He who can no longer pause to wonder and stand rapt in awe, is as good as dead; his eyes are closed

-- Albert Einstein

University of Alberta

Aversive Conditioning on horseback: A management alternative for grassland systems threatened by sedentary elk populations.

by

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To Antje, Mia and Finn who always stand behind me – despite all.

ABSTRACT

Loss of migratory behaviour in ungulates has been observed worldwide and invites new tools for managing the habitat degradation that results from these sedentary populations. We assessed use of aversive conditioning on horseback as a means of reducing grazing pressure and restoring migratory behaviour in elk (*Cervus elaphus*) at the Ya Ha Tinda Ranch, which is an important wintering range. We conditioned elk by herding them daily in the direction of their historic migratory route and monitored changes in elk distribution and grassland biomass each year. After three summers of aversive conditioning treatments, summer elk presence on the targeted grassland had declined substantially and grassland biomass had increased. Although elk use shifted in the desired direction, we did not detect any longer-distance migration in targeted elk. Our research suggests that aversive conditioning on horseback can temporarily reduce grazing pressure on threatened grasslands, but is unlikely to change migratory behaviour.

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CHAPTER ONE: INTRODUCTION

OVERVIEW AND RATIONALE FOR MANAGING SEDENTARY UNGULATE POPULATIONS WITH AVERSIVE CONDITIONING.

Worldwide millions of animals migrate between habitats. Migration is a regular, periodic movement of populations away from and back to their place of origin (Baker 1978). A single round trip may take the entire lifetime of an individual, as with the Pacific salmon (*Oncorhynchus*), or an individual may make the same trip repeatedly, as with many of the migratory birds and mammals. The animals may travel in groups along well-defined routes, as with many bird and ungulate species, or individuals may travel separately, congregating for breeding and then spreading out over a wide feeding area, as for some seal species (Aidley 1981). Migration distances vary between a few hundred meters in several amphibian species (e.g., wood frogs (*Rana sylvatica*), or eastern newts (*Notophthalmus viridescens*; Regosin *et al.* 2005) and thousands of kilometers as in purple martins (*Progne subis;* Stutchbury *et al.* 2009). The record for long-distance flying is held by the Eskimo curlew (*Numenius borealis*), a shorebird that navigates from Alaska to Tierra del Fuego, a distance of 16,000 km (Jukowsky 1995). Not only costs migration an enormous amount of energy (Bohlin *et al.* 2001), a great number of animals suffer injury or death in an attempt to migrate, the most famous example for this being salmon (Cooke *et al.* 2004). For these reasons, migration must have a net positive effect. For ungulates, this benefit

mostly stems from the migration triggered "grazing succession" (Vesey-Fitzgerald 1960), basically triggering a foraging facilitation effect (Sinclair and Arcese 1995). Despite the ancient history of migration in many species, migratory behaviour has changed in recent decades in a host of species (reviewed by Berger 2004). Many of the massive and historically described overland treks by herd-dwelling mammals have been lost from Asian steppes, African savannas, and North American grasslands (Berger 2004). The ecological changes connected with the loss of migratory behaviour are sometimes drastic; the changes in population distributions caused by loss of migratory behaviour influences natural predator-prey relationships, leading to hyper abundant populations (Ripple and Beschta 2006), and triggers loss of diversity in wildlife and vegetation communities (Warren 1991, Soulé *et al.* 2003). When ungulates cease to migrate to summer ranges, which are, in Canada's Rocky Mountains, typically at higher elevations (Hebblewhite *et al.* 2008), continued summer grazing on lower-elevation wintering ranges can threaten ecosystem health (Derner and Whitman 2009). When the viability of these important grasslands is compromised, the entire ecosystem that is built on it may be threatened as well (Derner and Whitman 2009). This is mainly because summer grazing has been shown to remove deep-rooted, and grazing-resistant grasses such as Parry oat grass (*Danthonia parryi*; Dormaar and Willms 1990) and rough fescue (*Festuca campestris*; McInenly 2003). On top of this, grazing may cause growth suppression and regeneration delays, as well as mortality among seedlings that are repeatedly browsed or pulled out of the ground (Crouch 1976, Tilghman 1989).

There are several widely used management tools to limit the changes in animal distributions caused by loss of migration. Nonlethal methods such as repellents and animal-activated frightening devices are often employed to reduce damage to areas of interest (VerCauteren *et al.* 2005, 2006). The Kenya Wildlife Service, for example, has been recognized as a world leader in wildlife power fencing by being among the first in the world to use modern high powered electric fencing for the exclusion of problem wildlife (Kassilly, 2002). Largely because of the high rate of habitat destruction, relocation has become an increasingly prominent conservation tool over the last couple of decades (e.g. Conant 1988, Fisher and Lindenmayer 2000, Kleinmann 1989). Destruction of problem wildlife is often called for as a management tool in ranching communities; e.g. farmers called for destruction of problem wildlife more so than non farmers in location (McIvor and Conover 1994). Especially in urban settings destruction of wildlife threatening humans is accepted (Hansen and Beringer 1997).

Each of the management tools mentioned above has limitations. Repellents and frightening devices are largely ineffective for elk and other cervids due to rapid habituation (VerCauteren et al. 2005). Moreover, fencing and frightening devices usually cannot distinguish between target and non target animals and thus can have undesired effects on ecosystems. More invasive methods such as relocation can cause mortality rates as high as of 50% (Wright 1977; Rosatte and Macinnes 1989). Although live capture and relocation is accepted by the general public, this impression assumes that the animals will live "happily ever after" in their new location (Craven *et al.* 1998). This reaction

seems to stem from the appreciation people have for urban wildlife, and the empathy they have for individuals as opposed to populations (Runde and Milsap 1994). For the same reason, the public is generally strongly opposed to lethal management of problem animals (Braband and Clark 1992).

Aversive Conditioning (AC) is widely used for predator control (reviewed by Smith *et al.* 2000) but it has rarely been used to change animal distributions (but see Kloppers *et al.* 2005). The advantages of AC are that it is inexpensive (relative to many alternatives) and its effects are, given that the contact to the target species is maintained directly, usually limited to the species of concern (Jelinski *et al.* 1983). AC can generate short-term changes in both distribution and wariness of elk (Kloppers 2005), but AC can produce rapid habituation in both deer (*Odocoileus*; Craven and Hygnstrom 1994, Curtis 1995) and black bears (*Ursus Americanus*; Leigh and Chamberlain 2008). AC seems to be most effective if it is implemented either before or at the initial stages of a conflict situation as behavioural patterns are difficult to modify once they have been established (DeNicola *et al.* 2000).

The underlying theory for AC is based on the assumption that the target species is responsive to negative associative learning. Learning can be defined as a relatively permanent change in behaviour that results from experience (Klein 2008). However, learning reflects a change in the potential for a behaviour, it does not automatically lead to a change in behaviour, also, the changes in behaviour are not always permanent (Klein 2008). Avoidance learning is an AC procedure in which a response terminates a primary aversive event. Through

negative reinforcement, a target species will learn to avoid conditions that are painful or unpleasant. Through avoidance learning, the necessary coping responses can be acquired without undue physical suffering. Avoidance training involves using a signal or cue to alert the animal or person to impending danger (Klein 2008). With punishment, in contrast to avoidance learning, the animal is presented with an aversive stimulus in response for a given behaviour of its own. This does not simply suppress ongoing behaviour, it also strengthens behaviour directly associated with its termination (Lindsay 2000). Additionally as a result of implementing punishment, cues occurring prior to the onset of punishment become emotionally conditioned with fear (Lindsay 2000). As a direct contrast of terms, avoidance is sometime termed active avoidance and punishment is termed passive avoidance. In this thesis, I test the efficacy of AC on horseback as a means of changing the distribution and habitat use of elk conducted a research project at the Ya Ha Tinda Ranch, just east of Banff National Park, in Alberta, Canada, during the summers of 2005 – 2007. This elk population has partially lost its migratory behaviour which appears to be threatening the grassland ecosystem that provides its winter range (Hebblewhite *et al.* 2005). The main objectives of this research project were to (1) determine whether it is possible to use horseback riders to aversively condition elk to change their distribution (Chapter 2) and (2) determine whether it is possible to detect changes in elk use in the response of a rough fescue grassland at the Ya Ha Tinda Ranch (Chapter 3). If it is possible to manipulate elk distribution in this way with concomitant

changes to grassland health, the work has implications for a variety of grasslands threatened by altered migratory patterns and overgrazing elsewhere.

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CHAPTER TWO

USE OF HERDING TECHNIQUES TO ENCOURAGE MIGRATION IN SEDENTARY ELK

Holger R. Spaedtke, Colleen C. St. Clair, Mark Hebblewhite[1]

INTRODUCTION

Ungulate migration is widely known as a strategy to maximize fitness in the face of seasonal and spatial variation in resources (Boyce 1979, Swingland and Greenwood 1983). Enormous migrations of ten thousand elk (*Cervus elaphus*), a hundred thousand caribou (*Rangifer tarandus*) or millions of wildebeest (*Connochaetes taurinus*) define and shape ecosystems through movement, predator-prey dynamics and expansive herbivory (Houston 1982, Sinclair 2003, Johnson *et al.* 2005). For the migrating individuals, migration is broadly hypothesized to reduce predation and increase forage availability (Bergerud *et al.* 1984, Fryxell *et al.* 1988).

Drastic changes in migratory behaviour have been observed worldwide which is, given the ecological importance of migration, concerning to managers and researchers (Schaller 1988, Berger 2004, Johnson *et al.* 2005). In Africa for example poaching and changes in cultivation threaten Serengeti wildebeest migration (Thirgood *et al.* 2004). In Asia, market hunting has been directly responsible for population declines of migratory Mongolian gazelles (*Procapra*

[1] This chapter has been formatted for submission to the Journal of Wildlife Management with these authors.

gutturosa), Saiga antelope (*Saiga tatarica*), and Tibetan antelope (*Pantholops hodgsonii*; Schaller 1988, Lhagvasuren and Milner-Gulland 1997, Arylov *et al.* 2004). Declines in migration in North America have recently been explained by habitat fragmentation connected to oil and gas development for pronghorn (*Antilocapra americana*; Berger 2004), diamond mine exploration for barren-ground caribou (Johnson *et al.* 2005), general over harvest for elk (Toweill and Thomas 2002), hydroelectric developments for woodland caribou (Mahoney and Schaefer 2002) and differences in hunting pressure on different sub groups of migratory elk (Boyce 1989, Smith and Robbins 1994). Additional factors are known to include the creation of agricultural crops that attract elk year-round (Burcham *et al.* 1999) and the creation of artificial predator refugees such as town sites, etc. (Isbell and Young 1993, Riley *et al.* 1998). Once acquainted with a refuge area, elk often cease migratory behaviour (Geist 1982). The ecological changes connected with the loss of migratory behaviour are drastic; natural predator-prey relationships are influenced, leading to hyper abundant populations (Ripple and Beschta 2004), and diversity in wildlife and vegetation is potentially lost (Caughley 1981, Warren 1991, Soulé *et al.* 2003).

Our study site, the Ya Ha Tinda Ranch in Alberta, Canada, is home to one of Alberta's 3 largest elk (*Cervus elaphus*) herds (Morgantini 1995), which, historically, spent each winter at the Ranch, and then migrated to the front and main ranges of the Rocky Mountains in Banff National Park during summer (Morgantini and Hudson 1988, Hebblewhite and Morgantini 2003). There, these elk provided the primary prey base for up to 4 wolf (*Canis lupus*) packs that range

widely in BNP, and also provided a high-quality food resource for other predators and scavengers. Elk on and adjacent to the Ranch also serve as prey for predators outside the park, including grizzly bears (*Ursus arctos*) and human hunters. Recent research at the Ya Ha Tinda Ranch (Hebblewhite 2005) however, has found a gradual change in the migratory behaviour of the elk. Whereas only 25 – 50 elk (2-8% of the herd) remained on the Ranch during the summer in 1981 and 1982 (Morgantini and Hudson 1988), that number increased to a maximum summer count of 481 animals (55% of the current herd) in 2003 (Hebblewhite and Morgantini 2003). The reasons for the dramatic reduction in elk migration from the Ranch stem from a combination of habituation to humans and predator avoidance. By tolerating human activity at the Ranch, elk avoid higher predation rates in the adjacent areas (Hebblewhite 2005).

The Ranch is also one of the largest remaining parcels of rough fescue (F*estuca campestris)* in Canada. Fescue grasslands comprise some of the most threatened communities in the Canadian Prairie Provinces (Vujnovic 1998) and have recently been described as endangered by Environment Canada (Trottier 2002). Concern about their loss due to development, woodland encroachment, exotic species and overgrazing has increased because only 5% of these grasslands remain in pre-settlement condition (Vujnovic 1998). Continued summer grazing by elk at the Ranch may ultimately threaten the viability of the fescue and, consequently, the entire ecosystem that is built on it, including their own survival. Although fescue is resilient to winter grazing (Willms *et al*. 1986), growth is reduced when clipping or grazing is extended into the growing season (McLean

and Wikeem 1985). At the Ranch, this means that the grassland can likely sustain grazing by elk in the winter, but it likely cannot sustain continued grazing in the summer (McInenly 2003; AGRA Earth and Environmental 1998). Reinforcing migratory behaviour is, thus, in the best interest of both range and wildlife management at the Ranch.

We applied aversive conditioning (hereafter AC) trials on horseback to reinforce migratory behaviour in elk. AC is a form of operant conditioning (Brush 1971, Davey 1981) that can involve either avoidance conditioning or punishment (Domjan 2003). It has been used widely to protect livestock from predators (Andelt 1992) and has successfully been used to remove elk from the townsite of Banff in Banff National Park (Kloppers *et al.* 2005). In brief, AC in this study consisted of herding elk off the grassland each spring morning in the direction of their former migratory route. Because elk minimize energy expenditures while maximizing forage intake (Geist 1982), we hypothesized that herding elk from the grassland would eventually cause them to avoid that area. We believed that such an association would be possible because others have shown that human disturbance can evoke predator-avoidance responses even in the absence of predation events (Frid and Dill 2002, Beale and Monaghan 2004). Our objectives were to determine whether it was possible to use humans on horseback to aversively condition elk away from target areas during the spring and summer by herding them from the target grasslands. We assessed the efficacy of this approach by monitoring the movement of radio-tagged, resident

elk (i.e., those that have previously remained at the Ranch during the spring and summer) for both short- and long-term changes in behaviour.

METHODS

Study area description

Field work was conducted at the Ranch and surrounding area east of the Banff National Park boundary in Alberta, Canada (51º45' N - 115º35' W). The Ranch is ~4000 ha in size and is situated in a montane ecoregion with an average elevation of 1550 m. Most of the Ranch consists of grasslands described as 2 different types of fescue communities by Willoughby (2001). . The most extensive grassland community described in the Ya Ha Tinda area is Rough fescue-Sedge-Junegrass (Willoughby *et al.* 2001). The other community type was described on western portions of the grasslands and represented a Sedge-Junegrass community type.

The Ranch has served as the wintering range for ~160 horses for Parks Canada Warden service since the 1930's and is also the wintering range for approximately 1000 elk that summer in the upper elevations of the front and main ranges of Banff National Park. Historically, these elk spent each winter at the Ranch, and then migrated to the front and main ranges of the Rocky Mountains in Banff National Park during summer (Morgantini and Hudson 1988, Hebblewhite and Morgantini 2003). Elk migrate as far as 80 km to the Bow Valley and even areas in Kootenay and Yoho National Parks in B.C. (Morgantini and Hudson

1988). Elk are the most common member of a diverse ungulate guild in the study area, with wolves being the primary predator in the system. The Ranch ecosystem has been described more thoroughly by Morgantini (1995).

Radio-collaring

We identified resident and migrant elk using data previously collected by the Ya Ha Tinda Elk and Wolf Ecology Project (Hebblewhite 2005). Resident elk were identified by using the percentage of time they were present at the Ranch during the previous 1 to 3 summers. Once identified, resident elk were divided in 4 target classes, depending on the accuracy and the amount of location information available, with class 1 (good information available for more than 2 years) elk to be the main trapping targets. Target resident elk were primarily captured using corral trapping during winter months (January – March), supplemented with helicopter netgunning where necessary. The principle method of capture was a 0.3ha large circular corral trap baited with hay during winter months. This trap was situated in a permanent location at the Ranch, on the winter range for the majority of this elk population. Once herded from the corral trap into a connected chute and squeeze system, the restrained elk were blindfolded, ear-tagged for identification, examined for injuries, and fitted with either global positioning system (GPS) or very high frequency (VHF) radio collars. The GPS collar fix rate was set to 15 minutes at daytime (5 a.m. – 8 p.m.) and 1 hour at night time.

Aversive Conditioning treatments

Aversive conditioning of elk began each spring at the beginning of the critical growing period for fescue (~May 15th), which also coincides with the beginning of elk migration. Each morning before conditioning began, a worker drove a truck down the ranch road (~13 km) to detect and record the positions of elk in the main grassland. We used near-daily applications of controlled movements by 2 - 15 people on horseback to herd elk groups off the grassland into nearby habitat. Treatments continued virtually daily until approximately the middle of August of each year.

Horse riders were equipped with handheld GPS units that logged continuous information on the location of horses (Figures 2-1 a and b). During the conditioning treatments, we attempted to reduce stress to elk by excluding cows with newborn calves on the ground and discontinuing trials when calves that moved with the group were imperiled by deep river crossings. Elk movement was monitored with the use of both conventional VHF radio-collars and GPS collars (Figures 2-1 a and b). In addition, every trial was observed by one worker who was positioned strategically to see and record the beginning group sizes, changes in group sizes, collared animals in the group, location of the group at periodic intervals, and additional remarks such as number of riders included in the trial.

