University of Alberta

Aversive Conditioning for Management of Habituated Elk (*Cervus elaphus*) in Banff National Park, Canada.

by

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A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

Spring, 2005

0-494-08101-5

ABSTRACT

Wildlife habituation near urban centres can disrupt natural ecological processes and threaten public safety. Research in Banff National Park in 2001-02 compared efficacy of human (audio and visual stimuli), dog (border collie herding) and control (non-) aversive conditioning treatments on 24 moderately-habituated elk (*Cervus elaphus*). Flight response distance increased following both human and dog conditioning treatments. Vigilance decreased for all treatment groups, while elk distance from town increased following only the human treatment. Research in 2002-03 assessed effects of conditioning frequency on behaviour of elk with different initial habituation levels. Flight response distance increased with conditioning frequency, particularly for more habituated elk. Neither conditioning frequency nor habituation level affected elk distance from town. Treatment effects did not significantly decrease within 8 weeks of application. This research demonstrates it is possible to temporarily modify behaviour of moderately-habituated elk using aversive conditioning, providing a solution for managing hyper-abundant and habituated urban wildlife.

ACKNOWLEDGEMENTS

Generous funding, equipment, logistical support and housing for this research were provided by Parks Canada (Banff National Park). A grant to Dr. Colleen St. Clair from the Canadian Foundation for Innovation gave us the use of our beloved 'Tundra' truck, in addition to other essential field equipment. Dr. Evelyn Merrill also generously loaned telemetry gear.

I would like to thank my supervisor Dr. Colleen St. Clair, without whose faith in me, encouragement, advice and rigorous scientific guidance this degree would never have happened. My committee members, Dr. Evelyn Merrill and Dr. Suzanne Bayley (from the University of Alberta), and Tom Hurd and Dr. Cliff White (from Banff National Park), all provided indispensable project advice and encouragement throughout the planning, fieldwork, analysis and writing stages.

Fieldwork was made possible by the dedication, humour, patience and wonderful elk-chasing efforts of Julie Mills (assistant first year, field supervisor the second year), Paula Ashby, Ron LeBlanc, Robi Gareau, Christine Aikens, John Zehnder (with herding dogs Blue and Duke), Mike Bartlett, Steve Anderson, Diane Volkers and Arian Spiteri. Other members of the Banff National Park Warden Office also provided generous project support, in particular: Glen Peers, Tom Davidson, Dr. Todd Shury, Ian Syme, Dennis Herman, Doug Eastcott, Ian Pengelly, Brian Low, Heather Dempsey, Cathy Hourigan and all of the dispatch team.

I am very grateful to people from other Banff National Park wildlife research projects that shared essential data with me: Cliff Nietvelt, Katy Holm and John McKenzie from the Elk Monitoring Project (elk telemetry data); Dr. Anthony Clevenger, Kari Gunson and Bryan Chruscz from the TransCanada Highway Project (predator data from crossing structures); Haley Breniser and Eric Knight from the Corridor Study (snow transect data); and Jennifer Wasylyk, Andrea Kortello and Simon Ham (Wolf and Cougar Projects) for elk sightings and kill reports. Your generosity aided my study design, elk monitoring efficiency and data analysis. Efficient data management and GIS assistance were provided by Darrel Zell, Jeff Truscott, Tao Gui, Alanah Woodland, Sarah Spence, Dale Bartrom and Charlene Nielsen.

My St. Clair lab partners and other fellow Terrestrial Ecology group members at the University of Alberta shared excellent ideas, stressful long nights, insightful conversations, happy dinners, hikes and road trips with me: Heather Hinam, Neil Darlow, Cam Gillies, Dr. Jan Murie, Cathy Shier, Paul Frame, Lana Ciarniello, Judith Toms, Boyan Tracz, Jalene LaMontagne, Warren Bernhardt, Evan Richardson, John Brzustowski, Dr. Scott Nielsen, Mark Hebblewhite, Jacqui Frair, Jim Allen, Dr. Susan Hannon and Dr. Mark Boyce.

