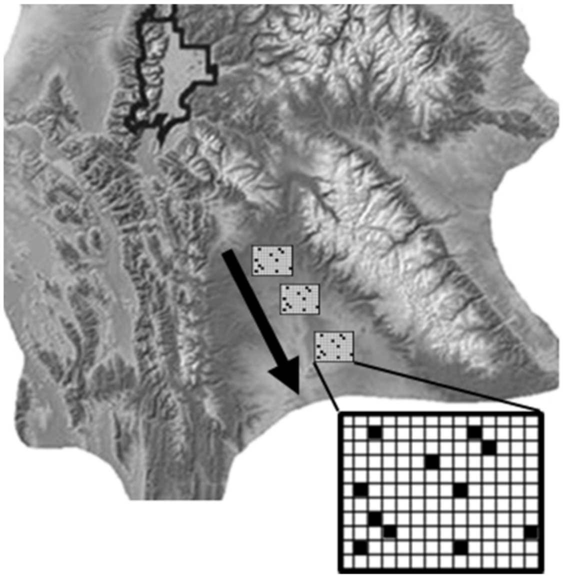


Figure 2 Sampling sites (not to scale) along the snow gradient in the Upper Green River Basin. Arrow indicates direction of snow gradient from deep to shallow.

Methods

In summer 2011, I sampled three sites within the snow gradient: one with deep snow, one with medium snow, and one with shallow snow. Sites were identified based on data collected by Beckmann *et al.* (2008), weather stations (US Historical Climatology Network 2011), and preliminary data collected in March 2011. At each of the three ~10mi^2 sites I overlaid a grid of 200m x 200m cells and sampled 15 randomly-chosen grid cells (3 sites with 15 cells each, for a total of 45 grid cells; Figure 2). In each grid cell I indexed jackrabbit and ungulate density using pellet counts from 10’ x 2” plots, with 5 plots per grid cell (Hodges and Mills 2008). Pellets were identified to species using standard field marks (Elbroch 2003). Snowdepth will be measured in each plot once per year in March 2012 and 2013.

Preliminary results

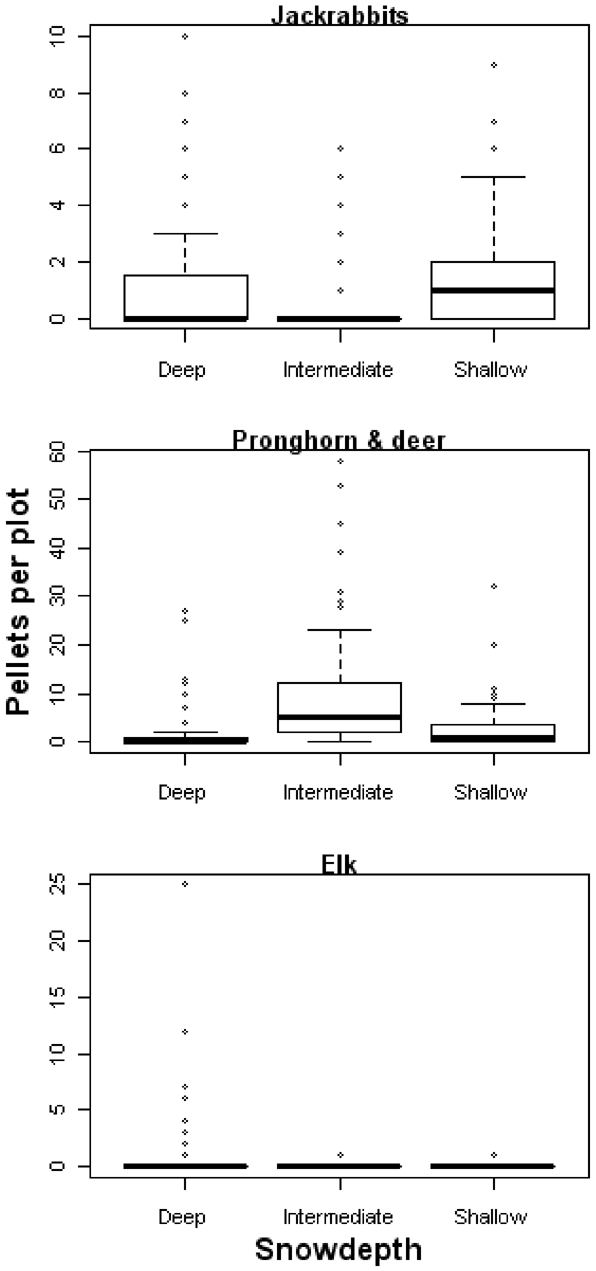
White-tailed jackrabbit scat density is significantly different between the three sites (X^2, $p<0.0001$), with jackrabbit scat density lowest at the intermediate snowdepth site. There are also differences between sites in elk density (X^2, $p=0.0001$) and deer/pronghorn density (X^2, $p<0.0001$), but not in the same directionality as jackrabbits (Figure 3). I found no associations between jackrabbit density and elk, cattle, or deer/pronghorn density when analyzing data either across all sites or within sites. Sagebrush density differs between the sites, as sagebrush canopy cover is greater at the deep snowdepth and intermediate sites than at the shallow snowdepth site. However, there is no association between jackrabbit scat density and sagebrush canopy cover (permutation test on jackrabbit scat density between sparse and dense sagebrush canopy cover, $n=129$, $p=0.23$).