Wolf presence and weather data

Activity data were obtained from wolves collared in previous studies (Hebblewhite 2005) and a concurrent wolf study that partially overlapped temporally and spatially with our research (Webb 2008). Given that wolves in

our study area were collared with VHF equipment only, we did not obtain frequent wolf locations but instead categorized wolves as being absent or present based on our ability to detect their VHF frequency. Each morning just prior to an AC trial, a worker scanned all known wolf frequencies and recorded the absence or presence of each individual. Weather data (wind direction and speed, precipitation and temperature) was obtained from the provincial weather station at the south end of the Ranch.

STATISTICAL ANALYSES

Aversive conditioning trial distance

To assess the relative success of an individual herding trial, we recorded the GPS locations of riders at the beginning and end of each trial and subsequently calculated the measured straight line distance between them using ARCGIS 9.2 (ESRI Redlands,CA, USA). To identify the predictors of trial distance, we recorded a set of relevant variables including the number of elk in each trial (#elk), the number of riders participating in the trial (riders), the temperature at the beginning of a trial (temp), the mean precipitation on the day (rain) and the mean wind speed (wspeed) and direction (wdirect) on the day of the trial. We used a set of candidate generalized linear models including logical combinations of variables to explain variation in trial distance. The most parsimonious models were determined, from a competing set of all possible candidate models, using an information theoretic approach based on AIC_c and Aikake weights (w) (Burnham and Anderson 1998)

Daily changes in elk distribution

To determine how daily movement patterns of elk were influenced by AC treatments, we used GPS data of radiocollared elk that were known to have participated in a trial. Beginning and end time of a conditioning trial was determined by visually inspecting GPS data collected from riders in the trial. Using ARCGIS 9.2 (ESRI, Redlands, CA, USA) we established a 'Mason-Dixon Line', which bisected the grassland perpendicular to the natural direction (SW) of migration (Figure 2-1 a and b), along the Red Deer River Valley. This Mason-Dixon Line represented the demarcation between more desired elk locations (west of line, numerically indicated by positive distance from line) and non desired elk locations (east of line, numerically indicated by negative distance from line). We used the elk GPS data to calculate the distance of each individual location collected during a conditioning trial in a 90 degree angle to the Mason-Dixon Line. We calculated hourly means of all locations for GPS-collared elk, using the start and the end of an AC trial and midnight as cutoffs, and including all conditioning trials conducted in each year. In this way, we created 3 periods per day: pre conditioning hours (midnight – start of conditioning), hours during a conditioning treatment (start of conditioning – end of conditioning) and post conditioning hours (end of conditioning – midnight). Given the complexity of the dataset, we conducted separate analyses on 3 subsets of the data. Firstly, as a measure of mean elk displacement from morning to evening and an indication of the overall success of conditioning trials, we tested for a difference in means of

pre, during and post conditioning distances to the Mason-Dixon Line in each year. Secondly, within the pre conditioning dataset, we tested the mean distance of the last hour pre conditioning vs. the mean of all earlier hours pre conditioning in all project years as a measure of response to conditioning trials. We did this to explore our hunch from field observations that elk learned to flee to the east immediately before conditioning started. Lastly we tested the distance of the last conditioning hour vs. all hours post conditioning in all project years as a measure for post conditioning behaviour of elk. We did this to determine whether there was an increase over years in the duration of time post-conditioning that elk remained farther from the line. Because these datasets were normally distributed, we used a random effects maximum likelihood estimator (xtreg command in STATA 10.0, StataCorp 2006) to account for the dependence among repeated observations on the same elk (Wooldridge 2002).

Within season changes in elk distribution

To measure the response of elk to AC trials over the temporal scale of seasons, we established 5 concentric circles using ARCGIS 9.2 (ESRI, Redlands, CA, USA; Figures 1a and b). The inner circle was fitted to encompass the target grassland and the 4 remaining concentric circles were placed with an increasing radius of 1km. We then plotted all elk data (GPS and VHF) of known residents in 2002 – 2008 on top of the circle layer. Pre conditioning years were represented by data from 2002 – 2004 and years with AC from 2005 – 2007. In the next step we calculated the percentage of elk points in each circle per individual, divided in

pre and post conditioning periods for each month (April – August). For statistical testing we used a subset of data (circles 1, 3 and 6) representing the focus grassland area (circle 1), an intermediate distance (circle 3) and distances outside of the target system (circle 6). We then used a set of candidate general linear models to examine the effect on the percentage of elk positions of our main effects (month, AC treatment, and circle number) and their 2 and 3 way interaction terms. The most parsimonious models were determined using AIC (see above).

Among season changes in elk distribution

To determine changes in elk distribution among seasons, we measured the amount of overlap in GPS locations between seasons for each elk. We assessed spatial overlap with static interaction, which compares the amount of overlap between 2 home ranges (Millspaugh *et al.* 2004, Fieberg and Kochanny 2005). We described monthly home ranges with utilization distributions (hereafter UD), which describe both the location and intensity of use within a home range. To measure UD overlap we used the Volume of Intersection Index (VI; Seidel 1992) which describes the volume of overlap between two 3 dimensional UDs. VI ranges from 0, for no overlap, to 1, for complete overlap. We used hourly data from known resident elk that were GPS collared in both pre- and post-conditioning years to develop monthly UDs, using fixed kernel analysis (Worton 1995) and the reference bandwidth method to determine the smoothing factor 'h' (Worton 1989, Seaman and Powell 1996). We used April as a reference month,

representing winter habitat use, because UDs for all elk were identically positioned in the center grassland in all winter months including April. We then calculated monthly VIs for each pairwise combination of UDs for April and each of the summer months for each collared elk. We used Generalized linear latent and mixed models (gllamm) (Rabe-Hesketh *et al.* 2001) in STATA 10.0 (StataCorp 2006), to determine whether the pattern of VIs differed as a function of conditioning treatment (pre vs. post) and related variables. Individual elk were identified with random effects to take account of multiple observations from individuals in each UD (Rabe-Hesketh *et al.* 2005). We used AIC to determine the most parsimonious models (as above).

RESULTS

Aversive conditioning trial distance

We used data from 113 AC trials to examine the changes in elk distribution within days, within seasons and among seasons (below). The mean trial distance was 2,681 m (± 111.5 SE) with a minimum distance of 295 m and a maximum distance of 6,479 m. Of the 15 candidate models, 3 best explained increases in trial distance (Table 2-1). In the top model (AIC *weight, w* = 0.63), trial distance increased slightly with the number of elk included in the trial, the temperature of the day and the number of riders conducting the trial. The distance covered during a conditioning trial, if other factors were left constant, increased by 3.5% per additional rider in the group (Table 2-2). Higher temperatures decreased the distance riders could move elk by -1.4% per degree (Table 2-2).

The second-ranked model was much weaker (AIC $w = 0.23$), and it included the same factors plus wolf presence. Interestingly wolf presence increased, not decreased as might be expected, the distance covered in a conditioning trial. The third ranked model, which was very weak (AIC $w = 0.14$) included rain instead of temperature (Table 2-1). Summing AIC weights of individual models (Anderon et al. 2000) suggested that the best model would always contain number of elk and number of riders as factors, and would contain temperature 86% of the time. Using conventional significance tests on the best model (Frair *et al.* 2004), only the number of riders and temperature were significant predictors of trial distance (Table 2-2).

Daily changes in elk distribution

To examine the response of elk to AC treatments within days, we used 13,399 data points collected from 38 elk wearing GPS collars. In this analysis, we used the Mason-Dixon Line as an arbitrary measure of trial success. Positive distances indicated movement in the SW direction of historic migration and negative values indicated that elk were moving in the opposite direction of our herding efforts; to the NE. Our first analysis showed that the distance to the line varied significantly among both years and the 3 diel periods of conditioning: pre, during and post. (Table 2-3; Figure 2-2) In all 3 years, we were able to move animals in the distance of their historic migration, but there were differences among years in the average position of elk both before and after conditioning (Table 2-3).

Our second and third questions (above) addressed these periods. For the second question, we explored the apparent increase in distance to the line that occurred immediately before conditioning began in the second and third years of conditioning. There was no difference in the pre-conditioning position of elk for the hour immediately before conditioning began in 2005, but this distance increased dramatically in 2006 and 2007 (Table 2-3, Figure 2-2). In addition, the average position of the elk through all the pre-conditioning hours increased in 2006 and 2007. Together, these results suggest that elk learned over time to move farther east in response to conditioning. Our third question addressed the way average elk positions changed in the post-conditioning period relative to the final hour of the conditioning period. Mean SW distances to the line remained relatively constant immediately after conditioning in 2005, declined in 2006, but increased in 2007 (Figure 2-2), causing a significant effect of year on the difference between the final hour of conditioning and the average of the post-conditioning hours.

Within season changes in elk distribution

We used GPS and VHF data from known resident elk collared in years with and without conditioning treatments to determine within season changes in elk distribution as a response to AC, yielding a dataset of 260 090 data points. We analyzed the proportion of points within each circle as a function of circle number, month, treatment (pre- vs. post-conditioning), and the interactions among these variables. Of the 13 candidate models, 4 were identified as the best set of

models (Table 2-4). All 4 top models included month, AC treatment, circle number and the interaction between month and circle. The 3 way interaction term (month, circle number, and AC treatment) was included in the 2 best fitting models, which together had a 64% chance of being the most parsimonious models (AICw = 0.41 and AICw = 0.23). Among years, AC treatments decreased use of the inner circle by 8.4% on average (Table 2-5, Figure 2-4). Within seasons, use of the inner circle was decreased by 14% between May and August, whereas the use of the outer area (circle 6) increased by 20% in the same period (Table 2-5, Figure 2-4).

Among season changes in elk distribution

We used hourly GPS data from 6 elk pre conditioning and 20 elk post conditioning, yielding an average of 6,535 ± 420 SE data points per animal per year, to measure the overlap of three-dimensional habitat use with volume of intersection indices (VI; Seidel 1992). The goal of this analysis was to identify changes in elk distribution both within seasons and among years using a more comprehensive measure of distribution (Figure 2-5). The top model in this analysis had strong support (Table 2-6). Using April as a reference month, this model revealed that VI decreased in the AC treatment years (2005-2007), but it also decreased through the conditioning season AC Table 2-7; Figure 2-6). On average, VI decreased by 53% between May and August and by 37% with AC (Table 2-7; Figure 2-6). Although the second best model (AIC = 0.25) included the interaction term between month and AC, this term was not significant with

conventional statistics (Table 2-7). The top 2 models together were 100% likely to be the most parsimonious models (Table 2-6).

DISCUSSION

The results of this research show that AC can significantly change elk distribution and land use on several temporal and spatial scales. Using this technique, we were able to reduce the time elk spent on a grassland targeted for protection within days, within seasons, and among years. Our results provide some insights about elk behavioural response to this form of AC and identify several additional factors that influence their responses. Exploring these patterns will help to reveal the utility of AC for altering resident behaviour in other ungulate species (e.g., Bolger *et al.* 2008, Skinner 1993, Lott 2002) with potential relevance to the management of other sedentary populations.

The distance over which we could move elk on a given day varied by a factor of 20 and in response to several factors. Most of this variation was explained by 2 variables; the number of elk in the trial and the number of riders. The positive association between trial distance and herd size may stem from the greater safety elk felt moving in a large group. Grouping behaviour is a common response to predation for many prey species, with the primary benefits being dilution of predation risk and reduction in vigilance required (Bertram 1978, Pulliam and Caraco 1984, Lima 1995). Because animals in larger groups can spend less time being vigilant (Turner and Pitcher 1986, Dehn 1990), elk may have felt less stress in larger groups (Hebblewhite and Pletscher 2002), which

may have increased their willingness to be herded. A similar effect of group size has been reported in cattle herding by Smith (1998). The effect of the number of rides presumably stemmed from the tighter control more individuals could provide on the edges of the group (personal observation). Again, similar to cattle, elk moved best when herding pressure was directed towards the sides of the herd while avoiding intense pressure from behind and leaving the desired direction open for movement (Cote 1999). When many riders were present, it was easier to provide consistent pressure to the sides of the herd, to cut-off elk that broke away from the group, and to prevent circling back in the direction from which elk were being moved. A final important contributor to the distance we could herd elk was temperature. Again, cattle provide some insights for this response; they are less willing to travel in warm weather (Cote 1999) when heat stress is common (Berman 2008). On warm days, we observed in elk some of the signs of heat stress, which include bunching, panting, restlessness, congregation around water sources, lack of coordination and trembling (Holt 2009). To counteract this effect, we began trials even earlier in the morning when warm weather was forecasted. Finally, there was equivocal evidence that trial distance increased with wolf presence, but this result counters previous research in the same ecosystem which showed that elk avoided habitats where wolves more commonly occurred (Hebblewhite *et al.* 2005). The weak positive effect of wolf presence on elk distance in our study may reflect the safety from wolves elk perceived in the presence of humans and horses, particularly as they traveled along the forest edge where wolves are more likely to occur (Hebblewhite *et al.* 2005).

Our analyses of the daily patterns in elk movement revealed several dimensions of their response to conditioning. As expected, elk consistently moved in a southwesterly direction in response to our conditioning treatment, but aspects of this response changed among years. In the second 2 years of the project, the distance to the Mason-Dixon Line, which divided the target grassland perpendicular to the direction of conditioned movement, actually increased in the hour before conditioning trials began. This described an increasing tendency for elk to move in the direction opposite the conditioning trials in the early morning just before trials were to begin. We believe this was a learned response by the elk which was cued by the pre-conditioning reconnaissance trip made each morning by truck (see methods) to determine the position of the elk. This response is easily interpreted as avoidance conditioning (Domjan 2003) whereby elk behaved in a way that reduced the likelihood of an expected negative stimulus. Indeed, some elk did avoid being conditioned by 'hiding' in the shrubs on the northeast side of the target grassland (Figure 2-1 a and b). Once we identified this tendency in 2006, we attempted to counteract it by approaching elk from locations further east and moving conditioning hours to earlier times. Nonetheless, it was difficult to overcome this tendency, perhaps because established movement patterns in ungulates are hard to change (DeNicola *et al.* 2000).

Learning on the part of both elk and our team might be responsible for the changes in distance to the Mason-Dixon Line that occurred among years at the end of conditioning trials. Relative to 2005, we were able to move elk farther from the line in 2006, perhaps because we learned the more effective techniques

for conditioning (above). But the elk quickly doubled back towards the grassland in 2006, reducing the average post-conditioning distance to the line, and perhaps revealing what they had learned to actively resist the distribution goals of conditioning trials. But by 2007, the distance to the line actually increased at the end of the daily conditioning period, which reduced the time elk spent on the central grassland (below). This response may have occurred because sufficient repetition enhanced the message contained in the AC treatments (*sensu* Kanwisher 1987, Henson 1998). In addition, the greater movement momentum in 2007 may have stemmed from a conspecific effect. In cattle, nonstimulated steers react in conjunction with a partnered stimulated steer to detour from a site connected with a negative stimulus (Tiedemann *et al.* 1999). This mechanism may have reduced the tendency for elk to return to the target grasslands (above) in 2007 to increase the average distance to the line in the post-conditioning period.

To examine the effect of AC on elk distribution within seasons, we established non-overlapping concentric circles over the target grassland and measured the percentage of elk positions contained in each circle. Elk moved from the centre of the target grassland to the periphery in the course of each season, but this tendency was more pronounced in the years with conditioning. Whereas we observed almost no difference in the percentage occupancy in different circles between pre and post conditioning years in April and May (conditioning typically started in mid May), the patterns in June and July were pronounced. On average the percentage of locations in the target grasslands (circles 1 and 2) decreased from 46% to 16% in June and from 30% to 8% in July.

Some of the within-season effect is likely due to the greater human activity in the centre of the grassland in summer (Hebblewhite and Merrill 2007). Elsewhere, elk move away from areas with biking, hiking and even horseback riding (Naylor *et al.* 2009), all of which occur in the area of the Ranch. Indeed, a synergistic effects may have occurred between the negative stimulus of our horse-based conditioning trials and the negative effect on elk of recreational horseback riding (Domjan 2003). Such an association may increase the reinforcement of this technique to increase its efficacy in the long term (below).

Our final measure of the effect of AC on elk behaviour also compared the overlap in elk use of areas both within and among seasons. Summer changes in utilization distributions were compared to the winter distributions (represented by April) using volume of intersection indices (VI), similar to Milspaugh *et al.* (2000) who used this technique to investigate overlap in the habitat use of hunters and elk and Schauber *et al.* (2007) who used VI to show that direct contact rates between GPS collared deer were higher in autumn and spring than in summer. In our study, measures of VI provided more comprehensive support for the between-season concentric circle analysis to indicate that elk spent more time further away from the target zones in years with conditioning. According to Hebblewhite *et al.* (2006), winter use of the grassland did not change between his mid (1986 – 1994) and late (1995 – 2004) study periods, but summer use by a resident portion of the population increased dramatically. Our AC technique appears to have decreased the VI over all summer treatment months relative to the years without AC. We overcame some of the sample size and bias issues that concern UD approaches by

using hourly GPS locations (as recommended by Fieberg and Kochanny 2005) to generate a sample size >200 (as recommended by Garton *et al.* 2001).