My family and friends were an indispensable part of my productivity, sanity and happiness these last few years, offering support and encouragement, shoulders to lean on, quiet times and diversions like wilderness excursions and music jam sessions. I thank my parents Dr. Jacobus (Kobie) and Wilhelmina (Miensie) Kloppers; my brother Martin

Kloppers; my bouncy dog Kayli; and friends (those not yet listed elsewhere): Eloise Pulos and Dr. Jay Gedir; Annie and Craig Paterson; Rob and Chrys Kaye; Ryan, Kirsten and baby Rowan Zapisocki; Christine and Jonathon Hornung; Theresa and Kevin Hannah; Mark Wendlandt, Amy Leach, Darcey Shyry, Jeff and Nathalie Sleno; Wayne and Tori Johnston; Dr. Shelley Pruss and Dr. Gary Scrimgeour; Joanna Myers, Richard Richter, Tom Yonge, Allison Twiss, Karina Houle, Tansy O'Connor- Parsons, Dani Thompson, Rebecca Rothgeb, Kathy Burden, Trinity Brooks, Graham Cline, and Max Darrah. I especially thank Jonathon Ensor for his extraordinary patience, understanding, support, and for sharing many laughs and adventures with me. I could not have done it without you all! Thank you.

TABLE OF CONTENTS

LIST OF FIGURES

CHAPTER ONE – INTRODUCTION

Wildlife-human conflict management is a relatively new, yet rapidly expanding, field of ecological research with application for diverse species, conservation issues and jurisdictions (Fall and Jackson 2002). Issues such as crop damage by herbivores (i.e. Belant et al. 1996, Bender 2003, Ward et al. 2004), wildlife-vehicle collisions (Madsen et al. 2002, Rea 2003) and livestock depredation (Andelt 1992, Smith et al. 2000) are prevalent in many countries, while other issues have evolved in response to unique circumstances within particular regions, requiring specialized solutions.

An emerging conflict in many urban areas and parks in North America is the habituation of wildlife to humans and human-use areas (Bounds and Shaw 1994, Thompson and Henderson 1998). Habituation is, by definition, a waning of an animal's response to repeated exposure to stimuli that carry no discernible biological consequence (see Jope 1985, Taylor and Knight 2003). Some degree of wildlife habituation to humans is likely necessary to ensure future wildlife survival as human populations and development expand (Whittaker and Knight 1998). The degree of habituation in many North American jurisdictions, however, has rapidly moved beyond acceptable ecological and public safety limits, particularly where habituation of large concentrations of ungulates such as deer (*Odocoileus* spp.) and elk (*Cervus elaphus*) has occurred (e.g., Warren 1991, Conover et al. 1995, Baker and Fritsch 1997, Coffey and Johnston 1997).

By contrast, habituation of similar ungulate species (red deer (*Cervus spp.*) and roe deer (*Capreolus capreolus*)) to humans within urban and protected areas has typically not occurred in Europe, a difference that demonstrates how geographic and cultural elements may interact to promote the habituation of wildlife. Thompson and Henderson (1998) outlined four major accelerants of elk habituation to humans in North America: high elk population density, sanctuary from hunting, human presence on elk winter range, and consistent and predictable human activities. The European and North American situations differ on some of those elements, but also vary regionally: average North American ungulate densities are high (e.g., Underwood and Porter 1997), while European ungulate densities are variable but high in some areas (e.g., Staines and Welch 1989, Focardi et al. 2002, Kuiters and Slim 2002); hunting in Europe is often permitted within core ungulate habitat including protected areas (e.g., Morellet and Guibert 1999) while the majority of North American protected and urban areas prohibit hunting (Messmer et al. 1997, Porter and Underwood 1999). European ungulate harvest rates in many areas have increased within the last 40 years (e.g., Hromas 1990, Morellet and Guibert 1999), while hunter participation and effort substantially declined over a similar period in North America (e.g., Enck et al. 2000, Riley et al. 2003). Significant human presence in the form of urban centres on critical elk winter range exists in the narrow montane valleys of Rocky Mountain parks of western North America (Thompson and Henderson 1998), whereas a substantial overlap of humans and ungulates on important winter range is less common in the European context (e.g., Mysterud 1999, Lamberti et al. 2001). Human densities are far higher in Europe than North America (Linnell et al. 2001), but it is not known whether there is a difference in predictable and consistent human activity levels in ungulate ranges between the regions.