Discussion

Sites in the Upper Green River Basin vary in three ways that might influence white-tailed jackrabbit density: snowdepth decreases from north to south, sagebrush canopy cover is reduced where snow is shallow, and ungulate densities shift along the snowdepth gradient. My preliminary data suggest that jackrabbit density is not associated with either ungulate densities or sagebrush canopy cover. As of yet I am unable to investigate possible associations between jackrabbits and snow, because I do not have direct snow measurements at each scat plot. I am collecting these data in March 2012 & 2013, which will enable a more thorough analysis of associations between snow and jackrabbit density.

My data on the relationship between white-tailed jackrabbit density and snowdepth show an unexpected relationship. I had initially hypothesized white-tailed jackrabbit density to either steadily increase with increasing snowdepth, steadily decrease with increasing snowdepth, or to maximize at intermediate snowdepth. Snowshoe hare (*Lepus americanus*) survivorship is maximized at intermediate snowdepths in early winter (Kielland *et al*. 2010), so it is surprising that white-tailed jackrabbit density appears to be minimized at intermediate snowdepth.

From the perspective of evaluating the suitability of snow conditions in GRTE for white-tailed jackrabbits, my results are thus far inconclusive. Snowdepth is deeper in GRTE than in the Upper Green River Basin. Thus if I find a decline in jackrabbit density as snowdepth increases, I would then conclude that snow conditions in GRTE would not be favorable to white-tailed jackrabbits. Since jackrabbit density does not appear to decline as snowdepth increases, my preliminary results suggest that increasing snowdepth does not limit white-tailed jackrabbit density. However, my data are still far too preliminary to support any firm conclusions or management recommendations.


Jackrabbits

Pronghorn & deer

Elk

Figure 3 Jackrabbit, pronghorn & deer, and elk scat density at sites across a snowdepth gradient in the Upper Green River Basin.

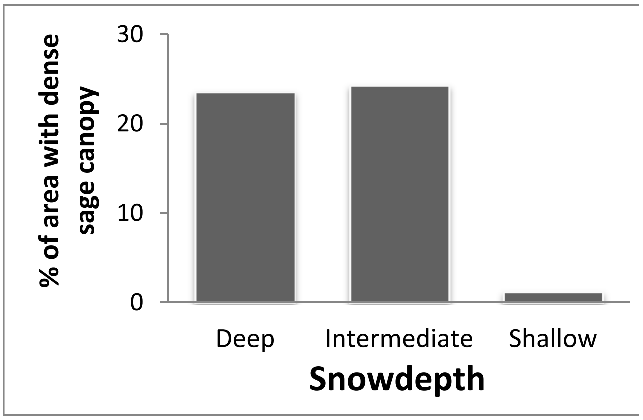


Figure 4 Sagebrush canopy cover along a snowdepth gradient in the Upper Green River Basin.