In sum, we have shown that AC can reduce the amount of time spent by elk on a target area within days, within seasons, and among years of use. Despite this success, not a single individual elk that was known to be a summer resident at the beginning of the study (see methods) exhibited a migratory pattern comparable to migrating individuals (*sensu* Hebblewhite *et al.* 2006) in any year of the study. An aerial survey, conducted in the last year of the project supported this observation (Appendix III). Thus, AC seems limited and perhaps ineffectual, at least with this intensity, as a means of reinstating migratory behaviour. Instead, the resident elk that were moved off the grasslands discovered new habitats close to the Ranch (Figure 2-1 b) and distribution changes rarely exceeded the outer limits of the Ranch area. The modesty of this change over a 3 year period might be expected from the decades over which migratory behaviour was lost (Hebblewhite *et al.* 2006) and more time will be needed to know the longer-term efficacy of AC. AC did not appear to affect vital rates of elk as measured by mortality rates, cow:calf ratios, or pregnancy rates, but a decline in population size occurred in the years in which it was conducted (H. Spaedtke, unpublished data).

MANAGEMENT IMPLICATIONS

A comprehensive approach to combat the world wide loss of migration should include a wide variety of management tools. Typically methods to tackle

animal distribution issues, such as loss of migration, include highly invasive methods such as fencing and relocation. Those methods are rarely accepted by the public and are usually connected to high mortality rates (Frair *et al.* 2006) and considerable financial costs (e.g. Romin and Bissonette 1996). Depending on habitat type, animal species, and local infrastructure, AC on horseback could be a viable alternative. AC can sometimes be employed as a low-cost, low-impact supplement to other management options in systems similar to the Ranch. In addition, moving wild animals on horseback appears to be much more acceptable to the public. Indeed, the technique could even serve as a tourist attraction to the benefit of some local economies. At the Ranch, Parks Canada has committed to continue AC treatments on horseback for the foreseeable future. Other systems that already employ horse-based techniques, such as the Greater Yellowstone Ecosystem, may benefit from simple horse-based herding techniques to manage ungulate populations.

Table 2-1. Conditioning trial distance model selection for the Ya Ha Tinda elk population, Alberta, Canada for 113 conditioning trials conducted in years 2005 – 2007. Models were ranked by Akaike's Information Criterion (AIC_C) values (Rank 1 = best) and normalized AIC_C weights (W). We only report models with $\Delta AIC \leq 3$.

Rank	Model	K	AIC_c	ΔAIC_c	AIC_w
1	#elk + riders + temp	4	493.1	0.00	0.63
2	#elk + riders + temp + wolves	5	495.1	1.99	0.23
3	#elk + riders + rain	4	496.2	3.04	0.14

Table 2-2. Parameter estimates, unconditional SEs and significance levels for the top model explaining variation in AC trial distance.

Parameter	Description	β	SE	P
#elk	number of elk in AC trial	0.0258	0.018	0.158
riders	number of riders in AC trial	1.8691	0.595	0.002
temp	temperature at start of AC trial	-0.7334	0.278	0.008
constant		38.4707	3.414	≤ 0.001

Table 2-3: Parameter estimates from random effects maximum likelihood estimator (xtreg) for a three individual models conducted on subsets of diel movement datasets of elk collected at the Ya Ha Tinda Ranch in 2005 - 2007.

Test	Parameter	β	SE	P
Test 1: Main Diel Periods	Year	1009.69	13.73	0.001
(Pre conditioning, Conditioning,	Period	263.75	28.71	≤ 0.000
Post Conditioning)	Constant	530882.40	57600.40	≤ 0.000
Test 2: Within pre conditioning	Year	-29.18	38.59	0.450
(Last hour pre conditioning,	Period	-752.34	102.54	≤ 0.000
previous hours pre conditioning)	Constant	57893.87	77415.20	0.455
Test 3: Post Conditioning Period	Year	-438.20	195.50	0.025
(Last hour Conditioning, Post	Period	422.85	38.08	≤ 0.000
Conditioning)	Constant	845742.70	76384.54	≤ 0.000

Table 2-4. Concentric circle use model selection for the Ya Ha Tinda elk population, Alberta, Canada for years without (2002-2004) and with (2005 – 2008) AC. Models were ranked by Akaike's Information Criterion (AIC_C) values (Rank 1 = best) and normalized AIC_C weights (W). We only report models with $\Delta AIC \leq 3$.

Rank	Model	K	AIC_c	ΔAIC_c	AIC_w
1	Month + AC + circle + int3 + int4	6	-217.1	0.0	0.41
2	Month + AC + circle + int2 + int3 + int4	7	-216.0	1.2	0.23
3	Month + AC + circle + int2 + int3	6	-215.2	1.9	0.16
4	Month + AC + circle + int1 + int2 + int3 + int4	8	-214.6	2.5	0.11

Note: Int1 = (month * ac), int2 = (ac * circle), int3 = (month * circle); int4 = (ac * month * circle)

Table 2-5. Parameter estimates, unconditional SEs and significance levels for the top model explaining variation in concentric circle use.

Parameter	Description	β	SE	P
AC	Aversive Conditioning treated population	-0.0727	0.0213	0.001
Month	Month of the year	-0.0254	0.0045	≤ 0.001
Circle	Concentric circle # (1 = inner - 6 = outer)	-0.0648	0.0088	≤ 0.001
Int3	2 way interaction (month * circle)	0.0043	0.0011	≤ 0.001
Int4	3 way interaction (ac * month * circle)	0.0029	0.0007	≤ 0.001
Constant		0.5031	0.0380	≤ 0.001

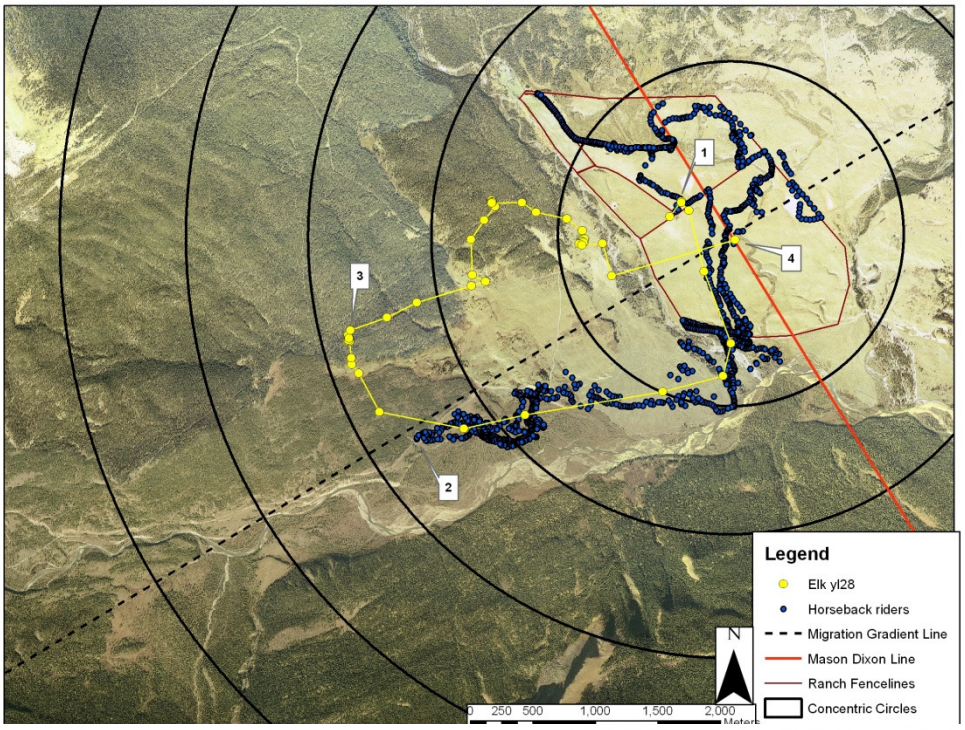
Table 2-6. VI model selection for the Ya Ha Tinda elk population, Alberta, Canada for years without (2002-2004) and with (2005 – 2008) AC. Models were ranked by Akaike's Information Criterion (AIC_c) values (Rank 1 = best) and normalized AIC_C weights (AIC_w).

Rank	model	K	AIC_c	ΔAIC_c	AIC_w
1	AC + month	5	-75.0	0.00	0.75
2	AC + month + AC*month	6	-72.9	2.16	0.25
3	AC + AC*month	5	-62.6	12.39	0.00
4	AC	4	-21.2	53.79	0.00

Table 2-7. Parameter estimates, unconditional SEs and significance levels for the top model explaining variation in VI.

Parameter	Description	β	SE	P
AC	Aversive Conditioning	-0.16247	0.047	0.001
Month	Month of the year	-0.11947	0.013	≤ 0.001
Constant		1.257195	0.096	≤ 0.001

A)



B)

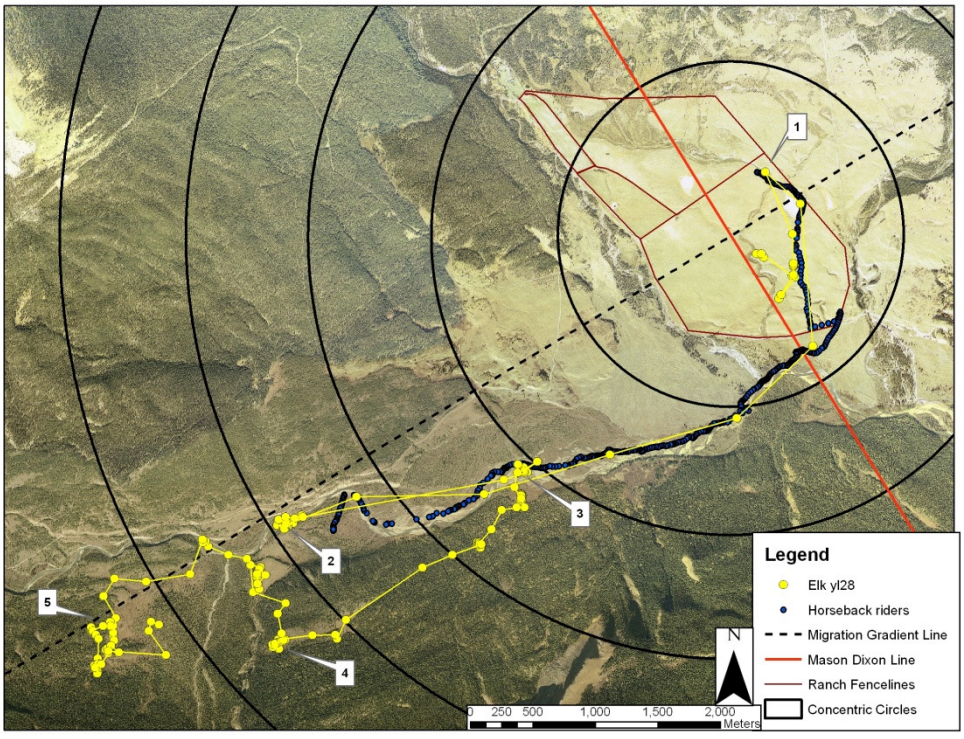


Figure 2-1 a – b. Ya Ha Tinda Ranch grasslands and surroundings with GIS established measurement tools: 5 concentric circles dividing the grassland in 6

areas (1 = within inner circle - 6 = area outside last circle); Mason-Dixon line (in red) drawn through the middle of the target grassland, with the migration gradient indicated as black dotted line in 90degree angel to Mason-Dixon line. Yellow dots indicate sample elk data of a 24 hour period with AC. In figure a) the elk returns immediately after the end of the AC trial, whereas in figure b) the elk moves on beyond the end location of the AC trial. In both Figures, 1 indicates the elk location at the beginning of AC, 2 the location at the end of AC and subsequent numbers indicate clusters of elk locations after AC.

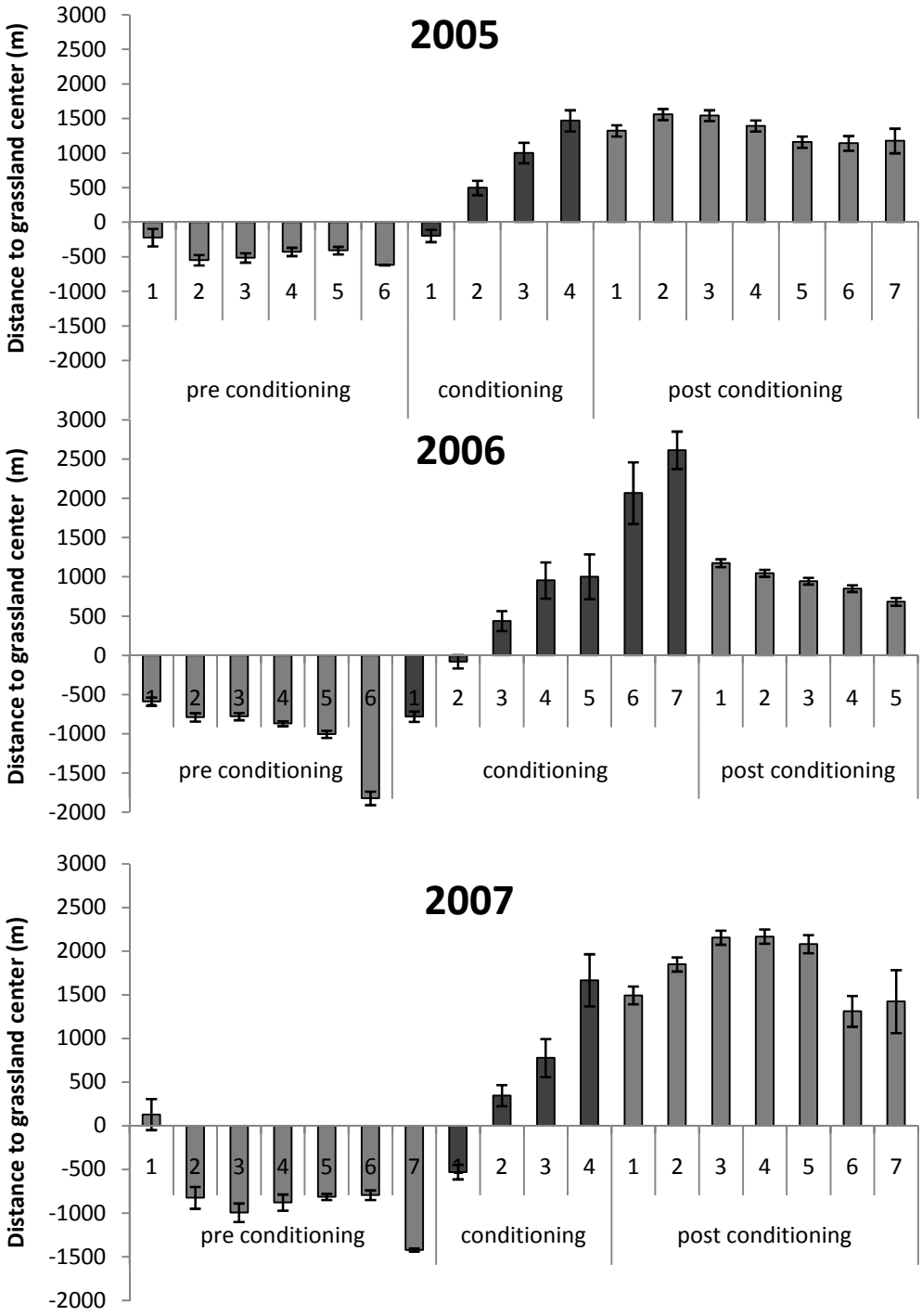


Figure 2-2. Hourly mean elk distance (m) to a Mason-Dixon Line dividing Ya Ha Tinda Ranch target grasslands in eastern and western portions. Negative values indicate eastern, positive values indicate western elk distance to the Line in the

hours before during and after a conditioning trial for 3 years of AC application. Error bars indicate Standard Errors.

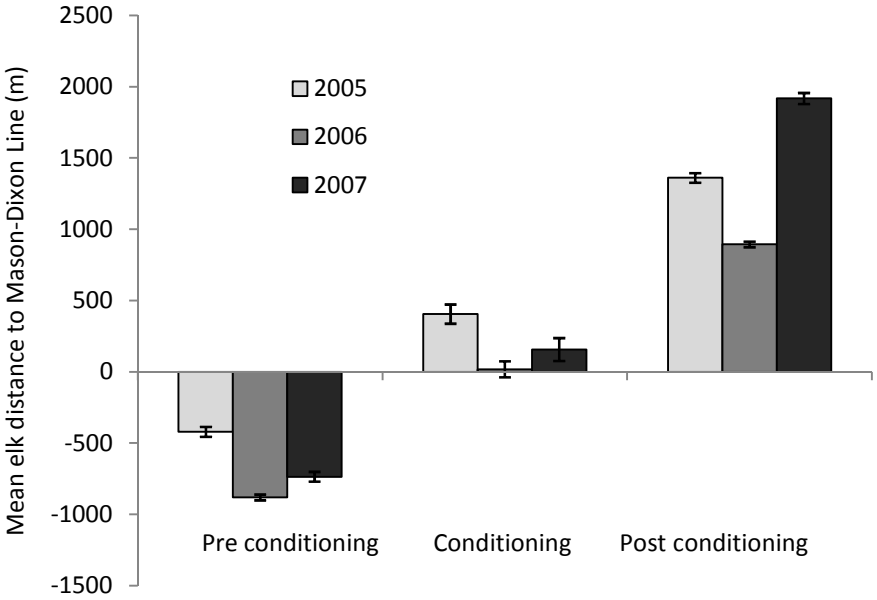
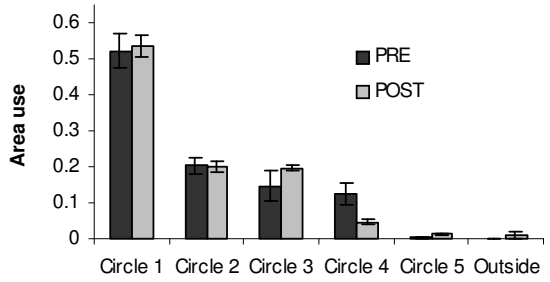
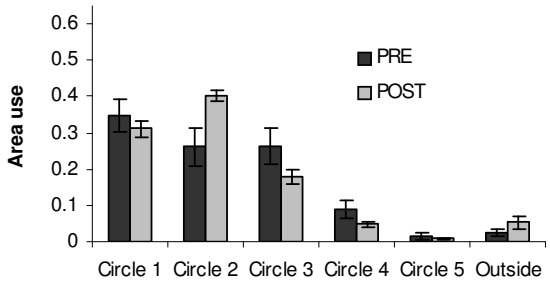


Figure 2-3. Annual mean elk distance (m) to a Mason-Dixon Line dividing Ya Ha Tinda Ranch target grasslands in eastern and western portions. Negative values indicate eastern, positive values indicate western elk distance to the Line in the hours before during and after a conditioning trial for 3 years of AC application. Error bars indicate Standard Errors.