An additional important factor, which was not described by Thompson and Henderson (1998) that may contribute to ungulate habituation to humans in North America is a strong predation risk gradient between human-use areas and surrounding areas (e.g., McKenzie 2001). Predators are less widespread in Europe (e.g., Okarma 1995) and generally occur at lower densities than in North America, although they are increasing in several areas (e.g., Breitenmoser 1998, Swenson et al. 1998, Linnell et al. 2001) where similar situations may exist or develop in the future.

Perhaps due to these regional differences in ungulate-human interactions, the scientific community has not recognized the magnitude of the wildlife habituation problem (Thompson and Henderson 1998). Consequently, very little published research has experimentally evaluated methods to prevent its occurrence. Many areas in North America are currently managing the issue using traditional 'problem-wildlife' tools: translocation (e.g., Beringer et al. 2002) and destruction of the offending animals (e.g., Rondeau and Conrad 2003). Within protected areas such as National Parks, however, legislated mandates require maintenance of ecological integrity, and policies discourage use of these tools except to individual animals under outstanding circumstances (National Parks Service 1991, Government of Canada 2000). Furthermore, the Parks Canada mandate guarantees visitors' 'benefit, education, and enjoyment' of park resources, and wildlife viewing is one of the most popular activities (Parks Canada Agency 2003).

These dual mandates of ecological integrity and visitor enjoyment currently challenge protected area managers to find alternate methods of redistributing and managing 'wild' ungulate populations such that they do not experience conflict in the human-use areas, yet are not entirely inaccessible to carnivores within the ecosystem, or to park visitors.

In response to this management paradox, I conducted a research project in Banff National Park, Canada, during the winters of 2001-02 and 2002-03 to test and refine aversive conditioning techniques for modifying the behaviour of human-habituated elk concentrated within the town site of Banff (Fig. 1-1). Aversive conditioning, a form of negative operant conditioning (see Domjan 2003), had previously been applied to livestock-depredating and 'problem' carnivores with mixed results (e.g., Bounds and Shaw 1994, Smith et al. 2000); its application to ungulates in published literature appeared to be uncommon and with mixed results (e.g., Nolte 1999, Gallagher and Prince 2003, Nolte et al. 2003). The overall goals of my research were to determine if aversive conditioning can modify habituated elk behaviour, and distinguish the more effective of two techniques (Chapter 2); and ascertain how the frequency of aversive conditioning affects and maintains changes to habituated elk behaviour (Chapter 3). The results of this research reveal important elements of elk behavioural response to operant conditioning, with application to numerous jurisdictions in North America that are seeking to manage and prevent the continued habituation of hyper-abundant ungulates.

Figure 1-1. Satellite photograph of the townsite of Banff (within Banff National Park), with the aversive conditioning zone delineated (Photo scale: 2.5 cm = 1 km). Inset shows the location of Banff, Alberta, Canada.