Objective 2: Effect of white-tailed jackrabbits on pronghorn fawn survivorship

Background

Hares, including jackrabbits, are medium-sized herbivores that often persist at high densities with high reproductive rates, making them attractive prey for medium-sized predators

(Flinders and Chapman 2003). As such, white-tailed jackrabbits may have strong effects on coyote predation of pronghorn fawns. Although a multitude of predators prey on hares, in several systems one hare species is the primary food source for one carnivore species, the best documented association being that between lynx and snowshoe hares (Stenseth *et al.* 1997). Less well known is that hares in the genus *Lepus* appear to be particularly important for coyotes (Bartel and Knowlton 2005). Unlike lynx that specialize on one hare species and are unlikely to persist in its absence (Krebs *et al.* 2001), coyotes are capable generalists and will switch to other prey species when *Lepus* are not available. Neonate ungulates are especially favored in such cases of prey switching: across several sites, coyote predation on neonate ungulates increases when *Lepus* density declines to low levels (Patterson *et al.* 1998; Stoddart *et al.* 2001; Arthur and Prugh 2010). Such outcomes result from *Lepus* altering both the predation behavior of individual coyotes and increasing the abundance of coyotes (Gregg *et al.* 2001). A similar relationship may exist between white-tailed jackrabbits, coyotes, and pronghorn fawns. White-tailed jackrabbits are a preferred prey item for coyotes (Flinders and Chapman 2003), and coyotes are the main predator of pronghorn fawns in southern GYE and elsewhere (Byers 1997; Gregg *et al.* 2001; Berger 2007). Since coyotes strongly interact with both jackrabbits and pronghorn, there is a high likelihood that white-tailed jackrabbits have indirect effects mediated by coyotes on pronghorn.

White-tailed jackrabbits could influence coyote predation rates on pronghorn fawns in three ways. **(1)** First, the presence of jackrabbits could effectively subsidize the coyote population by providing coyotes with more food and causing the coyote population to increase (i.e. jackrabbits alter coyotes' numerical response). With more coyotes to prey on pronghorn, we would expect to see increased predation rates on pronghorn fawns. This would be an example of apparent competition (Holt 1977). **(2)** Alternately, the presence of jackrabbits may cause coyotes to preferentially prey on jackrabbits instead of pronghorn fawns (i.e. jackrabbits alter coyotes' functional response). In such a scenario we would expect to see reduced predation rates on pronghorn fawns when jackrabbits are present. This would be an example of apparent facilitation. **(3)** Lastly is the null, where white-tailed jackrabbit presence has no effect on coyote predation rate on pronghorn fawns.

White-tailed jackrabbits disappeared from Grand Teton National Park (GRTE) sometime between the 1970s and 1990s for unknown reasons, after being described as "commonly in the vicinity" during the 1930s and 1940s (Berger *et al.* 2006; Berger 2008). Despite disappearing from GRTE, jackrabbits persist in nearby areas outside GRTE boundaries including one site (Gros Ventre Drainage) less than 10 miles from the Park border (Figure 3). Sites where jackrabbits persist are broadly similar to areas in GRTE where jackrabbits once occurred, including in vegetation, coyote density, and ungulate species composition and density (USGS Gap Analysis Program 2010; see Preliminary Results). Wolves are present in GRTE and the Gros Ventre Drainage, but not in the Upper Green River Basin (Jimenez *et al.* 2011). Since wolves limit coyote populations in GRTE and the Gros Ventre Drainage (Berger *et al.* 2008), we might expect coyote densities to be higher where wolves are absent in the Upper Green River Basin. However, there is an active coyote removal program run by Wildlife Services in the Upper Green River Basin to protect livestock, and my preliminary data suggest that it has roughly similar effects on coyote densities as the presence of wolves.