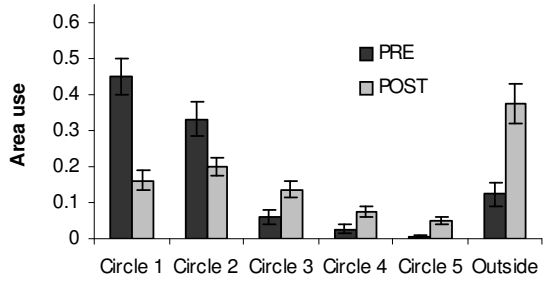
A) April



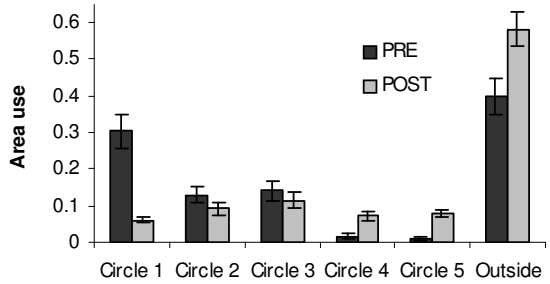
B) May



C) June



D) July



E) August

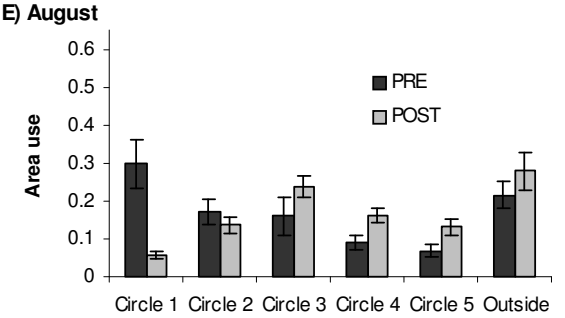
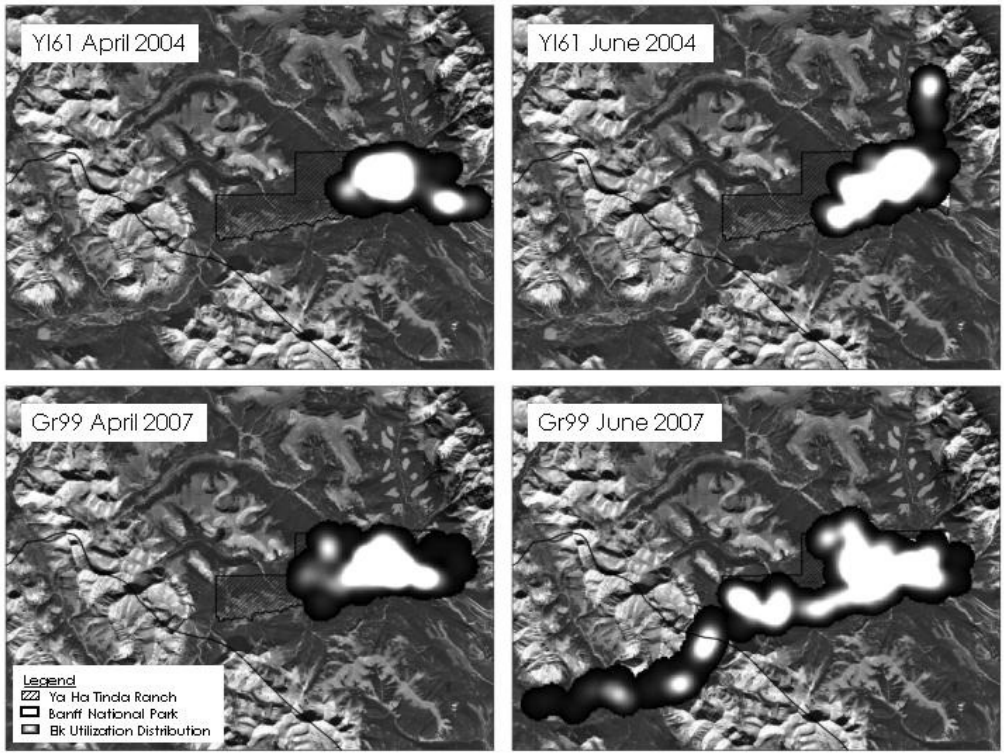


Figure 2-4: Mean proportion of elk use in areas defined by concentric circles (diameter increasing by 1km per circle) around the target grasslands at the Ya Ha Tinda Ranch for month April – August in pre (2002 – 2004) and post (2005 – 2007) years. Error bars indicate Standard Errors.

A)



B)

Figure 2-5: Utilization Distributions of sample elk in April and June of 2 sample elk. A) without conditioning and B) with conditioning.

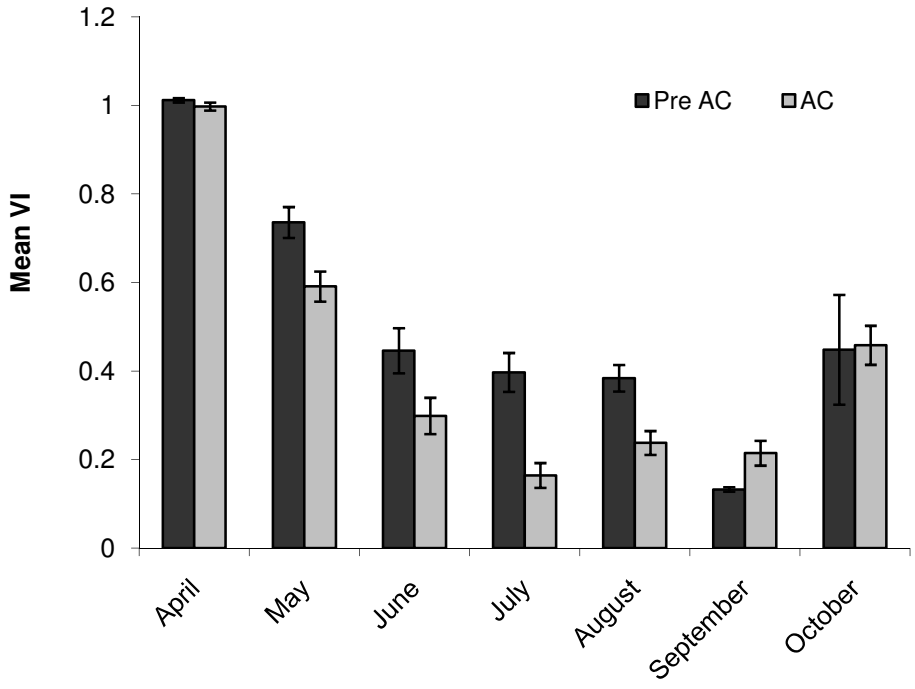


Figure 2-6: Mean Volume of intersection (VI) index for elk locations compared to the April locations of the same individual. Note: VI in April must be approximating 1 given that April locations are compared with themselves.

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CHAPTER THREE

MANIPULATING ELK DISTRIBUTION AFFECTS BIOMASS IN A MONTANE FESCUE GRASSLAND

Holger R. Spaedtke, Colleen C. St. Clair, Clifford A. White[2]

INTRODUCTION

Migration can allow animals to increase access to food resources (MacArthur *et al.* 1972), avoid environmental factors, e.g. heat exposure (Belovsky 1981) and evade the accumulation of predators (Festa-Bianchet 1988). By migrating, grazing animals also provide an opportunity for rangelands to recover from intense utilization, similar to rotational grazing in modern farming systems (Asamoah *et al.* 2003). The absence of migration is, thus, assumed to increase the potential for habitat degradation (McInenly 2003). As evidence of this effect, overgrazing by livestock is recognized as one of the main impediments to grassland health (Yong *et al.* 2003, Fleischner 1994). Wild ungulates may also be sedentary. For example, wildebeest (*Connochaetes taurinus*) and caribou (*Rangifer tarandus*) both exhibit sedentary sub populations (Banfield 1954; McNaughton 1985), which presumably increase the grazing pressure on their associated habitats (McNaughton 1985). Indeed, rangeland health is predominantly determined by the grazing pressure it sustains (Grant *et al.* 1982).

[2] This chapter is formatted for submission to the Journal of Range Ecology and Management with these authors.

The extent to which sedentary populations degrade rangeland habitat typically depends on their size and management (Van Soest 1994). Whereas well-managed forage systems have the potential to increase plant production and the nutritional quality of forage (Pedreira *et al.* 1999), excessive use of grasslands causes a reduction in plant cover, followed by a decrease in plant diversity (Heady and Child 1994). Grazing impacts both above and below ground productivity (Milchunas and Lauenroth 1993) and even moderate levels of increased grazing pressure can decrease primary production (Milchunas and Lauenroth 1993, Manseau *et al.* 1996, Milchunas *et al.* 1998). Although light to moderate removal of leaves may stimulate plant productivity, too much grazing negatively affects plant production (De Mezancourt *et al.* 1998). If too many leaves are removed from a plant, its photosynthesis is inefficient and root systems shrink in response, making plants vulnerable to drought (Adams *et al.* 2005). At the same time, less decadent vegetation is left as litter, which is essential to water absorption and nutrient cycling. Once a grassland has experienced overgrazing, it can take decades to recover to a healthy state (Hui and Chen 2006).

One community type that appears to be susceptible to the effects of overgrazing is the rough fescue grasslands of Canada, which are highly productive by North American standards (Willms *et al.* 1996). Despite their importance, healthy fescue communities are found at a minority of surveyed sites (13%), despite the prevalence (33%) of fescue plants in the same locations (Holcroft Weerstra 2003). This disparity suggests that rough fescue communities are not being sustained at some of the sites where they historically occurred,

prompting a threatened designation (Trottier 2002). The loss of rough fescue communities is important because this grass provides particularly important winter forage for ungulates and it makes good-quality hay for livestock (Call and Maser 1985). Fescue is resistant to grazing in winter (Willms *et al*. 1986), but it does not appear to be robust to grazing or clipping in the spring and summer growing seasons (McLean and Wikeem 1985). Summer grazing is especially likely to reduce the abundance of ungulate forage plants in grass meadows (Bråthen & Oksanen 2001).

Some degradation from overgrazing is evident at one of the largest remaining parcels of rough fescue in Canada, which occurs just east of Banff National Park on the historic Ya Ha Tinda Ranch (hereafter 'Ranch'). There, the influence of warm westerly winds combined with the configuration of the surrounding mountains (rain shadow effect) have favored the development of an extensive Rough Fescue grassland (Morgantini and Hudson1989). This area covers approximately 3000 ha (McInenly 2003) and provides critical winter range for one of Alberta's three largest elk (*Cervus elaphus*) herds (Morgantini 1995). In recent years this elk population has become partially sedentary with up to 55% of the current herd spending their summers on the winter range at the Ranch (Hebblewhite *et al.* 2006). Previous work at the Ranch has indicated that those changes in the elk population may have a major negative impact on the fescue community under certain conditions (McInennly 2003).

Because of the sensitivity of fescue to summer grazing, continued year round residency by elk is likely to compromise the viability of both the fescue and

the grazing wild ungulates that depend on it. The Ranch is managed by Parks Canada and it provides a winter home for its working horse population, in addition to a wintering range for wild ungulates. Parks already controls the seasonality (mid-November until early May) and volume (a reduction from ~200 to 90 animals in winter; and to ~20 in summer) of horse grazing. What remains is to control summer grazing by elk. Paradoxically, by residing year-round on the Ranch, elk are potentially reducing the overall carrying capacity of the winter range. Reinforcing migratory behaviour is, thus, in the best interest of both range and wildlife management at the Ranch.

Here we describe the effects on the Ranch grassland of a research project that that used aversive conditioning to manipulate elk distribution during the summer months. In brief, elk were herded on horseback from the grassland to the direction of their historic migratory route each morning for three years (Chapter 2). To test of the efficacy of AC as a tool for protecting grasslands, we measured the grassland response with methods similar to other studies of rangeland health. We used pellet counts as an indicator of ungulate distribution and grazing pressure (e.g., Edge and Marcum 1989, Rowland *et al.* 1984) and additionally measured grazing as the percentage of grazed biomass in sample plots (e.g., Adams *et al.* 2005). We measured forage use by comparing biomass in caged and uncaged plots (e.g., Bonham 1989, Bork and Werner 1999). We assumed that all three measures would reflect effects of aversive conditioning on grassland health. If aversive conditioning can cause substantial changes to elk use in summer, it could provide a cost-effective means of preventing further damage to this

endangered and ecologically-important rough fescue grassland, with potential application to other jurisdictions in Alberta and across North America.

METHODS

Study Area

Field work was conducted at the Ranch and surrounding area east of the Banff National Park boundary in Alberta, Canada (51º45' N - 115º35' W). The Ranch is ~4000 ha in size and is situated in a montane ecoregion with an average elevation of 1550 m. Most of the Ranch consists of grasslands described as a Rough fescue-Sedge-Junegrass community type, but the western area mainly represents a Sedge- Junegrass community type (Willoughby 2001). Since the 1930's the Ranch has provided a wintering site for up to 160 horses for the Parks Canada Warden service and up to 1000 elk. Until recently, most elk migrated as far as 80 km to the Bow Valley (Morgantini and Hudson 1988) and a broad assemblage of ungulates and predators uses the range year round (Morgantini (1995).

Aversive Conditioning Treatments

Aversive conditioning of elk involved sequential applications of controlled movements by 2 –15 people on horseback, who applied herding techniques, known from cattle, to move elk in the direction of historic migration routes west of the Ranch. Elk were moved as groups off the target grassland areas (Figure 3-1) into nearby habitat beginning in the critical growing period of fescue (~May

15th of each year), which coincides with the beginning of elk migration. Treatments continued throughout the summer whenever elk were seen in the target areas. Elk movement was monitored with the use of both conventional VHF radio-collars and global positioning system (GPS) collars. For a more thorough assessment of the aversive conditioning methods applied see Chapter Two.

Vegetation Plot Design

To identify the change in grazing pressure over short (within season) and longer (among seasons) time periods, we used two methods: elk pellet counts and grass biomass measurements. These methods have been used in previous graduate research at the Ranch (McInenly 2003, Hebblewhite *et al.* 2006) which allowed us to use those results as 'pre-treatment' data and to establish a database for longer term monitoring. McInenly (2003) determined the spatial extent of grasslands at the Ranch by digitizing a large polygon from a satellite image (excluding continuous forest portions), and by field verification of non-forested classifications based upon canopy covers of less that 60%. Using this method, she created 277 points on a systematic grid located at 250 m intervals. Each point was placed at the center of a 25m² (5m*5m) plot, in which all fresh elk pellets were counted. We modified that grid to create a 500m grid with 45 plots in total (Figure 3-1). Every plot was permanently flagged at each corner with 20cm steel nails wrapped with flagging tape. Each plot was revisited monthly between May and September of 2005 – 2007.

Elk Pellet Counts

To provide a finer-scale and within-season assessment of elk grazing pressure, we counted elk pellets in the vegetation plots during each of the monthly samples. At each of the 45 permanent plots, elk and horse pellets were counted following the method described in McInenly (2003). A pellet group was defined as at least 8 pellets and the distribution of the pellets was considered for distinguishing between groups. Only when > 50% of the pellet group was within the plot border, was it included in the count. We determined pellet age and counted only fresh pellets in the initial visit (May) of each year. After this, pellets were evenly distributed within the plot after counting, to ensure that subsequent visits counted only the new pellets groups. We did not remove pellets because of the effect that would have on available nutrients (and hence vegetation growth) within the plot. Unlike McInenly's methods, we counted pellet groups on a monthly base, summarizing May – September counts as 'total summer count' resulting in identical and therefore comparable measures. Although pellet counts in 25 m^2 plots overestimated those in 100 m^2 plots (McInenly 2003), we continued using the 25 m^2 design to make our results comparable to that earlier study and to increase sample efficiency (Neff 1968). Thus, our results may provide slightly higher absolute estimates of ungulate density, but this bias is consistent among years.

