A portion of our First Year Progress Report to the National Science Foundation for Award 1556248

LTREB: TESTING FOR FACULTATIVE SWITCHING BETWEEN MIGRATORY STRATEGIES IN A PARTIALLY MIGRATORY, LONG-LIVED LARGE HERBIVORE POPULATION

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What are the major goals of the project?

1) What determines switching between migratory and resident strategies in a long-lived large herbivore, elk?

1. Is switching between strategies conditionally dependent on intrinsic (age, reproductive history, learning) factors?
2. Or is switching dependent on extrinsic (density, forage, predation risk) factors?

2) What are the population consequences of switching between migratory strategies in a partially migratory population?

1. What are the ultimate population consequences of this switching behavior between strategies?
2. How will changes in density, forage or predation risk ultimately affect the ecological balance between migratory strategies?

Major Activities:

In our first year of our LTREB grant, we made progress towards our long-term research goals of first understanding the mechanisms causing switching behavior in a long-lived partially migratory elk population, and second, towards understanding the population consequences of this switching behavior. **Our first major activity continued to be the long-term collection of our core ecological data on adult female elk, which we summarize in specific objectives below.** These field data on elk will be used to study migration, survival, mortality causes, habitat selection, and population ecology including aerial population estimates, calf recruitment, etc., that are the foundation of our long-term questions.

Our second major activity focused on the collection of data on the hypothesized ecological covariates predation risk and forage driving resource selection, switching behavior between strategies, and population dynamics. This includes estimating predation risk by major predators, which included capture and radio-collaring of 3 new gray wolves in 2 of the 3-4 overlapping wolf packs in the study area with Iridium GPS collars. Furthermore, we also made significant investment in application of new technology (remote cameras) to study predation risk by multiple large carnivore species across the entire study area, as well as finalizing our second year of a MS research project focused on combining non-invasive DNA collected from carnivore scats to integrate with our remote camera and GPS datasets. Finally, we continued development of remote-sensing based applications to link to in-situ field methods to track changes in elk forage quality over time, and conducted annual vegetation sampling to estimate primary productivity of key elk forage plants on the winter range following our long-term protocols.

Scientifically, **we also made significant progress in the reporting period in publishing the first analyses of our hypotheses of the determinants of switching behavior of elk** using the first 11 years of our long-term data (Eggeman et al. 2016). We also completed a PhD dissertation and several associated publications on the development and application of a remote-camera monitoring network to monitor predation risk by multiple large carnivores for our elk population (Steenweg 2016; Steenweg et al. 2017; Steenweg et al. 2016). We also submitted a synthesis of 11 years of our demography data from 2001 – 2012 to *Oikos*, and published another paper on comparative elk population ecology including our Ya Ha Tinda database in *Ecology*. Our main scientific activity in the last year was the recruitment and training of our new PhD student, Hans Martin, at the University of Montana, as well as collaboration with the MS in Environmental Journalism at the University of Montana. At University of Alberta, our graduate students made continued progress in their research.

Specific Objectives:

Our first specific objective for year 1 were continuing the long-term collection of our core ecological data on adult female elk. Specifically, this included capturing and handling of 20 new adult female elk in winter 2016/2017 to obtain blood samples for pregnancy analysis, extract a tooth for estimating age, record body condition metrics using a portable ultrasound, and to replace /refurbish existing GPS collars and deploy 5 additional new GPS collars. We currently have ~ 78 VHF/GPS collared female elk, with ~ 50 GPS collared in the population. In addition, we captured and radio-tagged 30 neonatal elk calves in spring of 2016, the last year of our 4-year investigation into elk calf survival using marked calves being led by our PhD student Jodi Berg. We documented cause-specific mortality of elk adults and neonates as well through the year. We now have 4 years of marked neonatal calves, combined with 5 years of mark-resight calf survival monitoring to estimate calf survival by migrant strategy, and will be returning to our standard long-term monitoring method mark-resight in year 2 (2017/18) for the duration of our LTREB grant.