Since factors that are likely to have a strong effect on pronghorn fawn survival are broadly similar across southern GYE sites with and without white-tailed jackrabbits, these sites approximate a 'natural experiment' to test the effect of jackrabbit presence on pronghorn fawn survival.

Study design

The local extirpation of white-tailed jackrabbits from GRTE represents a substantial management challenge for the Park, but it also provides an excellent opportunity to study food webs in the form of a natural experiment in the presence and absence of white-tailed jackrabbits – an exclusion treatment that is not ethically or logistically feasible to experimentally replicate. Although not as strong as manipulative experiments, natural experiments in the presence and absence of a key species can provide deep insights into the functioning of food webs (e.g. Estes *et al.* 2010; Dorcas *et al.* 2012). I will study the coyote-jackrabbit-pronghorn food web in five sites of the southern GYE that are similar in vegetation and herbivore species composition, but have variable jackrabbit presence (Figure 5).

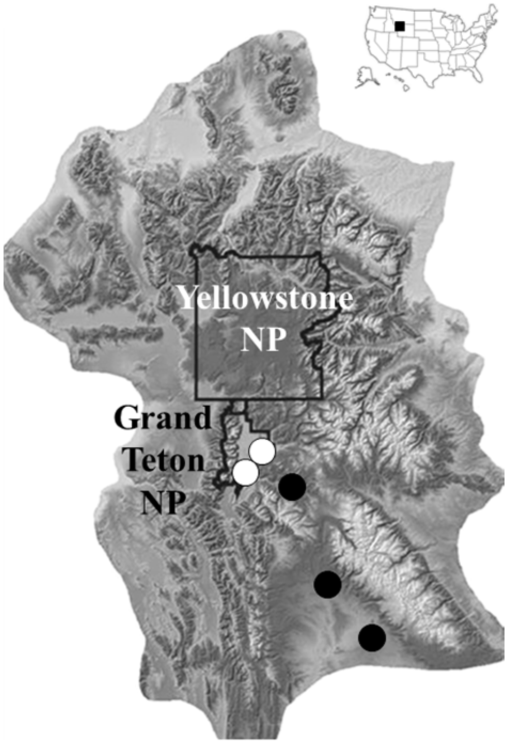


Figure 5 Study sites in the southern Greater Yellowstone Ecosystem with (black dots) and without (white dots) white-tailed jackrabbits.

Methods

I am investigating how white-tailed jackrabbits affect coyote predation on pronghorn fawns by measuring jackrabbit density, coyote density, and pronghorn fawn survival at each of the five sites. Coyote density was measured at each site using 5 separate 1-mile scat transects along abandoned two-tracks, which were initially cleared and subsequently re-checked for coyote scats once per week for two weeks (Gese 2001; Berger *et al.* 2008).

I measured white-tailed jackrabbit density using three methods. First I used pellet counts in ~80 randomly placed 10' x 2" plots at each site (for a total of ~400 plots; Hodges and Mills 2008). Second, I used DISTANCE sampling from ~15 mile spotlight transects carried out along roads and two-tracks at study sites outside GRTE (Smith and Nydegger 1985). Spotlight transects were not conducted in GRTE due to jackrabbits' absence. Third, I estimated jackrabbit density using capture-mark-recapture methods.

To measure pronghorn fawn survivorship, I used fawn:doe ratios in late summer as an estimate of fawn survivorship (Berger and Conner 2008). In the southern GYE more than 99% of adult females become pregnant each year and give birth during a three week period in May-June. Fawns stay hidden for the first 2-3 weeks of life before beginning to travel with their mothers, and 95 percent of predation events occur in these first 17 days of life. Coyotes account for the majority of fawn predation in all areas where it has been studied, including southern GYE (Byers 1997; Gregg *et al*. 2001; Berger *et al*. 2008). Female pronghorn give birth to a mean to 1.90 ± 0.019 fawns (reviewed in Berger and Conner 2008), meaning that any downward deviation from a 1.9 fawn:doe ratio represents fawn mortality.