Biomass Estimation

During every visit, biomass was determined using a "disc-pasture-meter" measurement (Vartha and Matches 1977, Dorgeloh 2002) in each of the 4 corners of each plot. This method was previously used by Hebblewhite *et al.* (2006). Briefly, this method consisted of sliding a 0.25m² base plate (weight 222g) over a 1m long calibrated aluminum rod (meter stick). After dropping the disc from the top of the meter stick, the settling height (accurate to 0.5cm) was recorded as a measure of overall biomass per sub-plot. For every disc measurement, the average % cover was determined for the broad vegetation classes of grasses, forbs, shrubs and bare ground, to improve drop disc biomass representation. The accuracy of the drop disc method was calibrated by conducting 282 clip plots, directly adjacent to the permanent vegetation plots, over the three years of the project. At each of these control plots a drop disc measurement, as described above, was taken and all standing biomass (green and old) greater than 2cm height (to simulate that available to elk cropping) was clipped, dried at 100 degrees for 24 hours and weighted. A linear regression of biomass dry weight and drop disc height explained 76% of the variation in dry weight and the overall fit was significant [$(F_{1,278}) = 882.15$, $p \leq 0.001$, $R^2 = 0.76$]. Thus, we used the final model predicting dry weight [Dry weight (g/m^2) = 4.698*(Disc Height) - 16.206 (Figure 3-2)] to estimate biomass (below).

Grazing percentage and biomass growth difference

As a measure of grazing pressure on the grassland, we determined, using an ocular method, the percent biomass that had been grazed per sub plot by identifying fresh (< 1 month) bite marks in the vegetation and estimating the total percentage of biomass grazed (*sensu* Keigley *et al.* 2003). In the main project years 2006 and 2007, range cages ($1.5m^2$, 1.8m high) were added to additional plots adjacent to our study plots. These locations were typically within 10 m in a randomly-chosen direction with visually-similar habitat. Their purpose was to provide measures of biomass removal from grazing within seasons, providing another measure of the effectiveness of aversive conditioning measurements for grassland protection. Biomass underneath the cone was measured at the point of setting up the cone to achieve an 'original state' measurement and during the next revisit approximately 1 month later. The difference between the two measurements was calculated to determine growth per month. At the same time the paired plots were measured, using identical methods, producing identical growth estimates for the unprotected sample plot. The cones were moved after each revisit (monthly) to avoid cage effects on vegetation growth.

Precipitation

To control for the effects of precipitation on biomass during our study, we compared biomass measures to precipitation over several additional seasons using data collected by Hebbelewhite *et al.* (2006), Sachro *et al.* (2005) and the Monitoring and Evaluation Branch of Alberta Environment. Hebblewhite *et al.*

(2006) collected vegetation data with the same protocol we used, but Sachro *et al.* (2005) determined biomass availability by placing a 20 cm x 50 cm frame in the center of each plot and clipping biomass within. Clipped samples were air-dried in the field and then weighed. Field sampling was conducted from June 25 to August 16, 2001. As we have shown (above), these biomass measures from clipping are tightly correlated to those derived by the drop disk method. Thus we corrected Sachro's measurements for plot size and used $1m^2$ total biomass estimates to compare data from all three studies. Precipitation data (June – August in mm per month) for long-term comparisons were obtained from Environment Canada for Blue Hill tower 20 km south east of the Ranch for 2001–2007.

STATISTICAL ANALYSES

Elk Pellet counts

We tested the hypothesis that aversive conditioning changed the distribution of pellet groups in summer while leaving the distribution unchanged in winter using negative binomial regression (Hilbe 2007) similar to what others have done with pellet count data (Boyce *et al.* 2001, Rowland *et al.* 1984). We assessed model fit by fitting both zero-inflated negative binomial and zero-inflated poisson regression models to the pellet data (Nielsen *et al.* 2002), and testing for improvements to model fit using the Vuong test (Vuong 1989). In all cases, models fit the negative binomial distribution better (all Vuong tests P-values > 0.18). Because of missing data in 2000 and 2001 and a strong confound effect

between year and AC treatment, we used 2001as a reference year and tested for differences among years (with 2001 representing pre AC and 2005 – 2007 representing years with AC) using separate negative binomial models for winter and summer. We fit random effects negative binomial regression (xtnbreg) in STATA 10.0 (StataCorp 2006). As a complement to this test, we used a simpler approach to assess the similarity in pellet counts among treatments, seasons, and years, by conducting a bootstrap analysis to derive the 95% confidence estimates for each of our means (Hoyle and Cameron 2003). For this, we used the bootstrap() function from the "bootstrap" package for R (version 1.0-21; Efron and Tibshirani 1993) and 1000 bootstrap samples to estimate the shape of the t function for each year / season combination and 200 resamplings to estimate the standard deviation within each of those 1000 simulations.

Grazed Biomass and Re-growth

We tested for differences in grazed biomass and biomass re-growth between years and between revisits (within years). To meet assumptions of normality, we arcsine transformed the biomass data prior to analysis (Zar 1999). Given that re-growth data were normally distributed we did not use data transformation on this dataset. For both analyses we used a random effects maximum likelihood estimator (xtreg command in STATA 10.0; StataCorp 2006) which accounts for the dependence among repeated observations on the same vegetation plot (Wooldridge 2002). Because the variance associated with the random effect was small ($\sigma_u_{grazing} = 0.051$, $\sigma_u_{re\text{-}growth} = 0.003$), we conducted a Breusch-Pagan

Lagrange multiplier test for random effects (xttest0 – command in STATA 10.0, StataCorp 2006) which indicated that the random effect should remain in both models ($\chi^2_{\text{grazing}} < 0.001$, $\chi^2_{\text{re-growth}} < 0.001$).

Precipitation

To incorporate the effect of precipitation on biomass, we calculated the annual sum of precipitation using data from the month of June until August of each year. Our biomass data approached normal distribution and fit a Gaussian distribution better than a Poisson distribution, therefore we analyzed the data with a generalized linear mixed effects model and a Poisson link, using the lme4 package in R 2.7.1 (R Development Core Team 2007). Explanatory variables included AC (0 = no conditioning, 1 = conditioning) and PRECEP (average annual summer precipitation). We included Vegetation plot ID (PLOTID) as a random effect (separate intercept for each plot) because changes in biomass could vary between vegetation plots due to changes in topography and soil type in different parts of the study area. YEAR was initially included as a covariate, but was dropped due to strong colinearity with conditioning treatments. We also tested for variation in AC effects among levels of precipitation by examining the interaction of AC and PRECEP. We used likelihood ratio tests for model selection (Zar 1999).

RESULTS

Elk pellet counts

Between 2000 – 2002 and 2005 – 2007, we counted a total of 844 individual pellet groups during 445 plot revisits. Mean pellet counts declined by approximately 50% in the years post AC during summer, but they remained relatively unchanged following winter (Figure 3-3). We found a decline in pellet counts subsequent to the pre-conditioning year of 2001, indicating an effect of AC. The constant decline of pellet counts from year 2001 – 2007 indicated that the AC effect was weaker in 2005, than in either 2006 or 2007 (Table 3-1, Figure 3-3), suggesting that the response of elk to AC increased over time. During winter, there were no significant differences among years (Table 3-1). The bootstrap approach supported this analysis. In winter, it showed no differences (overlapping confidence intervals) between pre and post AC pellet counts , but in summer, the 2007 count differed from both 2001 and 2005; 2006 did not differ from any other year (Table 3-2).

Grazed Biomass and Regrowth

We conducted 2168 sub plot measurements in 47 different vegetation plots over the three years of the project. The percentage of biomass that was grazed declined precipitously in successive revisits in every year, but there were also differences among years and in a year by revisit interaction (Table 3-3, Figure 3-4). The amount of biomass grazed decreased significantly as a function of both year and time of revisit. The interaction term between these variables was also

significant, indicating that the way in which grazing pressure changed throughout the season was different across years (Table 3-3). Unexpectedly, we discovered that 2007 had higher grazing than 2006 in the first visit but this difference diminished throughout the revisits (Figure 3-4).

We additionally measured the growth difference between 284 revisits in 47 plots with enclosures in 2 years of the project. Mean growth inside enclosures was slightly higher than outside the enclosures in the first revisit of both years, but that difference disappeared for the second visit in 2007, and became dramatically negative in the third visit of that year (Figure 3-5). This pattern produced a strongly significant effect of year, visit number, and year by visit interaction (Table 3-4), indicating that the way in which growth patterns changed throughout the season was very different between years (Figure 3-5).

Precipitation

Mean biomass measured in the years before conditioning (2001 – 2004) was less than half the value (87.14 g/m^2 ± 9.13 SE) than in the years with AC (183.31 g/m^2 ± 5.79 SE). This difference is likely partially an effect of the approximately 45% increase in mean precipitation that occurred between the years before conditioning (197.9 mm ± 7.36 SE) relative to after conditioning (290.9 mm ± 5.6 SE ;Figure 3-6). Biomass increased significantly with rainfall, but it also increased with aversive conditioning (Table 3-5). These effects appeared to be additive, because the interaction between rainfall and aversive conditioning was not significant and the inclusion of this term did not improve

model fit (Table 3-5; LRT = 1.546, p-value = 0.214). Biomass increased by an average of 210 % with aversive conditioning in low precipitation conditions (100 mm) and by 25% in higher precipitation conditions (375 mm)

DISCUSSION

Results from three metrics suggest that changing elk distribution with aversive conditioning had a measurable effect on the target grassland. First, we observed a decline in pellet groups on the grassland within and between years of the project (excepting 2007). Among years, this decline was most pronounced between 2005 and 2006. Second, we observed a within-season decline in the percentage of biomass that was grazed in vegetation plots. This difference was most pronounced between our initial visit in May and the subsequent visit in each of the conditioning years. Although this within-season trend was consistent throughout all years of the project, a between-season decline in grazing occurred only for the first two years of the project (2005 and 2006). In 2007, grazing percentages were higher than other years in the first three revisits but following the expected trend in the last revisit. Our third measure of the effect of aversive conditioning on the grassland was more equivocal. Whereas regrowth measurements in caged and uncaged plots showed slightly higher growth inside cages in the first revisit of both measurement years, growth was much higher outside the cages by the last visit of the second year. Overall, our results suggest that AC had a generally positive effect on vegetation, which could not be explained by interannual differences in precipitation. Although biomass increased

in wet years, it was higher still in the years with aversive conditioning, suggesting an additive effect of precipitation and reduced summer grazing. Despite the generally positive effect AC appeared to have on grassland growth, there are some subtleties of interpretation to explore.

Using pellet counts as a measure of habitat use by ungulates has been extensively debated in the literature. In some early ungulate studies, there appeared to be no association between pellet counts and controlled animal use of an area (Collins 1979, Collins and Urness 1979). In subsequent studies, a strong correlation was found between pellet counts and telemetry locations (Loft and Kie 1988, Edge and Marcum 1989), suggesting that higher resolution of information about ungulate activity is needed to identify the correlation with pellet counts. On balance, it appears that pellet counts can provide a relative measure of ungulate activity, but are less effective as a measure of absolute abundance or density (Harkonen and Heikkila 1999). At the Ranch, pellet counts have been used previously as a measure of apparent habitat quality (Morgantini and Hudson 1988) and local activity (Morgantini and Russell 1983). In keeping with these relative metrics, our results suggest that pellet counts reflected a decline in elk use of the targeted grasslands both within and among the summer seasons in which aversive conditioning was applied. However, over the same period, there were no differences in winter pellet counts, indicating the effect of AC on elk distribution was limited to the months in which it was applied.

As measured by the percentage of plots that were grazed, our results demonstrated an overall decline in grazing throughout each of the years in which

AC was applied. Although the pattern of reduced grazing was highly consistent between early and subsequent visits within seasons, it did not hold across seasons. Elk grazed significantly more biomass in the first revisit of 2007, relative to 2006, suggesting that they had limited abilities to remember the effects of AC between seasons. Although this explanation is plausible, our measurements did not permit us to identify the amount or quality of biomass that was removed; only a ocular estimate of the percentage of vegetation that had been grazed. Thus, it is possible that elk removed a higher percentage of biomass in 2007, but they may not have obtained higher forage quality or amount by doing so. This scenario is also plausible because 2007 was the third high-precipitation year in a row and the effects of high precipitation on biomass growth can be lagged by one or more years (Dunnett *et al.* 1998; O'Connor *et al.* 2001 Wiegand *et al.* 2004). Because forage quality actually decreases with biomass abundance (Wilmshurst *et al.* 1999, Fryxell *et al.* 2005), elk may have needed to consume more of the lower quality biomass in order to achieve energy intake that was comparable to years with higher quality biomass (Demment and Van Soest 1985).

A second potential explanation for our grazing results is, that an accumulation of biomass reduced forage quality, may be supported by our 2007 results for regrowth in caged vs. uncaged plots. In that year, regrowth outside the plots was dramatically higher than it was inside the plots by the final revisit. The areas outside the cages were subjected to grazing throughout the summer, albeit at lower intensity than in the pre-conditioning years. Particularly under conditions of high standing biomass, repeated grazing can stimulate fresh regrowth and

increase the nitrogen concentration of the vegetation (Drent and Van der Wal 1999). In this way, modest grazing by herbivores can facilitate forage growth (Arsenault and Owen-Smith 2002) to qualitatively improve the vegetation even while depleting it. Similar facilitation through repeated grazing has been shown to occur in barnacle geese (*Branta leucopsis*) (Ydenberg and Prins 1981), lesser snow geese (*Chen caerulescens caerulescens*) (Hik and Jefferies 1990) and brown hares (*Lepus europaeus*) (Van der Wal *et al.* 2000) and is the basic reason for the existence of grazing lawns (McNaughton 1984). In our study, the drastically increased biomass growth outside cages in that last revisit could thus be a response to the combined effect of three wet years and the facilitation of regrowth induced by modest grazing, which can begin within days (Holland *et al.* 1992). A third potential explanation is that our dramatically higher regrowth outside of cages may have been a cage or observer effect. Both seem unlikely, because we moved cages every month, reducing the effects of light and wind (Bonham 1989) and trained our field teams with identical methods and frequent calibration tests.

The relationship we found between biomass and precipitation was not surprising. Aboveground biomass production is typically positively related to both precipitation and temperature in grasslands and other ecosystems world-wide (Lauenroth 1979, Le Houe´rou *et al.* 1988, McNaughton *et al.* 1989, Paruelo *et al.,* 1999, Knapp and Smith 2001). The stronger effect usually results from precipitation (Sala *et al.* 1992), perhaps because warming typically lowers soil moisture (Rustad *et al*. 2001, Wan *et al.* 2002). For this reason, precipitation is the principal factor altering productivity of grasslands (Biondini and Manske

1996, Biondini *et al.* 1998, Heitschmidt *et al.* 1999). It is interesting that the effects of precipitation and AC were additive, not multiplicative because intensive grazing and drought in combination can cause severe declines in both the biomass of native plant communities (Loeser *et al.* 2004) and species richness (Fuhlendorf and Smeins 1997). No interaction between AC and precipitation was apparent in our study, perhaps because 2005 – 2007 were all relatively wet years.

In summary, our results suggest that AC changed the intensity of elk use of a grassland with measurable effects on plant growth, particularly within seasons, that could not be explained by differences in precipitation. Previous rangeland research has demonstrated that moderate levels of herbivory during summer are generally sustainable, but long-term heavy grazing intensities are not (Ibanez 2007, Mekuria 2007). This appears to be especially true for rough fescue grasslands (Strong and Leggat 1992) and many of the productive forage species within those grasslands (e.g. Parry oat grass (*Danonia parryi*; Willms *et al.* 1985) or Bluebunch wheatgrass (*Agropyrum spicatum*; McLean and Wikeem 1985).

MANAGEMENT IMPLICATIONS

Our results have supported the continuation of AC as a method for protecting the grassland at the Ranch and are being adopted there for the foreseeable future. Although the horse-based infrastructure at the Ranch makes the technique particularly tractable, there are other areas where it may also be practical. For example, in Yellowstone National Park there are ongoing discussions about problems of overgrazing of the northern range by elk and bison

(Huff and Varley 1999). There, aversive conditioning on horseback might be possible at a large enough spatial scale to supplement other possible management approaches. In horse-based cultures, such as parts of the American Midwest (Raber 2005) and Mongolia (Jagchid 1979), this form of rangeland management might provide an alternative to expensive relocation or fencing projects. In many other jurisdictions, herding wild ungulates by other means, such as all terrain vehicle or helicopter, may be a useful tool for rangeland management that will ultimately support, as we project to be the case at the Ranch, the long-term viability of those same populations.

Table 3-1: Parameter estimates from random effects negative binomial regression estimator (xtnbreg) for a model explaining variation in elk pellet counts at the Ya Ha Tinda Ranch, using year of the censuses (year) as fixed effects and the pellet plot id as a random effect.

	β	SE	Z	P	95% CI	
Winter						
Year	-0.03	0.02	-1.78	0.075	-0.07	0.003
Constant	73.20	39.30	-1.86	0.063	-3.83	150.24
Summer						
Year	-0.10	0.04	-2.20	0.028	-0.18	-0.01
Constant	192.11	87.32	2.20	0.028	20.96	363.25

Table 3-2: Bootstrap results for summer and winter pellet counts conducted in years without (2000 – 2002) and with (2005 – 2007) aversive conditioning at the Ya Ha Tinda Ranch, Alberta.

	Mean	95 % CI
Winter		
2001	3.53	2.57 - 5.07
2002	4.56	3.53 - 6.02
2005	3.76	2.92 - 5.14
2006	3.21	2.33 - 4.55
2007	3.38	2.53 - 4.64
Summer		
2000	0.5	0.25 - 1.15
2001	0.66	0.37 - 1.15 *
2005	0.65	0.38 - 1.05 *
2006	0.27	0.14 - 0.43
2007	0.14	0.04 - 0.32 *

Note: stars indicate non overlapping confidence intervals per season.

