

# **Do selective pressures of harvest drive an evolutionary change in the size of animal weaponry?**

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## **INTRODUCTION**

Understanding the ecological and evolutionary responses of wild populations to disturbance is critical for the management and conservation of wildlife. Human activities around the globe have led to increased global temperatures (Parmesan et al. 1995, Deutsch et al. 2008), fragmented and degraded habitats (Fahrig 2003, Ferraz et al. 2007), high levels of pollution (Verhoeven et al. 2006, Butchart 2010), and potentially, an evolutionary change to populations and species that results from human activities of harvest (Allendorf and Hard 2009). Harvest-induced evolution has important implications for both the management and persistence of many wild species across the world (Allendorf et al. 2008, Kuparinen and Festa-Bianchet 2016); yet, the true evolutionary effects of harvest on wild populations has remained relatively poorly studied on the temporal and spatial scales that evolution often acts. Even at limited temporal and spatial scales, however, evolutionary responses to harvest have been shown to occur across taxa (Coltman et al. 2003, Walsh et al. 2006, Allendorf et al. 2008). Systems that are subjected to sufficiently intensive and selective harvest may experience reduced weapon size, reduced growth rate, early sexual maturation, altered behaviors (i.e. foraging, courtship and migration behaviors), and changes to life history strategy over the span of only a few generations (Walsh et al. 2006, Hard et al. 2008, Allendorf and Hard 2009, Devine et al. 2012, Olsen et al. 2012, Monteith et al. 2013, Darimont et al. 2015). All species have the underlying requirements for evolution to act upon (heritability of traits and selective pressures on those traits; Darwin 1859), and harvest induced-evolution can occur when selection through harvest is severe enough (Kuparinen and Festa-Bianchet 2016), yet, the threshold of that severity is still unclear across most populations and species.

Although there is sufficient empirical and theoretical evidence that demonstrates harvest can influence life-history characteristics and result in demographic changes to populations, it is still uncertain to what degree harvest-induced evolution contributes to observed population-level changes (Hard et al. 2008). Changes to populations that result from harvest-induced evolution often mimic changes that are driven by changing environments and phenotypic plasticity (Kuparinen and Festa-Bianchet 2016). Consequently, disentangling the effects of selection through harvest from the effects of selection by natural processes is imperative to understanding the degree harvest-induced evolution is acting on both the population and species levels. In some fish species, for example, decreases in population density because of harvest may result in increased resource availability. Increases in resources can lead to accelerated juvenile growth and early sexual maturation, which consequently may result in small body sizes at sexual maturity (Sinclair et al. 2002, Kuparinen and Merilä 2007). These population level changes to body size are similar to population level changes that would occur because of harvest-induced evolution (Walsh et al. 2006). Alternatively, in ungulate species, increases in population density that reduce the resource availability per individual can result in a shift in investment from growth of secondary sexual characteristics (i.e. weaponry) to the growth and maintenance of somatic tissue. The plastic response of resource allocation to limitations in resources may result in negative trends in the size of weapons through time, which mimics the expected trends that would arise from harvest-induced

evolution (Festa-Bianchet 2016). Understanding how populations and species are evolving and responding to their environments is crucial to understanding the degree that harvest-induced evolution is occurring in natural systems.

Ungulate species specifically can be subject to accelerated changes in weapon size through selective removal of individuals with impressive sized horns and antlers under heavy harvest pressure (Festa-Bianchet et al. 2000, Hard and Mills 2006, Monteith et al. 2013, Pigeon et al. 2016). Identifying harvest-induced evolution is difficult, not only because of the intricacies of disentangling the effects of natural processes from selective pressures, but because long-term data of phenotypic measurements are critical to identifying change through evolutionary time (Hundertmark et al. 1998). Indeed, it remains unclear what harvest practices may produce evolutionary changes in weapon size, especially when most harvest practices for trophy species are selective to some degree (Festa-Bianchet 2016).

To understand the degree harvest-induced evolution acts on wild ungulate populations, we evaluated how demographic changes, selective effects of harvest, and environmental characteristics influenced horn size of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*), desert bighorn sheep (*Ovis canadensis nelsoni*), and Stone's sheep (*Ovis dalli stonei*) harvested across 12 United States and 2 Canadian provinces from 1980 to 2016. We evaluated three hypotheses to understand the effects of harvest and environmental factors on weapon size in mountain sheep throughout their North American range.