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CHAPTER TWO – PREDATOR-RESEMBLING AVERSIVE CONDITIONING TECHNIQUES FOR MANAGING HABITUATED ELK

Wildlife habituation poses important challenges for National Parks and other jurisdictions where humans and wildlife frequently interact. In many parts of North America, habituation occurs where wildlife protection policies are combined with a significant human presence and associated urban facilities. Habituation can be defined as a decrease in an animal's innate response to repeated exposure to stimuli that are biologically irrelevant (e.g., Jope 1985, Thompson and Henderson 1998, Whittaker and Knight 1998). Animals that are habituated to humans do not avoid contact with humans or areas where contact with them is likely, unlike the behaviour of wilder conspecifics. When habituation affects large animals like ungulates, it can cause a host of ecological and public safety problems. Ecologically, areas with human-habituated wildlife can create a 'refuge effect', where concentrations of ungulates such as elk (*Cervus elaphus*) or other wildlife are attracted to artificially fertilized lawns and gardens as food supplements (Lubow et al. 2002, Rubin et al. 2002), and where they also receive artificial refuge from predation (Isbell and Young 1993, Riley et al. 1998). This can lead to breakdowns in natural predator-prey relationships and hyper-abundant populations (e.g., Ripple and Beschta 2004), which can cause subsequent declines in diversity of associated wildlife and vegetation species (e.g., Caughley 1981, Warren 1991, Augustine and DeCalesta 2003, Soulé et al. 2003). In addition to these ecological effects, habituated animals can also compromise public safety through aggression or attacks directed at humans (e.g., Herrero 1985, Bounds and Shaw 1994, McNay 2002*b*, Yellowstone Center for Resources 2002, Beckman and Savage 2003), wildlife-vehicle collisions (Conover et al. 1995, Etter et al. 2002, Nielsen et al. 2003), transmission of diseases (Fanning and Edwards 1991, Steere 1994, Magnarelli et al. 1995, Salman 2003), and attraction of dangerous predators to human-use areas (Halfpenny et al. 1991, Beier 1996, McCullough et al. 1997).

In Banff National Park, Canada, concentrations of habituated elk in the town site of Banff cause both ecological and public safety problems. The refuge effect is evident as elk survival and nutritional intake are substantially higher within the town than in the surrounding valley (McKenzie 2001) where wolf use is less constrained by human activity (Duke et al. 2001). Consequently, high levels of herbivory by localized and hyper-abundant elk prevent regeneration of aspen and willow (White et al. 1998), with cascading effects on other herbivores in the ecosystem including moose (Hurd 1999) and beaver (Nietvelt 2001). A more pressing problem stems from wildlife-human conflict. Between 1993 and 2001 there was an annual average of 66 aggressive elk-human encounters, including an average of seven incidents per year in which elk physically injured humans (G. Peers, *unpublished report*). Since 2000, these habituated elk have also attracted predatory wolves, bears and cougars to the town site, habituating carnivores to hunting within human-use areas, and further threatening public safety (McNay 2002*a*, G. Peers, *personal communication*).

Despite the urgent need to prevent ungulate habituation to humans and human-use areas in Banff and other urban and protected areas, relatively little published research has addressed methods by which this can be accomplished (Thompson and Henderson 1998). Reactionary methods typically used to manage 'problem-wildlife' include translocations (e.g., Baker and Fritsch 1997, Beringer et al. 2002) or destruction (e.g., DeNicola et al. 1997, Schwartz et al. 1997, Rondeau and Conrad 2003), but these address consequences, not causes of habituation. Moreover, such methods can have negative ecological and social consequences (e.g., Craven et al. 1998, Lee and Millar 2003, Beringer et al. 2002, Rondeau and Conrad 2003) that may be ethically unacceptable in a park or urban setting. The field of ungulate damage management (e.g., DeCalesta and Witmer 1994, Fagerstone and Clay 1997, DeNicola et al. 2001, Fall and Jackson 2002) has experimented with a variety of more proactive methods to reduce vegetation herbivory using area repellents or fencing (e.g., Hygnstrom and Craven 1988, Milunas et al. 1994, Baker et al. 1999), reduce urban deer populations with contraceptives (e.g., Muller et al. 1997, Rutberg et al. 2004), and prevent collisions with vehicles using reflectors and lasers (e.g., Waring et al. 1991, Ujvari et al. 1998, VerCauteren et al. 2003). Even so, these damage management methods do not address the behavioural mechanisms that cause – or could prevent – ungulate habituation to humans in the first place.