Table 3-3: Parameter estimates from random effects maximum likelihood estimator (xtreg) for a model explaining variation in grazing percentage at the Ranch, using year of the project (year), number of revisit (visit) and their interaction (year*visit) as fixed effects and the vegetation plot id as a random effect.

	B	SE	Z	P	95% Conf. Interval	
Year	0.23	0.01	3.76	0.000	0.01	0.35
Visit	-0.02	0.005	-3.37	0.001	-0.03	-0.001
Year * Visit	-0.007	0.002	-2.96	0.003	-0.01	-0.002
Constant	0.07	0.01	4.81	0.000	0.04	0.10

Table 3-4: Parameter estimates from random effects maximum likelihood estimator (xtreg) for a model explaining variation in biomass re-growth between two vegetation plot revisits at the Ranch, using year of the project (year), number of revisit (visit) and their interaction (year*visit) as fixed effects and the vegetation plot id as a random effect.

	β	SE	Z	P	95% Conf. Interval	
Year	2.21	1.05	2.10	0.036	0.15	4.27
Visit	-0.96	0.36	-2.67	0.008	-1.67	-0.26
Year* Visit	-2.50	0.49	-5.13	< 0.001	-3.45	-1.54
cons	2.99	0.78	3.83	0.000	1.46	4.52

Table 3-5: Parameter estimates for a generalized linear mixed effects model on two candidate models. Explanatory variables included ac (0 = no conditioning, 1 = conditioning) and precip (average annual summer precipitation), random effect was the vegetation plot ID.

Model 1 = precip+ac	β	SE	DF	T	P
Intercept	35.01	16.61	79	2.11	0.038
Precipitation	0.24	0.07	79	3.55	0.001
AC	76.22	13.76	76	5.54	<0.001
Model 2 = precip*ac					
Intercept	0.82	32.27	78	0.03	0.979
Precipitation	0.41	0.16	78	2.66	0.009
AC	122.03	39.66	76	3.08	0.003
Interaction precept*ac	-0.21	0.17	78	-1.23	0.22

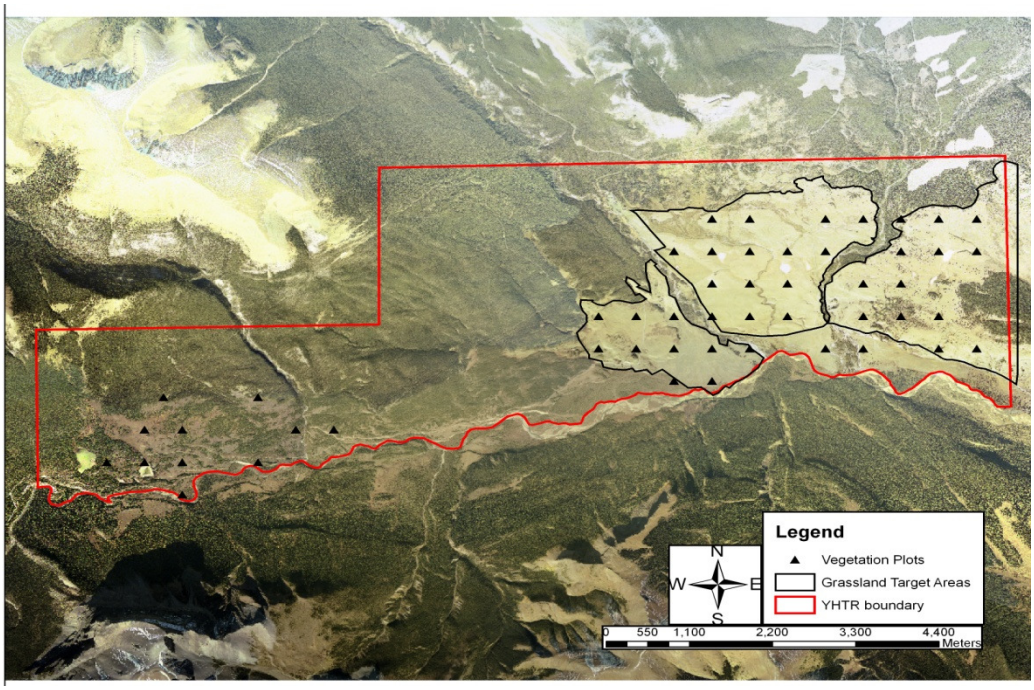

Figure 3-1: Locations for vegetation/pellet plots (black triangles) adapted from a grid developed by McInenly (2003). Revisits were conducted monthly for pellet and vegetation surveys between May and September 2005-2007 and for pellet analyses in May and September 2000 – 2002 by McInenly (2003). The red frame indicates the Ya Ha Tinda boundary and black framed indicates three main grassland areas targeted by Aversive Conditioning at the Ya Ha Tinda Ranch, Alberta.

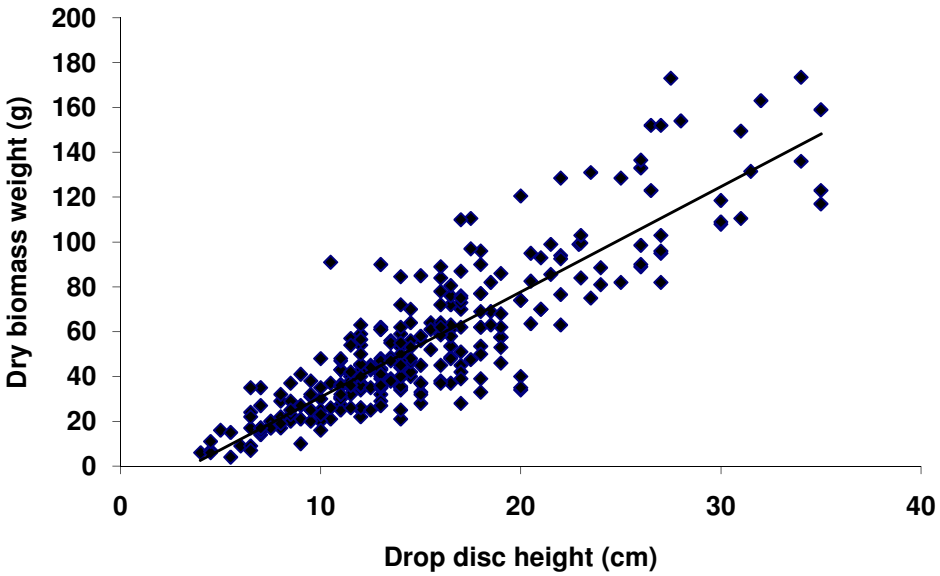

Figure 3-2: Correlation of dry weight of biomass (g/m^2) and drop disc height (cm). Data obtained for drop disc calibration at the Ya Ha Tinda Ranch, Alberta.

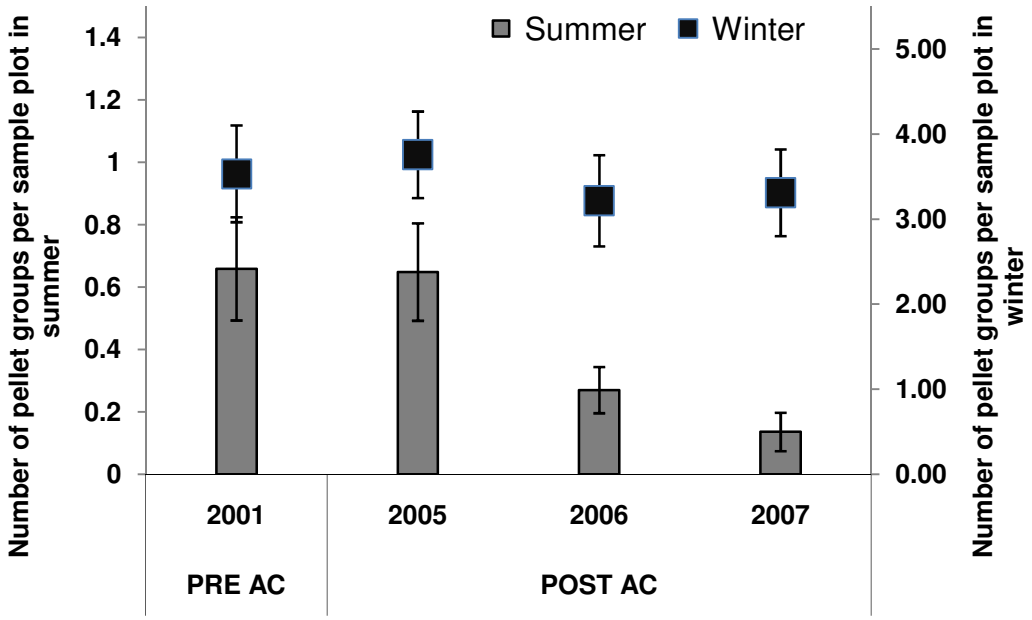

Figure 3-3: Means of winter and summer pellet group counts in years with (Post AC) and without (Pre AC) aversive conditioing counducted at the Ya ha Tinda Ranch , Alberta. Error bars indicate Standard Errors.

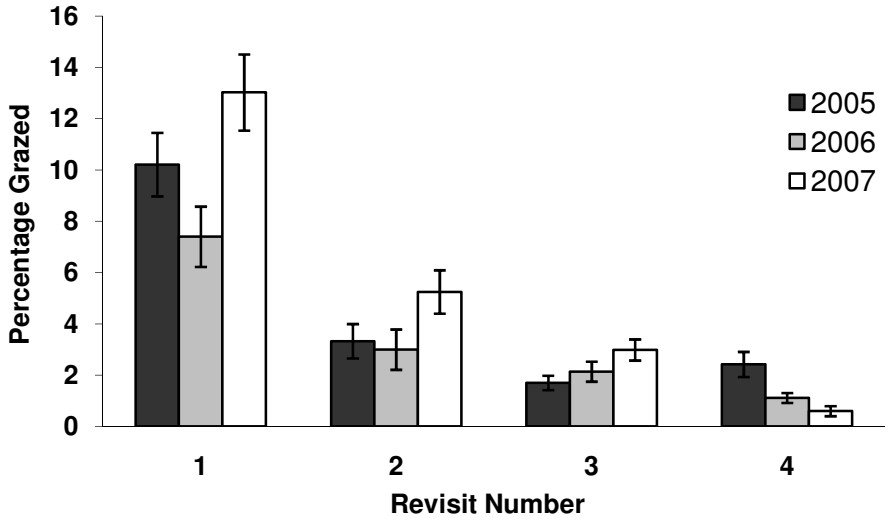

Figure 3-4: Mean percentage of grazed biomass deteced during monthly revisits of vegetation plots at the Ya Ha Tinda Ranch, Alberta. Error bars indicate Standard Errors.

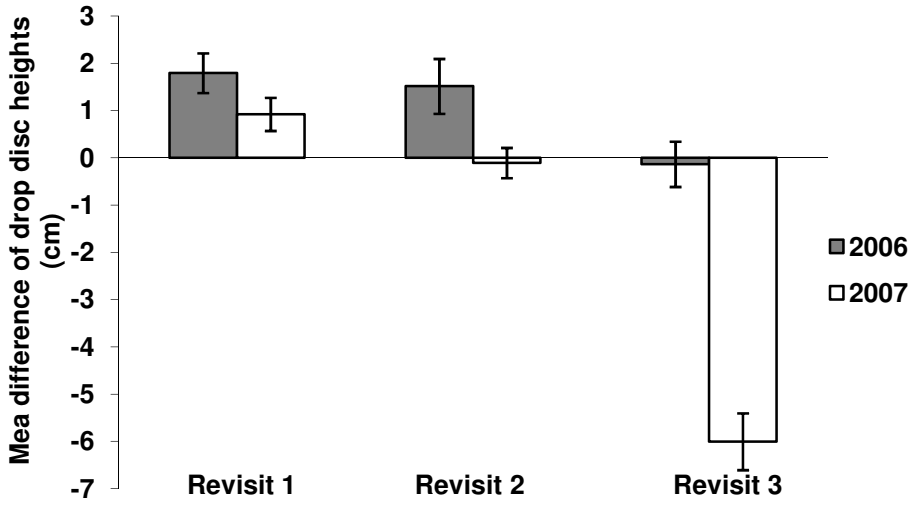

Figure 3-5: Difference of biomass re-growth between caged and uncaged plots per revisit of vegetation plots at the Ya Ha Tinda Ranch, Alberta. Positive values indicate that caged plots had higher regrowth whereas negative values indicate that caged plots had lower regrowth values. Error bars indicate Standard Errors.

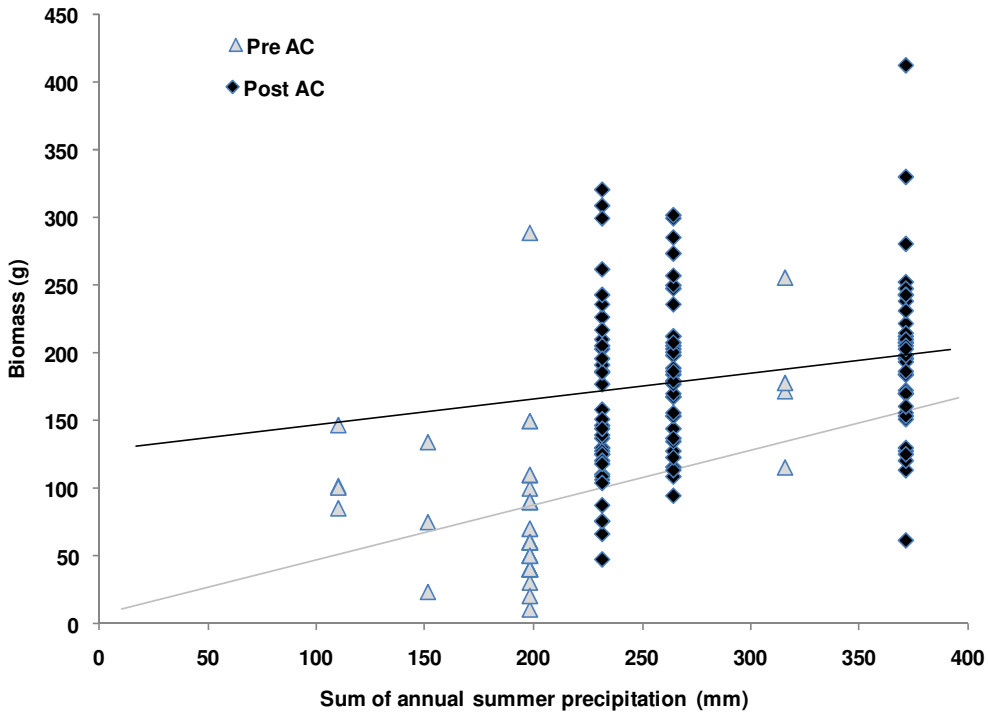

Figure 3-6: Regression of biomass (g/m^2) measured in grasslands and the sum of rain in the summer months (June – August; mm) in years without (Pre AC) and with (Post AC) aversive conditioning.

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CHAPTER FOUR

IMPLICATIONS OF AVERSIVE CONDITIONING ON HORSEBACK FOR MANAGING A SEDENTARY ELK POPULATION.

In this thesis, I assessed the feasibility of Aversive Conditioning (AC) on horseback as a management tool for sedentary elk. Specifically, I determined whether horse-based AC could change elk distribution and decrease summer grazing pressure on the targeted grasslands. My focus on the Ya Ha Tinda Elk population was prompted by previous work, which had shown that elk migratory patterns have changed significantly over the past decades (Hebblewhite *et al.* 2006), which, in turn, increased the proportion of the population that was resident year round. Locally overabundant populations of ungulates can exert enduring effects on the structure and composition of plant communities (Jewell and Holt 1981, Diamond 1992), with cascading effects on other species such as birds (Berger *et al.* 2001), insects (Miyashita *et al.* 2004) and soil arthropods (Wardle *et a.* 2001). Managing these sedentary ungulate populations with the traditional techniques of fencing, relocation and lethal control has revealed substantial limitations (Chapter 1). This thesis examined AC on horseback as an alternative method that is likely to offer affordability for managers and palatability for the public.

In chapter 2, I showed evidence for a change in elk distribution as a response to AC treatments on several temporal and spatial scales. Elk responded

directly to AC treatments on a daily basis, indicating responsiveness to the aversive stimuli of being herded. Elk distribution also changed both within and among seasons as a direct result of AC treatments, when compared to elk distribution without conditioning. AC distances were influenced by a combination of factors, including available numbers of horseback riders, the number of elk in an AC trial and, equivocally, wolf presence. Two main results provided some evidence that elk learned to avoid conditioning treatments. First, elk moved in an NE direction in the hour before conditioning began in the second two years of the project. It appeared that this movement was cued by the daily, early morning reconnaissance trips made by truck. This response appears similar to an avoidance response to snow mobiles observed in reindeer (*Rangifer tarandus*; Tyler 1991), and moose (*Alces alces*; Colescott and Gillingham 1998). Second, elk moved farther following conditioning in the final year of the project, suggesting a cumulative effect of conditioning treatments (Klein 2008). It is this cumulative effect that made it possible to reduce the amount of time elk spent on the grassland in summer, as shown by both the concentric circle and utilization distribution analyses.