*Demographic Shift Hypothesis (H1)* – We assessed the hypothesis that changes to the age structure of a population through time will result in temporal changes in the mean horn size of that population. Demographic changes as a function of harvest can affect age structure of the population. We predicted that an increase in the age structure of a population would result in a corresponding increase in the mean size of horns of that population through time. Conversely, we predicted that a decrease in the age structure of a population would result in a corresponding decrease in the mean size of horns of that population through time (Fig. 1).

*Selective Harvest Hypothesis (H2)* – We evaluated the hypothesis that selective harvest for males with large and fast growing horns will result in an evolutionary change in horn size through time by favoring the persistence and reproductive advantage of males with small and slow growing horns. We predicted that the removal of males with large and fast growing horns would result in decreases to the age-specific horn size of individuals in a population through time, regardless of the age structure of the population (Fig. 1).

*Environmental Factors Hypothesis (H3)* – Finally, we assessed the effects of environmental conditions, including climate and forage availability on horn size through time. Harsh climates and poor forage availability may result in decreases to the age-specific horn size of individuals. Conversely, mild climates and favorable forage conditions may result in increases to the age-specific horn size of individuals (Fig. 1). We assessed three predictions that were based on the environmental factors hypothesis. First, we predicted that environmental conditions in the year before an individual was born would have the greatest influence on lifetime horn size of an individual. Conditions of a mother during gestation has been shown to influence both body size and weapon size of her offspring throughout their life (Monteith et al. 2009). Second, we predicted

that environmental conditions in the first three years of life would have the greatest influence on lifetime horn size of an individual. Mountain sheep take several years to reach adult body size, and environmental conditions during that developmental period may influence the tradeoff between growth to somatic tissue and growth to horns. Finally, we predicted that environmental conditions throughout an individual's life would have the greatest influence on the horn size of an individual. Mountain sheep do not shed their horns annually, and continually grow their horns throughout their life, therefore environmental conditions throughout their life may have the greatest influence on lifetime horn size.

Changes to the horn growth curve of a population through time can occur through either the mechanisms described by the selective harvest hypothesis or the environmental effects hypothesis. Furthermore, the mechanisms of both selection by hunters and the environment can potentially confound each other, resulting in no detectable changes when in reality, selective pressures may be resulting in age-specific declines, but are simply washed out due to favorable environmental conditions. We aim to disentangle the different mechanisms of selection by accounting for environmental conditions during the three stages of life outlined in the environmental effects hypothesis. After accounting for environmental conditions, any age-specific changes that are occurring are likely the result of harvest pressure.

## **METHODS**

We evaluated the effects of harvest and environmental conditions on horn size of mountain sheep using harvest records collected by state and provincial agencies over the past four decades. We obtained harvest records of three subspecies of mountain sheep (Rocky Mountain bighorn sheep, desert bighorn sheep, and Stone's sheep) from 12 United States and 2 Canadian provinces. Wildlife managers and biologists throughout mountain sheep range routinely have collected data on both age and size of horns for harvested animals for decades. These data represent one of the only sources of phenotypic data that includes both age and a metric of size for any ungulate species over a vast spatial and temporal scale.

We used two different metrics of horn size in our analyses because of differences in available measurement data from state and provincial agencies: full score and length base score. Full score was calculated by summing the length of the outer edge of the horn and 4 circumference measurements equally spaced along each horn (Fig. 2). Length base score was calculated by summing the length of the outer edge of the longest horn twice and the measurements of the base circumference of both horns (Fig. 2). We used the measurement of the longest horn twice for the length base score to reduce bias that may arise if one horn was broomed heavily. We did not use the longest horn twice for the full score because agencies that provided us with full scores often did not have individual measurements available, only the cumulative score. Measurement protocol used by state and provincial agencies were identical to measurement protocols established by the Boone and Crockett Club (Buckner and Reneau 2009).

### **Weather and Plant Phenology Data**

We extracted spatially explicit data on precipitation, snow water equivalent, and minimum temperature from 1980 to 2015 using modeled values from DAYMET (1-km<sup>2</sup> resolution) from 1

October to 31 May. We calculated the mean values of precipitation, snow water equivalent, and minimum temperature during three different periods of life – year of gestation, the first 3 years of life, and the entire lifetime of an individual.