In protected areas such as Banff, habituating events may occur whenever residents or tourists (e.g., golfers, photographers, nature enthusiasts) approach elk at close range without invoking a negative consequence (*sensu* Domjan 2003). Over time, the elk not only cease to view humans as potential predators, but may even begin to perceive humans as potential competition for particular habitat, and show aggression towards humans if approached or provoked (Thompson and Henderson 1998). Dominance hierarchies also strongly influence inter-individual behaviour among herd animals, as higher rank can affect physiology (Buchanan 2000) and access to space and food (Geist 1982, Wirtu et al.

2004). Therefore, elk aggression directed at humans might also be an attempt at establishing or expressing such dominance.

Here I describe a research project predicated on the assumption that it is possible to reverse and prevent the habituation process with aversive conditioning. Aversive conditioning is a form of operant conditioning (for background, see Brush 1971, Reynolds 1975, Davey 1981, Hadley 1981). It can employ avoidance conditioning, in which the animal must perform a specific act to avoid or escape the aversive stimulus, or punishment, in which animals that exhibit a particular behaviour subsequently experience an aversive stimulus (Domjan 2003). Aversive conditioning is routinely used to teach predators avoidance of commercially valuable livestock (e.g., Andelt 1992, Smith et al. 2000) and it shows much potential in carnivore-human conflict situations (e.g., Ternent and Garshelis 1999). However, it is less commonly used to condition prey (but see Aguilera et al. 1991, Gallagher and Prince 2003, Nolte et al. 2003). Because elk, like all animals, are adapted to conserve energy, access essential resources, and avoid injury (Geist 1982), I hypothesized that habituated elk that experience negative predator-resembling stimuli (e.g. anxiety, stress, pain, energy loss and reduced foraging time) unpredictably when they approach humans or human-use areas should learn to flee from humans and eventually avoid both humans and the associated human-use areas altogether (see also Thompson and Henderson 1998, Whittaker and Knight 1998, Frid and Dill 2002, Nolte et al. 2003). To capitalize on likely combinations of genetic disposition, learned behaviour, and cultural transmission (*sensu* Whittaker and Knight 1998, Griffin and Evans 2003), I selected stimuli known to trigger natural predator-avoidance responses (see also Geist 1982, Hansen et al. 2001, Blanchard et al. 2003) in non-habituated 'wild' ungulates: a fear of humans (Schultz and Bailey 1978, MacArthur et al. 1982, Gander and Ingold 1997, Kilgo et al. 1998, Conner et al. 2001) and of human-dog combinations (Martinetto and Cugnasse 2001, Miller et al. 2001). I then drew from principles in stock herding (Smith 1998) and learning psychology (Domjan 2003) to employ these stimuli in a chase sequence that I expected would resemble predatory behaviour by humans, human-dog combinations, or wolves (*Canis lupus*). My objectives were to (a) test the hypothesis that habituated elk behaviour can be reduced with aversive conditioning and (b) compare the efficacy of two treatment types; human- and dog-based aversive conditioning. To assess the relative effectiveness of these two techniques, I measured three response variables for the elk: flight response distance from an approaching human (e.g., Altmann 1958, Stuwe 1986, Recarte et al. 1998, Taylor and Knight 2003); the proportion of time spent in vigilance postures as a measure of predator-wariness (e.g., Lima 1987, Dehn 1990, Frid 1997, Hunter and Skinner 1998, Kie 1999; Welp et al. 2004); and proximity to the town boundary based on daily radio-telemetry locations.