Preliminary Results

Although there are some differences between the five study sites, areas in GRTE are not systematically different from sites harboring jackrabbits in any of the variables I measured (Figure 6). Bison are present only in GRTE, whereas other sites harbor only cattle, but the substitution of cattle for bison seems unlikely to influence pronghorn fawn survivorship. White-tailed jackrabbit presence is the only factor I have found that is likely to affect pronghorn fawns and that consistently differs between GRTE and the other sites.

Live-trapping from 233 trap nights in July and August resulted in only 3 captures of two juvenile white-tailed jackrabbits (one was recaptured) in the Upper Green River Basin. Spotlight transect also had low success rate, as I only observed jackrabbits in 1 out of 8 spotlighting surveys. Due to the low success of these two methods, I relied on scat plots (*n*=367) from the five study sites (mean plots per site = 73.4; range: 62-84) to measure jackrabbit density. Pronghorn fawn:doe ratios conducted in early August succeeded in four out of the five study sites, but I failed to find a sufficient number of pronghorn in the Elk Ranch site in GRTE to estimate fawn survivorship. Thus data on the relationship between pronghorn fawn apparent survival, coyote density, and jackrabbit density are restricted to four sites. I found a trend of reduced pronghorn fawn survivorship as coyote density index increased. Pronghorn fawn survivorship generally increased with increasing white-tailed jackrabbit density index (Figure 7).

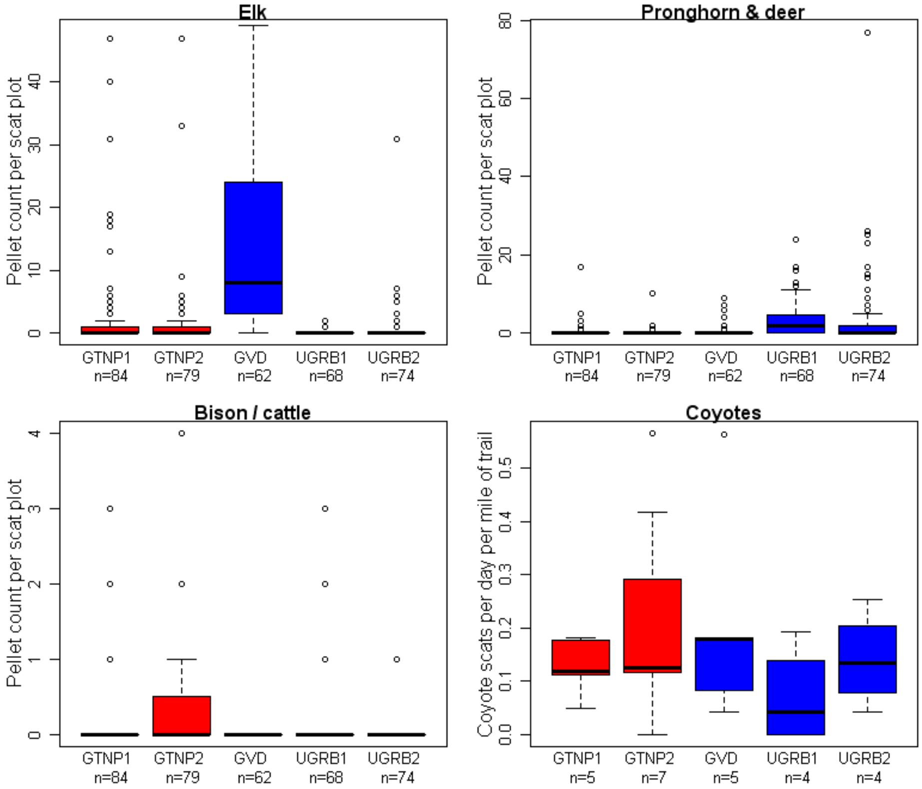


Figure 6 Index of ungulate and coyote density at each of five study sites, based on data collected in summer 2011. Areas without jackrabbits are colored red; areas with jackrabbits are colored blue. Sample sizes indicate number of plots or transects. GTNP=Grand Teton National Park, GVD=Gros Ventre Drainage, UGRB=Upper Green River Basin.