In the third chapter of my thesis I examined the response of the targeted Ya Ha Tinda fescue grassland to our AC treatments. Elk use of the grasslands decreased with AC, based on pellet counts, using methods similar to Campbell *et al.* (2004), which decreased grazing to increase biomass production, compared to the years without conditioning. The biomass response to AC treatments was obvious to observers; however the AC project was conducted in three relatively

wet years, directly following a drought in which previous biomass measurements were taken. Precipitation has frequently been shown to be the main influencing factor of biomass growth, even though it is sometimes connected to a time lag of 1 to 7 years (Sherry *et al.* 2008, O'Connor *et al.* 2001). In my study, precipitation could not explain the magnitude of the biomass response which was evident after conditioning even after the effect of precipitation was removed. The responses of elk to the AC treatments documented in this thesis are consistent with the tenets of learning theory. Avoidance conditioning occurs when animals learn not to exhibit behaviours that are associated with a negative stimulus. In this study, I created a negative stimulus in the form of herding on horseback, which caused energy loss for the target elk by forcing them to walk (and sometimes run) for up to several km. Our technique was more effective when there were more rides, which may have reflected the intensity of the stimulus (*sensu* MacKintosh 1974). My work suggests that it is possible to train animals to move away from areas or objects by repeatedly pairing their presence in that area with a negative, energy-demanding stimulus.

An important advantage of the AC approach I have described is its acceptability with the public. Every form of wildlife management is potentially negative for some individuals even if the management intervention improves the health of populations or ecosystems. Despite these gains, the public tends to be highly critical of techniques that appear to harm individuals (Loker *et al.* 1999). Moreover, public opinions on a given approach can vary with attitude, experience, and ecological knowledge (Purdy and Decker 1989, Curtis and Hauber 1997,

Decker and Purdy 1988). Perhaps because gentle herding on horseback is already part of a cultural norm in rural communities (i.e. for cattle; Cote 1998), our AC protocol appeared to be highly accepted by the public in our study area. This was not surprising, given that the culture at the Ranch, which is the site of a long-term horse facility for Parks Canada horse and an equestrian-based campground with up to 3000 horse nights per years (Rick Smith, personal communication). In this and potentially other jurisdictions, AC based on horse-based herding could be a valuable tool for managers because it can promote population and ecosystem health, without appearing to harm individuals.

Although I have shown that AC can be an effective tool for limiting damage to grasslands by sedentary elk, my technique has not addressed the root cause of the problem. Many other management solutions address the consequences, rather than the causes, of an ecological problem (e.g. management of habituated grizzly bears in the Canadian Bow Valley; Mueller *et al.* 2004). In the case of elk, it may be more biologically significant to prevent cumulative human impact in currently remote and rural elk home ranges, than to protect remnant habitats in heavily-impacted suburban areas (Thompson and Henderson 1998). Similarly, I suggest that preventing the formation of stationary populations is a better approach than attempting to manage them after they are established. Animal populations that are subjected to any change which might trigger a loss of migratory behaviour and resulting overabundance in parts of their range should be monitored and, if changes in migratory behaviour are observed, targeted early. Over thirty years ago, Skinner (1974) argued that a behavioural

pattern, once lost, could be restored most easily immediately after loss of that behaviour. That learning principle applies well to the management of migratory ungulates. At Ya Ha Tinda, elk have become more sedentary over several decades and each additional year makes it more difficult to change this behaviour. Nonetheless, Van Dyke and Klein (1996) reported significant shifts in elk ranges over a 10-year period and concluded that tradition and behaviour learned from maternal relationships may not persist indefinitely. This work suggests that persistent AC may eventually be capable of changing elk behaviour. Indeed, our work (Chapter 2), which is similar to work by Kloppers *et al.* (2005) and consistent with learning principles (Domjan 2003), suggests that persistent conditioning of habituated elk will be necessary to effect and sustain changes in their distribution or behaviour.

Despite the potential efficacy of AC, it is likely to be effective only when the destination habitat is suitable. Water is among the most important habitat variables for ungulates particularly in arid areas (Weaver *et al.* 1959) or years (Beale and Scotter 1968, Beale and Smith 1970). It would be counterproductive to move animals into areas with no water, or limited food, or high predation rates. In some cases, it may be possible to manipulate the target habitat to increase its attractiveness, and hence the viability of AC. For example, Brown and Mandery (1962) applied fertilizer to hayfields in Washington to increase habitat quality for elk and thereby reduce damage to adjacent private hayfields. However, when the protected hayfields improved their yields, the elk moved back again. Careful assessment, and potentially manipulation of targeted habitat may be necessary to

make AC effective because the net loss caused by conditioning (e.g. energy) must not be exceeded by the net gain (e.g. food) of returning. In summary, I have shown a measurable effect of AC on the distribution of a treated elk population and on the grassland that supports it. However, these effects were limited to what could be detected within and among three seasons. They were limited in space to the outer confines of the Ya Ha Tinda ecosystem. We did not find any indication of reinstatement of the historic migratory patterns that are still shown by other members of this population. Reinstating true migratory behaviour may be considerably harder. One of the impediments to this change may be the high site fidelity elk display to their calving grounds (Vore and Schmidt 2001). Nonetheless, the adjustment to elk distribution we achieved may be enough to facilitate recovery of the central grassland at this site and my technique appears to have long-term tractability at this site, as evidenced by the ongoing use of this approach. Particularly in other jurisdictions where horses are available (e.g., Greater Yellowstone Ecosystem, Inner Mongolia), this technique may have similar long-term potential as a low-impact tool for managing sedentary ungulate populations.

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APPENDIX I

ELK NIGHT TIME STEPLENGTH

Our daytime measures of elk use of the target grassland (Chapter 2) might have overestimated the reduction in use if elk compensated by foraging more intensively at night. To assess this possibility, we calculated elk steplength (straight line distance between two subsequent GPS locations) during night (defined as the interval between 6 pm and 6 am) for elk influenced by AC treatments during the project years (2005 – 2007). To correct for different sampling intervals between project years, we used locations at 3 hour intervals. We used negative binomial regression for this analysis, with area as a random effect to correct for multiple observations in each area. This analysis showed that night time steplength increased in years with AC compared to years without AC ($\beta = 0.24$; SE = 0.04; $P \leq 0.001$) and this effect was likely driven by the bigger effect size in areas with AC treatment . Night time steplenght decreased in areas without AC treatments compared to areas with AC treatments ($\beta = -0.03$; SE = 0.01; $P = 0.016$) . The interaction between these two factors was significant as well, indicating that the increase in night time step length that occurred in the post-conditioning period occurred only in the areas were AC was applied ($\beta = -0.08$; SE = 0.01; $P \leq 0.001$; Figure A.1.1.).

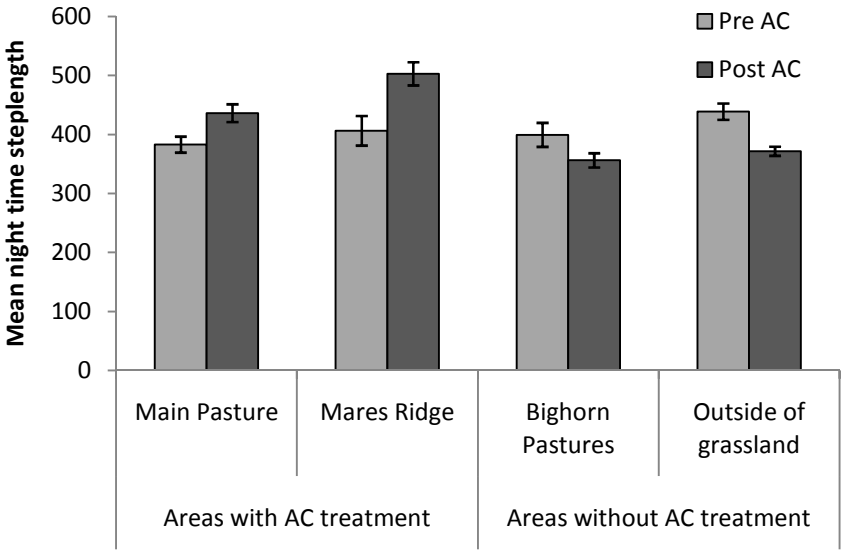

Fig A.1.1.

Mean nighttime (6 pm – 6 am) steplength (straight line distance between two subsequent locations) of elk in 2 treated and 2 untreated Areas of the Ya Ha Tinda Ranch, Alberta in years with AC. Error bars indicate Standard Error.

APPENDIX II

YA HA TINDA ELK HERD POPULATION DATA

Pregnancy Rates

To monitor elk pregnancy rates we sampled all adult (> 2 years) elk during capture by taking blood from the jugular vein and testing for pregnancy hormones (Sasser 1998). Blood analyses were performed by Bio Tracking, Moscow, Idaho, USA. Pregnancy rates of the collared sample declined between 2002 and 2007 (Negative Binomial regression = -0.215; SE = 0.103, P = 0.038), but there was no difference in pregnancy rates between migrant and resident individuals (Negative Binomial regression = -326.3; SE = 1799.4, P = 0.856) or in the rate of decline for the two groups (year by migratory status interaction; Negative Binomial regression = 0.16; SE = 0.90, P = 0.856). Because the AC years were in the latter part of the project, those years were characterized by generally lower pregnancy rates (Figure A.2.1.), but there was no categorical difference between pregnancy rates in the pre- and post-AC years ((Negative Binomial regression = -0.501, SE = 0.351, P = 0.154).

Herd size and calf-cow ratios

Elk herd size was monitored by visually counting elk groups in their winter range (at the Ranch) on the ground. Counts were conducted at times when migrants and residents group together in the winter range (November – March of each year) by observing elk with a spotting scope form distances of ≤ 500 m. During each observation period, the total elk number was determined and all elk

were classified by sex and age (adult cow, yearling cow, adult male, yearling male and calves of the year). The maximum count made each winter was used to determine herd size. These counts reflected a continuously declining population through all years (Regression equation: $-54.71*x + 874.6$; $R^2 = 0.89$). Because of that consistent decline, the years with AC exhibited lower population sizes than years without AC (ANOVA $F_{1,6} = 23.13$, $P = 0.008$). Paradoxically, calf-cow ratios demonstrated an increase over the same period with higher rates in AC years compared to years without AC (ANOVA $F_{1,126} = 7.36$, $P = 0.007$).

Mortality rates

Elk mortalities were detected by daily monitoring GPS and VHF collar signals throughout the AC season. The collars were set to indicate mortality after 6 hours without movement. All detected mortality signals were confirmed on the ground by visiting and investigating these locations. The percentage of detected mortalities (range = 5-7% per year) in the collared sample population was low and stable over pre and post ac years in the summer migratory ranges. However, the mortality rates at the ranch fluctuated more (range = 9 – 14 %) and reached its lowest level in the first year of AC treatments (2005) and its maximum level in 2003 and 2007. There was no difference in mean mortality rates between years with and without AC ($t_{Banff\ NP} = 0.80$; $P = 0.48$; $t_{Ranch} = -0.18$; $P = 0.87$; Figure A.2.3.).

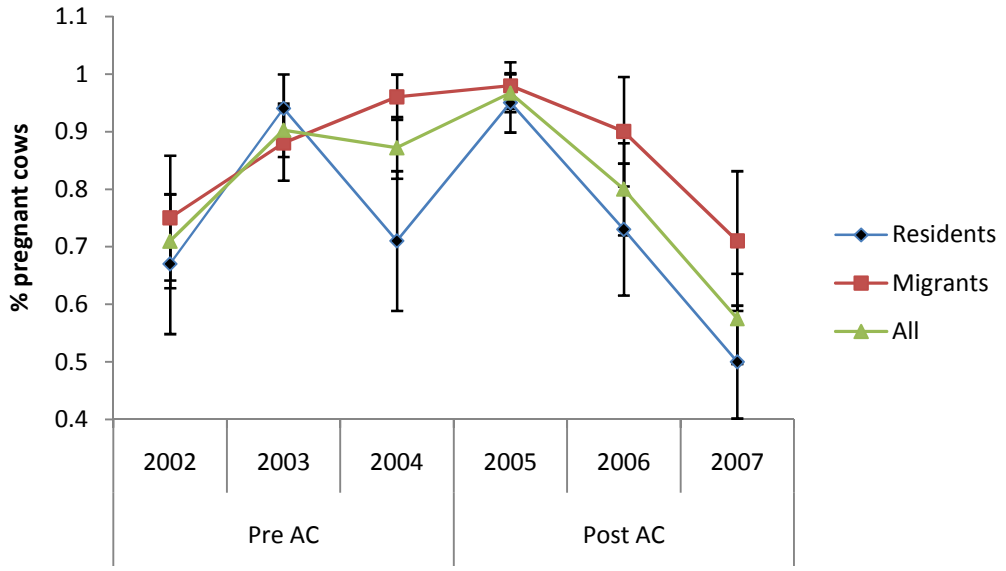

Figure A.2.1

Pregnancy rates determined by blood sampling adult elk cows during capture at the Ya Ha Tinda Ranch, Alberta in years with and without AC treatments. The data are displayed for resident elk (black diamonds), migrant elk (red squares) and all individuals independent of migratory status (green triangles). Error bars indicate Standard Errors.

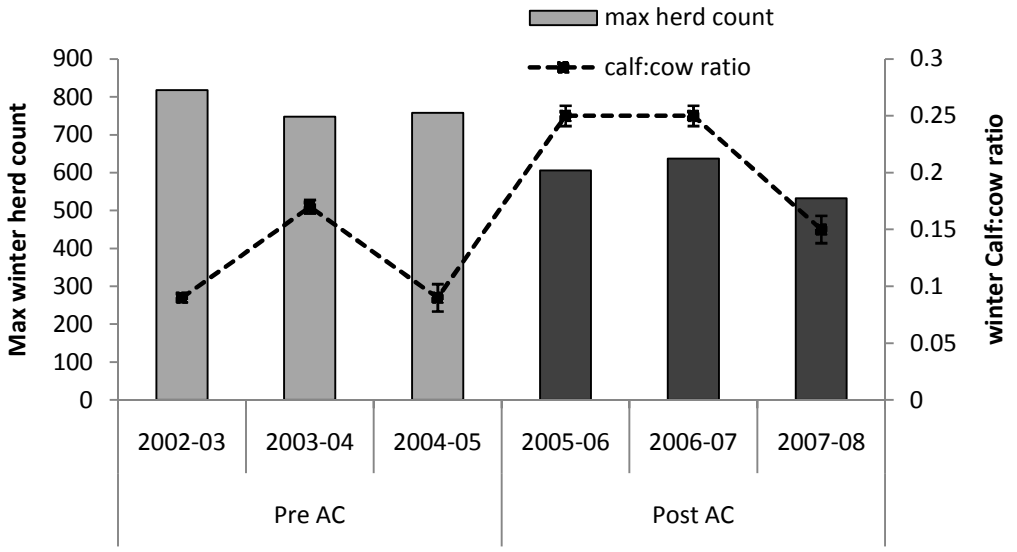

Figure A.2.2

Max winter count elk numbers and winter calf-cow ratios for winters of years with and without AC at the Ya Ha Tinda Ranch, Alberta. Calf-cow ratio error bars indicate Standard errors

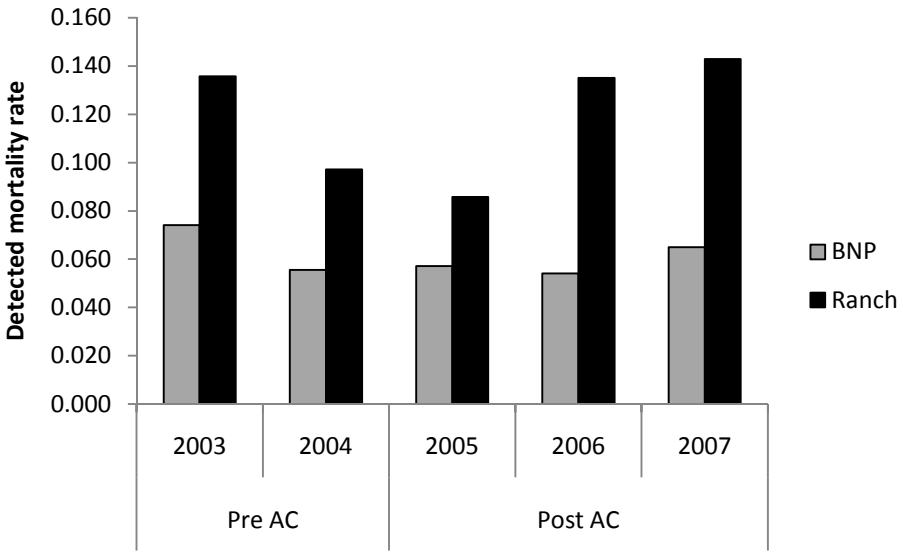

Figure A.2.3.

Elk mortality rates measured as a percentage of the collard sample that died each summer within Banff National Park (not influenced by AC treatments) and at the Ranch (influenced by AC treatments) in years with and without AC treatments.

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APPENDIX III

SUMMER ELK RANGE SURVEYS 27, 28, 29 JULY 2007[3]

INTRODUCTION

In this final year of the Ya Ha Tinda Aversive conditioning project, aerial summer range surveys were conducted in cooperation with Dr. Hebblewhite by repeating surveys that were completed in the summers of 1977, 1978 and 1979 (Morgantini 1982) and 2003 and 2004 (Hebblewhite 2006). This comparison will help to determine the larger-scale changes in elk distribution associated with this project. These surveys were intended to provide us with several benefits. Firstly, they enable us to directly compare and evaluate elk distribution in the summer ranges between the early years when the entire herd migrated (1970's), to the years where the loss of migratory behavior was discovered (2003/04) and, finally, to the year after 3 years of applying aversive conditioning (2007). Secondly, these surveys allow us to monitor elk calf productivity in the summer ranges especially for those elk that are exploring new habitat following aversive conditioning treatments. Continuing these aerial surveys every 2-3 years was one of the long-term management recommendations stated by Hebblewhite (2005) as a tool to monitor long-term population trends.