METHODS

Study area and schedule

Fieldwork was conducted in the town site and surrounding area of Banff, AB (51°15'N, 116°30'W), within Banff National Park, Canada, during the winter of 2001-2002. Banff town site is situated in the Bow Valley within the central Canadian Rockies at an elevation of 1,383 m. In the lower Bow Valley bottomlands, modest snowfall combined with occasional warm periods creates important winter habitat for ungulates (Holland and Coen 1983, Holroyd and Van Tighem 1983, Woods 1991). The town of Banff has a permanent human population of 7,135, but with park visitation approaching five million people per year (Banff-Lake Louise Tourism Bureau, *personal communication*). My 466.5 ha study area was composed of the urban land-use area of Banff in addition to an adjacent golf course, montane wetlands, forests and shrublands within 2 km of the town boundary. The total elk population in the town site area numbered 277 in the spring survey of 2001, showing a continuing decline in response to management actions and increased predation by wolves since a high of 533 elk in 1994 (Banff National Park, *unpublished data*). During this 2001-02 field season up to 18 wolves (*Canis lupus*) used the area surrounding the Banff town site (Banff National Park, *unpublished data*).

We collected pre-conditioning (before) data on three response variables (below) during the months of September and October, and collected post-conditioning (after) data between November and March. The winter season was specifically chosen for this conditioning research to coincide with the time that partially-migratory elk in Banff are most likely to concentrate in the lower-elevation urban areas (Woods 1991, McKenzie 2001, see also Kilpatrick and Spohr 2000) thus risking habituation to humans and their infrastructure.

Radio-collaring and treatment assignment

We radio-collared 19 moderately-habituated elk between September and December of 2001 using ground-darting immobilization which, in addition to five animals that were previously collared, provided a total sample size of 24 adult (> 2 years) female elk that were either without calves or had weaned calves produced in the previous spring. I defined 'moderately' habituated elk as those that had no known histories of year-round town site residency or aggression towards people, yet allowed human approach close enough for ground-darting (< 40 m). It was my subjective impression that the 24 study elk associated in large mixed herds that moved freely throughout the Banff town site and periphery both at the time of collaring and throughout the winter research. Thus, I expected that elk from the different treatment groups were subjected to relatively similar habitat, forage availability, predation pressure and other environmental factors that could influence my dependent variables. I evaluated this assumption using a home range overlap analysis to assess the relative similarity of habitat use between elk of the different treatment groups.

I divided the 24 study elk into three treatment groups of eight elk each: human, dog and control. The division was based haphazardly on the locations of three loose groupings of radio-collared elk on the first day of conditioning trials. On that day, these arbitrary groups were all located < 200 m from the town boundary and were separated by < 1000 m. Prior and subsequent to my start day, these elk dissolved into one or more large mixed herds and each elk was treated independently or in groups of a few individuals (below). I evaluated the independence of treatment groups with an association analysis to determine how the proportion of time that individual elk spent with elk of their own treatment group compared with the proportion spent with elk of the other treatment groups.

Aversive conditioning protocols

We applied ten 15-minute aversive conditioning treatments per elk between November 2001 and March 2002 when elk were found within an arbitrary boundary around the town. To create long-lasting and robust associations, we attempted to subject the elk to diligent yet unpredictable conditioning events (Brush 1971, Reynolds 1975), and researcher personnel and clothing were alternated between successive trials to help generalize the treatments to other humans (Rybarczyk et al. 2003).

The human conditioning treatment was applied by two people chasing the target elk for 15 minutes while using starter pistols (RG 300 Clip Launcher; Margo Supplies, High River, Alberta, Canada) to fire five pyrotechnic screamers and five cracker shells over their heads. We fired the screamer shells first to start the elk running and control their direction of travel, and then used the cracker shells towards the end of the treatment to maintain their sense of fear, anxiety and confusion. If dense traffic, facilities or people in close proximity posed a safety hazard during the trial, we moved the elk more slowly to the edge of town before firing any shells.