To assess forage availability and quality, we obtained 14-day composite NDVI with a spatial resolution of 1 km<sup>2</sup> recorded by the Advanced Very High Resolution Radiometer (AVHRR) weather satellites. We extracted NDVI values and calculated start of season, end of season, length of season, peak NDVI, amplitude, and integrated NDVI of each year from 1982 to 2016. We calculated mean values of each metric during three different periods of life – year of gestation, the first 3 years of life, and the entire lifetime of an individual.

### **Assessing Age Specific Changes to Horn Size**

To test for age-specific changes in horn size of individual hunt areas through time, we used mixed-effect models to predict horn growth curves for cohorts born in each hunt area from 1980 – 2004. We included age, natural log of age, state or province, and year of birth as fixed effects and an uncorrelated random slope and intercept varying among year of birth and hunt unit within year of birth.

For each hunt area, we used the predicted values from the model to estimate the size of 7-year-olds born in each cohort from 1980 – 2004. For each hunt area, we used a simple linear regression of the predicted size of 7-year-olds as the response variable and cohort year as the predictor variable to assess age specific changes through time. We used predicted size of 7-year olds because mean age of harvest from all records of harvested mountain sheep was 7, and the horn growth curve begins to asymptote between ages 6 and 8 for most hunt areas. This modelling approach allowed us to use all data points available to inform the predicted size of 7-year olds, therefore increasing our sample size and confidence in detecting age-specific trends through time.

### **Assessing Selection Strength in Hunt Areas**

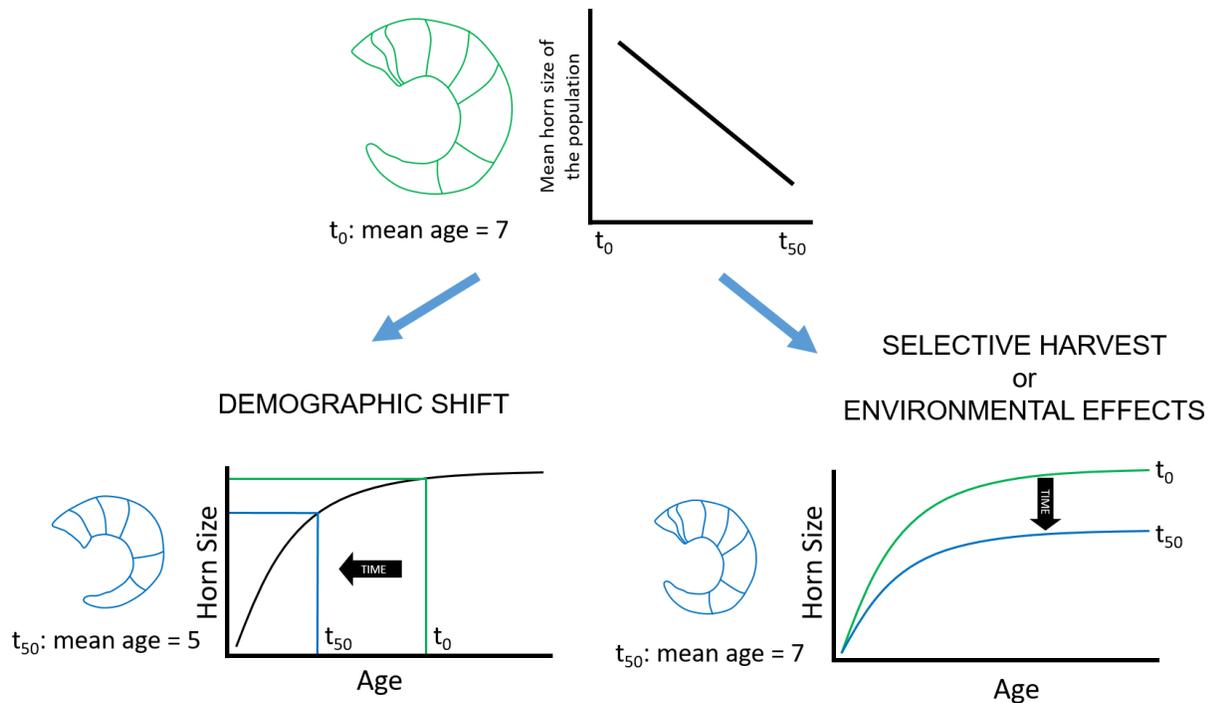
We developed a metric of selection strength on fast growing males to assess if the harvest pressure was intense and selective enough in each hunt area to produce a measurable effect on age at harvest of cohorts. To evaluate selection strength, we regressed the mean age at which a cohort was harvested against the predicted size of a 7-year-old in that cohort, weighted by the number of animals that were harvested in each cohort. If selection was strong enough, we expected a negative relationship between mean age of harvest of a cohort and the predicted horn size of 7-year-olds in that cohort, indicating that cohorts that produced larger males would be harvested at younger ages when compared to cohorts that produced smaller males.