[3] This Appendix is planned to be published with the following co-authors: Mark Hebblewhite, Luigi Morgantini and Colleen C. St Clair.

METHODS

Aerial survey methods followed closely those described by Morgantini and Hudson (1988) and are described briefly as follows: Elk surveys were flown from 06:00h to 12:00h on days of calm, clear, sunny conditions beginning at Ya Ha Tinda Ranch. All major summer ranges identified by radiotelemetry on 78 radiocollared elk were flown in a Bell Jet Ranger 206 at an average ground speed of ~80 - 100 km/hour. Major low elevation summer ranges were systematically searched at an average height above ground level of 100-200m, including Scotch Camp, Tyrell Flats, Scalp Creek Natural Area, the Ya Ha Tinda Ranch, Panther-Dormer Corners, Windy Meadow, Mid Panther Valley, and Hector Lake Meadows. All higher elevation grasslands and meadows were searched by flying at 100- 200m above treeline to afford views of subalpine and alpine areas. Ridge tops were searched in addition to flying along treeline. Flight paths were recorded with a Garmin GPS III at sampling intervals of 1 location per 00:30 – 2:00 minutes.

Personnel

On July 27th and 28th Holger Spaedtke, Mark Hebblewhite and Jesse Whittington participated in the surveys. On July 29th, only Mark Hebblewhite and Jesse Whittington conducted the surveys. These two observers were very experienced (> 500 hours) in conducting aerial surveys

Data Recording

Once an elk herd was sighted, one observer (MH) scanned for radiocollared animals, while the plane circled the elk herd at ~100m above ground obtaining a total and classified count, where possible, following criteria described by Anderson et al. (1998). Owing to probable errors in classification, no effort to distinguish female yearlings was made. The following ancillary data were recorded for each elk herd sighted:

1) Primary and secondary activity (feeding, resting, moving)
2) Relative canopy cover class following Hebblewhite (2000), namely 0 – 33% cover, class 0, 33-66% cover, class 1, 66-100% cover, class 2. Cover types were later confirmed using GIS cover layers and Satellite Photos.
3) Count confidence was recorded – i.e. if observers were unsure whether all elk were seen or observed, especially calves, then a class 2 count confidence was recorded whereas 'all elk seen' generated a count confidence of 1.
4) Summer range area, divided into 3 strata: 1) the areas around the Ya Ha Tinda Ranch including the Ranch, Dogrib ridges, and ridges North and NW of the Ranch, called the Ranch strata, 2) the Front Ranges including Divide, Peters, Condor, Forbidden, Red Deer, Panther, Snow Creek areas, and 3) the Main Ranges, including Pipestone, Molar, and Upper Bow River areas.

All other wildlife observations were recorded by identifying species and conducting a total count (ignoring sex distribution). No locations (or only rough

estimates of the location) were recorded, giving a total estimate of species and their numbers in the survey area.

Preliminary Sightability Estimates

In an attempt to understand how sightability affects summer elk counts (Unsworth 1994; Samuel et al. 1987), we collected data on whether we missed radiocollared elk in the survey area following methods in Hebblewhite (2000). One observer (HS) had a general knowledge of where to expect collared elk to be during the surveys, but this knowledge was not disclosed to other observers. If, after surveying an area where radiocollared elk were previously located no elk were found, MH used the aerial telemetry equipment to locate the 'missed' elk. While not as rigorous as methods described by Unsworth (1994) and Samuel et al. (1987), this approach may allow tests of a summer elk sightability model developed elsewhere (Anderson et al. 1998) for BNP.

RESULTS

A total of 15.3 hours and 1,294 km (including circling over found groups for identification) were surveyed on July 27th, 28th and 29th during excellent sighting conditions. A total of 238 elk (in 39 different groups) were counted on summer ranges in the survey area, composed of 187 female elk, 27 young of the year and 24 bull elk. Between 1 and 3 collared elk were present in 23 (59%) of the 39 elk groups sighted.

Elk sex class distribution

We used only 'confidence = 1' observations (98% of all sightings) to calculate calf:cow ratios, both by separation into the three ecological zones (i.e., Ranch, Front Ranges, and Main Ranges), and for the entire study area. Calf:cow ratios ranged from a low of 7% in the areas surrounding the Ranch to 18% in Front Ranges to a high of 44% in the Main Ranges (Table 1).

Preliminary Sightability Application

Clear differences in sightability existed between the three ecological strata areas of the survey. In the Ranch area, 95% of all radiocollared elk were sighted on aerial surveys, compared to 33% of all radiocollared elk in the Front Ranges, and 21% of all elk in the Main Ranges. Sightability percentages showed a similar pattern during Hebblewhite's (2005) surveys (Ranch = 93%; Front Ranges = 76% and Main Ranges = 31%; Table 2). We used the sightability percentages to adjust total elk numbers to achieve a rough estimate of the total elk population (Table A.3.3.).

Comparison to 2003 survey

Since 2003, elk numbers have decreased by 27%. This trend was most pronounced in the Ranch (63%) and in the Main Ranges (53%). The Front Ranges showed the opposite trend with a population increase of 93%. Using actual counts (not corrected for sightability) the same trends persist at the Ranch

and the Main Ranges, but a slight decrease (17%) is evident in the Front ranges. (Figure A.3.2. and Table A.3.4.)

DISCUSSION

Aerial surveys closely followed 1970's and 2000's surveys, and counted 239 elk across the survey area, representing 38% of the estimated winter elk population (637 elk) counted on January 27, 2007 by two independent observers at Ya Ha Tinda. Furthermore, at least 1 collared elk was found in over half of all observed elk groups. This high proportion of sampled groups with collared elk suggests that our survey design adequately sampled the distribution of elk in the survey area. However, the relatively low proportion of the winter population that was detected by summer aerial sampling suggests that this technique is better suited to simply identify summer elk ranges than it is to estimate population size.

Calf:cow ratios differed dramatically from previous aerial surveys as well as from ground counts in the two previous years (Table A.1.1.). Low sightability for adult elk suggests that detectability for calves was even lower, given their smaller body size. Winter calf:cow estimates confirmed the trend of lower calf:cow ratios in 2007/08 than in previous years (Appendix II).

The sightability estimates based on failure to detect collared animals, have changed slightly at the Ranch (93% in 2003; 95% in 2007) and in the Main Ranges (31% in 2003; 21% in 2007) but they have dropped dramatically in the Front Ranges (76% in 2003; 33% in 2007). The low sightability percentage in the Front Ranges combined with a larger number of smaller elk groups observed there

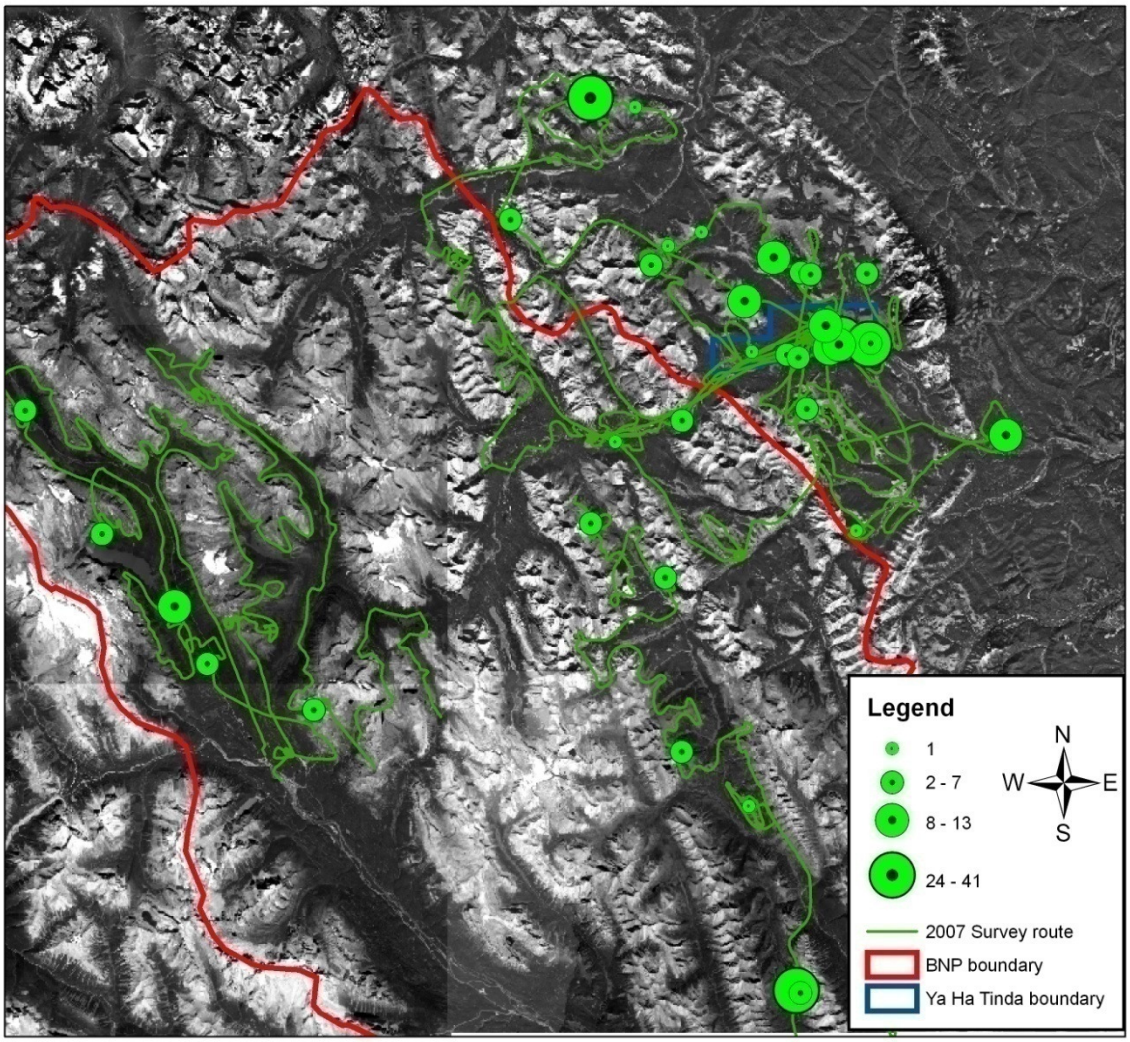
suggests that elk may be distributed in smaller subgroups and are thus easier to miss than in previous years. Sightability could also have been influenced by changes in vegetation biomass (especially shrubland and tree stand density) or a difference in elk behavior given the slightly later survey date (July 27 – 29 2007 as opposed to July 15-16 2003). Given this massive change in sightability we chose to present count data from 2007 using the more reliable sightability correction developed in 2003. (Table A.3.2.)

The general trend of a declining elk population indicated by Hebblewhite's survey (Hebblewhite and Morgantini 2003) from 2003 has continued. The total population detected during this survey was 27%. The largest population decline appears to have occurred on the Ranch grasslands where there was a 62% decline from 2003 estimates. This decline might be caused by the successful application of aversive conditioning treatments in the previous three years. Because sightability was very high in both years at the Ranch, population trends there are likely accurate. Moreover, elk observed at the Ranch seemed to behave differently compared to the years of Hebblewhite's project. In particular, fewer elk were found in the grasslands, and more elk were observed in areas just adjacent to the Ranch in 2007 relative to 2005.

The Front Ranges showed the opposite trend to what occurred at the Ranch by exhibiting a population increase compared to 2003. However, this apparent increase (93%) changed to a moderate decline (17%) when we corrected for sightability. The large range in values for this area limits the confidence with which we can interpret changes in either direction. If the apparent increase in the

summer population is real, it could result from the movement of conditioned elk away from ranch grasslands into the nearby Front Ranges. Analyses of the distribution of collared elk (Chapter 2) do not support this hypothesis. Our counts in the Main Ranges indicate a decline from ~250 elk (adjusted for sightability), to ~120. This is a large difference from previous surveys and surprising because Hebblewhite (2005) had found the population in the Main Ranges to be relatively stable compared to Morgantini's surveys in the 1980s. In sum we have shown that elk numbers have continued to decline, with no, or only slight, changes in distribution when compared to previous surveys. With decreasing elk numbers sightability correction calculations become increasingly important, but more difficult and potentially inaccurate.

Figure 1: Summary of elk summer range surveys conducted in July 2007. Green dots represent elk groups seen and green line represents the survey route flown.



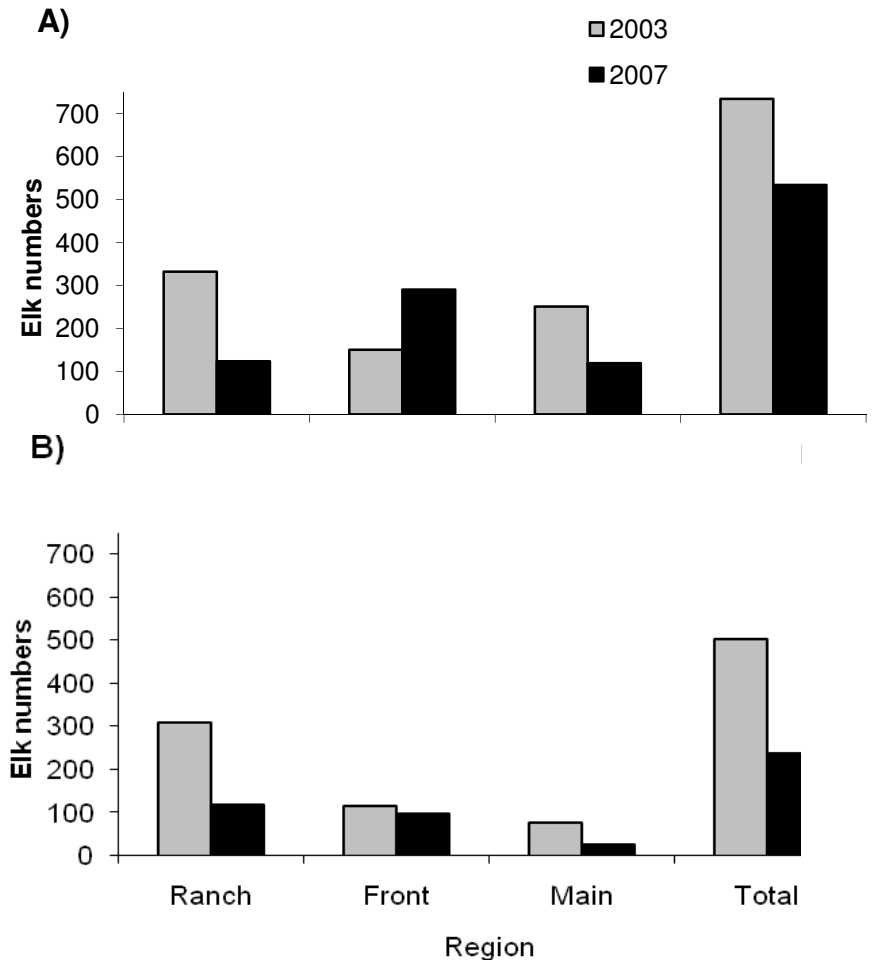


Figure 2. Sightability corrected (A) and actual count (B) data for elk observed during 2003 and 2007 surveys, organized by region.

Table A.3.1.: Cow:calf ratios and sex class distributions from reliable (confidence code 1) sightings where all cows and calves were counted during aerial summer range surveys in July 2003 and July 2007. Numbers in brackets indicate standard errors.

Region	Age class	Count 2003	Count 2007
Ranch	Female	206	91
	Calf	91	6
	Male	3	14
	Yearling male	N/A	4
	Total	300	115
	calf:cow %	0.44 (0.13)	0.07 (0.06)
Main Ranges	Female	77	16
	Calf	15	7
	Male	6	2
	Yearling male	N/A	0
	Total	98	21
	calf:cow %	0.19 (0.10)	0.44 (0.22)
Front Ranges	Female	95	78
	Calf	14	14
	Male	6	3
	Yearling male	N/A	1
	Total	115	96
	calf:cow %	0.14 (0.07)	0.18 (0.10)

Total	Female	378	185
	Calf	120	27
	Male	15	19
	Yearling male	N/A	5
	Total	513	232
	calf:cow %	0.32 (0.06)	0.15 (0.05)

Table A 3.2.: Sightability estimate based on radiocollared elk that were known to be alive but not observed during summer range surveys in July 2007 and sightability estimates, calculated using identical methods, from surveys in 2003 (Hebblewhite et al. 2006)

Region	Collared elk seen 2007	Collared elk missed 2007	2007 sightability %	2003 sightability %
Ranch	19	1	95	93
Main ranges	4	3	21	31
Front ranges	6	3	33	76

Table A3.3.: Elk numbers observed during 2007 summer range surveys and adjusted elk numbers using both 2003 and 2007 sigthability estimates for comparison.

Region	Elk observed 2007	Adjusted using 2003 sightability	Adjusted using 2007 sightability
Ranch	118	127	124
Front Ranges	96	126	291
Main ranges	25	81	119
Total	239	334	534

Table A3.4.: Sightability corrected and actual count data and population decrease percentages between 2003 and 2007 surveys for elk seen during 2003 and 2007 surveys.

Actual counts				Sightability corrected counts			
	2003	2007	Population decrease %		2003	2007	Population decrease %
RANCH	309	118	61.8	RANCH	332	124.2	62.6
FRONT	115	96	16.5	FRONT	151	290.9	-92.7
MAIN	78	25	67.9	MAIN	251	119.0	52.6
TOTAL	502	239	52.4	TOTAL	734	534.2	27.2

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