The dog conditioning treatment was applied for 15 minutes by one researcher and a professional dog handler with two border collies. The dogs silently herded the elk, potentially emulating wolf hunting, as directed by the dog handler using voice and whistle commands. The border collies were specifically chosen for this research, as preliminary trials indicated the elk responded to their silent movements with a 'flight response', whereas elk responded to a different breed of herding dog (New Zealand huntaway) that barked continuously, by stopping, turning and confronting the dogs aggressively, i.e. a mobbing or 'fight response' (see also Geist 1982).

The control group received a 'sham' treatment with two researchers standing silently within 50 m of the elk for the same 15-minute period. No other conditioning treatment was applied to the control group, but radio-collaring and response variable measurement was conducted in the same way as for the other treatment groups.

During each conditioning trial using humans or dogs, we moved the animals as far and as quickly as possible during the 15 minutes, typically at a running pace if it was deemed appropriate for animal, human and property safety. I considered this 'chase sequence' component of the treatment to be particularly important for emulating predation events, and maximizing elk energy loss and stress. If elk moved into dense hiding cover and we lost sight of them, we snow-tracked and continued the pursuit and application of noise and visual stimuli, again to better emulate predator hunting and stalking (e.g., Bateson and Bradshaw 1997). All aversive conditioning trials were tracked with a handheld global positioning system (GPS; Trimble GeoExplorer3; Trimble, Sunnyvale, California, USA) to accurately measure the distance elk were displaced, and the average frequency of treatment application (days between treatments) was recorded for each elk.

A final aspect of the conditioning protocol was the separation of elk into treatable units. Because elk from different treatment groups were often found interspersed with one another, a treatment was only applied if the appropriate treatment animals could be gently split away from the other animals. We split animals by walking slowly toward the elk and pushing them apart using subtle body movements and eye contact, employing standard low-stress stock herding principles (Smith 1998; Kloppers et al., *in preparation*). On some occasions, the whole herd reacted to the splitting and then we abandoned the conditioning trial. When we succeeded in splitting the selected treatment animal(s) from the rest of the herd, they were conditioned in a direction away from the remaining herd and the town site, and towards an area of suitable elk grazing habitat. While this splitting could be considered another form of conditioning, it was done consistently for all treatment groups (including control), and I expected it to have had the same relative impact on elk behaviour.

Response variables

To assess conditioning-induced changes, I collected data on each elk for three response variables: flight response distance, vigilance and distance to the town site boundary. I collected these data in two temporal phases: for six weeks prior to application of the conditioning treatments (before), and again at the latter half of the conditioning period (after). Specific details for each variable are provided below.

Flight response distance

Flight response trials were conducted opportunistically throughout the winter, but at a minimum of 24 hours following application of conditioning treatment on a given elk. Trials were conducted when the elk was neither bedded down nor travelling (moving purposefully at a steady pace without stopping to engage in other activities), and was > 25 m away from vegetation cover (visually determined to be of sufficient density and height to conceal an adult elk). When these conditions were met, one person approached the focal elk directly from a minimum distance of 75 m from the elk. Flight response distance (closest distance the elk could be approached before it moved > 5 m in any direction) was measured with a digital range finder (Bushnell Yardage Pro 500; Bushnell Corporation, Overland Park, Kansas, USA), accurate to within 0.5 m. For analysis purposes, the pre-conditioning flight response data for each elk was averaged into a 'before' value. To assess conditioning-induced change, I attempted to measure the flight response of all elk following their tenth aversive conditioning treatment. However, by that time, many elk had high levels of wariness and concealment in forest cover that precluded measurement of flight response, particularly for the human- and dog-conditioned elk. Thus, I derived my 'after' value from an average of whatever flight response data were available between the fifth and tenth conditioning treatments for each elk. I acknowledge that this metric undoubtedly provides a more conservative measure of treatment effects than might have actually existed after all ten treatments.