### **FUTURE DIRECTIONS**

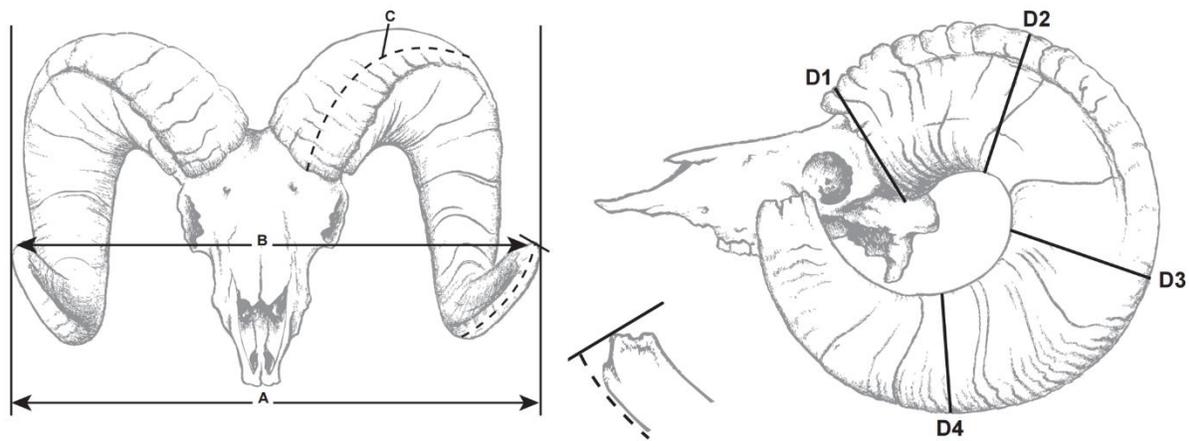
Our next steps are identifying the mechanisms of change in hunt areas that we detected age-specific increases or decreases. In addition to the aforementioned covariates, we will seek to identify a metric of harvest intensity based on harvest regulations. Complete data does not exist to identify the actual intensity of harvest (i.e., a known number of animals harvested from a known population size), however, using harvest regulations we will attempt to categorize intensity based on the morphometric requirements and quotas of different hunt areas. Finally, we are working through

the translocation history that was compiled by the WSWG to identify which hunt areas contributed and received animals via translocations and the relative influence that translocation may have based on the number of animals translocated and the abundance of the recipient population.

As we work through the results, we will continue communication with the WSWG and all collaborators on this project. Upon completion of analyses, we will send a formal update out to the WSWG and all collaborators for comments, feedback, and suggestions. Furthermore, we will keep collaborators involved as we develop and work through different drafts of the manuscript that will result from this work.



**Figure 1.** Conceptualization of the mechanisms that can influence population-level changes in horn size of mountain sheep through time. Population-level changes in horn size can occur through two pathways. First, changes in the demography that results in a shift to a decreasing age structure of the population can result in a change to the mean age of harvested animals over time. With a shift in mean age of harvested animals, there will be a corresponding shift in mean horn size, which manifests as a detectable change in the horn size of a population. Alternatively, harvest selectivity and intensity or changes in environmental conditions can result in age-specific changes to horn size through time, regardless of the age structure of that population. For example, high selective and intensive harvest or poor environmental conditions over life may result in a decrease to the horn growth curve through time, resulting in age specific decreases in the horn size of the population.



**Figure 2.** Illustrations of horn measurements for mountain sheep used by state and provincial agencies throughout western North America. Measurement criteria follow the protocols set by the Boone and Crockett Record Book Program. The full score was calculated as the cumulative sum of C and all D measurements for both horns. The length base score was calculated as the cumulative score of the C measurement for the longest horn twice, and the D1 measurement for both horns.

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