Our second specific objective was continuing to collect information on spatial predation risk by the major predators of elk in our study system, wolves. We captured and radio-collared 3 new wolves in 2 of the 3-4 wolf packs overlapping our study area, but were not successful in deploying 2 GPS collars on the main 3rd pack overlapping the winter range for our elk population. This is not atypical, as weather conditions during helicopter net-gunning to catch wolves during the 3 times we scheduled capture operations were not suitable for capture of wolves (no snow to either track or slow down un-collared wolf packs for net-gunning). We will attempt additional capture efforts in winter of 2017/18 for these 1-2 wolf packs that remain un-collared. However, the challenge and expense of continually trying to keep wolves radio-collared during or long-term study lead us to a long-term alternative approach, remote camera's, which overcome the field difficulties of maintaining 6-8 GPS collars on wolves, as well as collecting multispecies carnivore data including grizzly bear spatial distribution.

Thus, **our third major objective was developing and testing novel methods for measuring predation risk for multiple large carnivores** across our large, 5,000km^2 study area. In our initial research in this population from 2001 - 2005, we focused on monitoring wolf predation risk, the leading cause of mortality for adult female elk. However, continuing to monitor 3-4 wolf packs with GPS collars to estimate predation risk is extremely expensive (~ $50,000/year CDN) and sometimes infeasible due to logistical concerns (see above). Thus we needed to find alternative ways to monitor predation risk that provided comparable spatiotemporal information about exposure of elk to predation risk. Moreover, since beginning our neonatal elk calf tagging and survival/mortality monitoring (2012-2016) we found that wolf predation is the least important cause of mortality of neonatal elk calves, instead, grizzly bear mortality dominates, and that mountain lion predation may have been overlooked. Monitoring spatial distribution of multiple large carnivores is a significant methodological challenge, but one we felt achievable with developing, testing and calibrating a remote-camera based monitoring network across our study area.

Working with Parks Canada, we have successfully developed and implemented a network of over 200 remote wildlife cameras in our study area to monitor spatiotemporal occurrence and relative abundance of multiple different carnivore species. This calibration/validation research was led by PhD student Robin Steenweg at the University of Montana. We also collected a third data type from non-invasive DNA throughout the study area through the use of scat detection dogs that will be compared and integrated with remote camera data occupancy models; this research component was led by Eric Spilker in his MS thesis at the University of Alberta and is still in progress. Robin Steenweg's research lead to a number of significant achievements in the last year that we report below in significant achievements; Eric's work is still ongoing and is expected to be completed in the next year.

Finally, our last major specific objective was continuing to collect, process and manage spatial and in-situ plant vegetation plot data to track long-term variation in primary productivity of elk forage plants on the Ya Ha Tinda study area. We do this by conducting forage biomass sampling during the peak of the growing season (July/August) in repeat sample locations in and around the main winter range. In addition, we continue to download, process, and clean (correcting for cloud contamination, etc.) remotely sensed vegetation indices for the study area from the MODIS satellite platform. These vegetation indices (VI) include NDVI, EVI, fPAR, LAI, and NPP/GPP, as well as MODIS snow cover. We processed all remote sensing VI's for 2016 up to Jan 1, 2017.

Significant Results:

We made significant progress towards our first objective this year in understanding the **role of intrinsic versus extrinsic hypotheses in driving switching between migratory behaviors** in our population. This is one of the core objectives of our project, and we published a paper using the first 11 years of data from our study area in the leading ecological journal, Journal of Animal Ecology lead by one of our MS students, Scott Eggeman (graduated in 2013).

We tested variability in individual migratory behavior using a preliminary dataset from our first 11 years of our long-term project, using 223 adult female elk from our LTREB study site. We used net squared displacement (NSD) to classify migratory strategy for each individual elk-year (using methods we published in Spitz et al. (2017) using the same approach in the MigrateR R package). Individuals switched between migrant and resident strategies 15% per year, and migrants were more likely to switch than residents. We then tested how extrinsic (climate, elk/wolf abundance) and intrinsic (age) factors affected the probability of migrating, and, secondly, the decision to switch between migratory strategies. Over 630 individual elk-years, the probability of an individual elk migrating increased following a severe winter, in years of higher wolf abundance, and with increasing age. At an individual elk level, we observed 148 switching events of 430 possible transitions in elk monitored at least 2 years. Switching was density-dependent, where migrants switched to a resident strategy at low elk abundance, but residents switched more to a migrant strategy at high elk abundance. Older migrant elk rarely switched, whereas resident elk switched more frequently to migrate at older ages. Different strategies had opposing responses to density-dependent and intrinsic drivers, providing a stabilizing mechanism for the maintenance of partial migration and demographic fitness in this population.