Discussion

I found no systematic differences between study sites except in the presence of white-tailed jackrabbits. Thus, my study sites in the southern GYE provide a reasonable approximation of a “natural experiment” in the effect of jackrabbit presence on pronghorn fawn survivorship. Overall I found that – as expected – pronghorn fawn survivorship appears to decrease with increasing coyote density. My preliminary data also suggest that fawn survivorship increases with increasing white-tailed jackrabbit density, providing early but extremely tentative support for the apparent facilitation hypothesis between jackrabbits and pronghorn. Low sample size after only one year of data collection prevents a meaningful statistical analysis of these relationships, but sampling during the upcoming 2012 and 2013 field seasons will allow a robust analysis. If I continue finding support for the apparent facilitation hypothesis, my results would imply that lack of jackrabbits may be suppressing pronghorn fawn recruitment in GRTE. A similar, though less pronounced, effect may be occurring in the Gros Ventre Drainage, where white-tailed jackrabbits are present but at lower density than in the Upper Green River Basin.

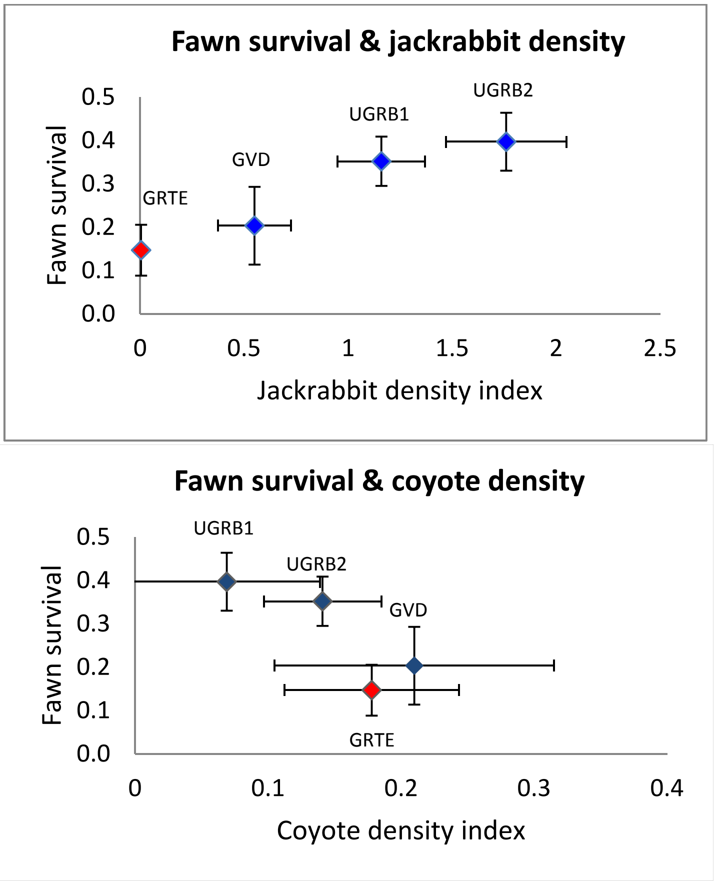


Figure 7 Apparent survival of pronghorn fawns in relation to coyote density and white-tailed jackrabbit density in summer 2011. Error bars represent standard errors. Blue dots indicate sites where jackrabbits are present; red dots sites where jackrabbits are absent (GRTE).

My data support the notion that white-tailed jackrabbits are functionally extirpated from GRTE but may be intermittently present at extremely low densities. I found white-tailed jackrabbit scat in 1 out of 163 (0.6%) plots in GRTE. For perspective, white-tailed jackrabbit scat was present in 21% of plots in the Gros Ventre Drainage and 50% of plots in the Upper Green River Basin. Data from my scat plots corroborate previously reported findings of an extremely small but functionally extirpated population of white-tailed jackrabbits inside GRTE boundaries (Berger *et al*. 2006).

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