This preliminary paper demonstrates that it is possible to understand the intrinsic and extrinsic drivers of switching behavior. However, our ability to disentangle density-dependence from conspecific competition versus density-dependent predation was limited because of the high correlation between elk density and wolf density within the short 11-year time series of this study. Since 2012, the elk population and wolf population have become increasingly decoupled, which we think will help us in further refining the role of predation and density on driving switching rates. Moreover, since 2012, an entirely new dynamic of elk switching back to becoming migrant again, but instead of migrating west towards traditional summer ranges inside Banff, they are migrating east to lands with far different predation risk and forage exposure. Therefore, in the next 3-4 years, one of our long-term goals will be to revisit this analysis to test whether factors affecting switching have changed with a larger dataset to better resolve some of these key uncertainties.

These changes in migratory behavior between resident and migrant status were reflected in spatial choice of migration routes. In preliminary analyses that are being finalized we found that across 867 elk-years of data, we identified 4 major migration routes from Ya Ha Tinda to summer ranges. The number of collared elk migrating east towards industrial forest lands increased from 4% in 2002-2005 to 37% in 2011-2014. In contrast, migration routes to the west into Banff National Park have been declining correspondingly, and the proximate correlate of declining western migration is higher exposure to wolf and grizzly bear predation.

We also made significant progress towards **development of alternative methods to monitor large carnivore spatial predation risk on elk** (summarized in Steenweg et al. 2016 *Biological Conservation* and Steenweg 2016 Dissertation). For species without uniquely identifiable spots, stripes, or other markings (e.g., wolves, grizzlies and mountain lions), cameras collect detection/non-detection data that are well suited for monitoring trends in occupancy as its own independent useful metric of species distribution, as well as an index for predation risk. We tested camera-based occupancy models as a method to monitor changes in occupancy of 13 multiple large carnivore and large mammal species (including elk, wolves, grizzly bears, and mountain lions), across 5 Canadian national parks (~21,000 km^2) including our LTREB study area in Banff. With n = 183 cameras, we report adequate statistical power to detect trends in species with occupancy ranging from a high of 0.81 (Grizzly bears) to 0.05 (wolverines). We had high statistical power to detect spatial and temporal trends in all of our focal species for our long-term work on monitoring predation risk of wolves, grizzly bears, and mountain lions.

We also made significant progress to understanding the population dynamics of our study population and the role of migration. We submitted a paper in revision to *Oikos* (Hebblewhite et al. 2017) focused on analyzing population vital rates and population growth rate over the first 12 years of our study. We tested for density dependence in adult female survival, adult cause-specific mortality rates and annual juvenile survival between migrant and resident elk in a population that underwent a 66% decline over 10 years. In contrast to predictions from predator-prey and life-history theory, we found only weak evidence of classic (negative) density dependence in adult survival and no evidence in juvenile survival. Predation by wolves was the leading known cause of mortality, yet stayed constant with declining elk density for both migrant and resident elk. Moreover, in contrast to bottom-up predictions, we found residents did not experience greater increases in vital rates than migrants. We also found only weak evidence for density-independent climatic drivers of adult female survival. Thus there were few differences between migrant and resident elk. **The constant predation rates across the study period supports equivalent fitness payoffs for migrants and residents, and suggests this population is being limited by density-independent predation.**

Finally, we published a complementary paper in the journal *Ecology* (Ahrestani et al. 2016) comparing population ecology of our population to 21 other elk/red deer populations using time-series data. First, we estimated density dependence applying Gompertz linear DD model in a Bayesian hierarchical framework. Second, we then tested the significance of environmental covariates (forage measured by NDVI, weather by Northern Hemisphere Temperature Anomalies) of direct and delayed density dependence. Most (15 of 19) of these exhibited a combination of weak to moderate density dependence, but there was no evidence for density-dependence in our Ya Ha Tinda population. The coefficient for the effects of density on population growth rate in the best fitting Gompertz model was B = 0.13 (Bayesian credible interval -0.48 – 0.59). Also, we did not detect an effect of summer forage (NDVI) or weather (NHTA) on the strength of density-dependence in our population. These combined results suggest that at least for the first 12 years of our study, the population was declining and that something else besides forage or climate was driving declines. **This is consistent with top-down regulation by predation consistent with our previous results and the cause-specific mortality reported in our *Oikos* paper.** Future analyses during this LTREB project will extend these analyses to determine if density-dependence is starting to increase population growth rate and vital rates as the population declined, and the role of wolf and grizzly bear predation on differences between migrant and resident elk.