I anticipated that several uncontrolled variables may also influence flight responses (LaGory 1987). Thus, for each trial I recorded herd size, nearest neighbour distance, distance to cover, and relative location within the herd (periphery, edge, centre). Snow depth at the time of each flight response trial was calculated *post hoc* from an average of snow transect measurements around the town site (H. Breniser, *unpublished data*). Because the proximity of wolves was likely to influence the behaviour of elk (e.g. Lima and Dill 1990), a relative index of wolf presence was also calculated *post hoc* using trackpad data from wildlife underpasses in the vicinity of the town site (A. Clevenger, *unpublished data*). Wolves and other animals concentrate their movements toward the town in these underpasses because a 2.4 m wildlife exclusion fence borders the highway that parallels the Bow Valley through Banff National Park (McGuire and Morrall 2000, Clevenger et al. 2001). To estimate wolf activity with this information, I averaged the number of wolf southbound passages (towards the town site) for the week preceding each flight response trial.

Vigilance

Vigilance trials were conducted opportunistically throughout the winter, but always more than 24 hours after a conditioning treatment was applied to the target elk. Trials were conducted when the elk was > 25 m away from vegetation cover and was not bedded down or travelling (as defined above). The elk was observed from a vehicle or at long range with binoculars or spotting scope, to avoid detection and influence of the observer. Each trial was five minutes in length, and was abandoned if the elk bedded down, became aware of the observer's presence, or was disturbed by other human or wildlife activity in the area. The amount of time of each predominant activity was recorded (feeding, scanning, grooming, defecating, moving, social interaction), and the proportion of time spent scanning (vigilant) was calculated. As in flight response, the pre-conditioning vigilance data for each elk was averaged into a 'before' value, and the vigilance data between each elk's fifth and tenth conditioning treatments were averaged into an 'after' value. Again I anticipated that other variables might influence vigilance behaviour, so I recorded herd size, nearest neighbour distance, distance to cover, and relative location within the herd (periphery, edge, centre). Average snow depth and wolf presence values for the time of each trial were calculated as per flight response (above).

Proximity to town site

To assess displacement from the urban area following conditioning, I recorded one morning visual sighting or radio-telemetry location per elk daily between September 2001 and March 2002. These locations were recorded prior to daily measurements of flight response or vigilance behaviour or the application of conditioning treatments. From those locations, elk distance to the closest point on the town site boundary was calculated using ArcGIS Spatial Analyst (Environmental Systems Research Institute, Redlands, California, USA; McCoy and Johnston 2000). Average snow depth and wolf presence values for the time of each location were calculated as per flight response (above). Again, the pre-conditioning distances for each elk were averaged into a 'before' value, and the distances after each elk had received ten conditioning treatments were averaged into an 'after' value per elk.

Statistical analyses

All analyses were conducted using SPSS 11.5 (Norusis 2002). Because of the relatively small sample sizes employed by this study (eight animals per group), I set *alpha* = 0.10 to balance Type I and Type II errors. One-way ANOVA was used in preliminary analyses to compare the average distance moved in each trial among treatments; the proportion of time each elk associated with elk of the same and other treatment groups (i.e., an association analysis), as well as the proportions of Minimum Convex Polygon (MCP) home range overlap within and among the different treatment groups (i.e. home range overlap analysis). Analyses of all three response variables were conducted using repeated measures linear mixed models (Norusis 2002). In the flight response and vigilance models, the variables group size, nearest neighbour, distance to cover, location in the group, snow depth and wolf presence were tested for significant univariate correlations and inclusion as possible covariates. The variables snow depth and wolf presence were tested for use in the model describing proximity to town site. All biologically plausible two-way interactions were also tested by adding them, one at a time, to the final main effects models and assessing their significance. Flight response data were log-transformed and vigilance data were square-root transformed to achieve normality.

RESULTS

During the 15-minute conditioning trials, the dog and human treatments moved the elk an average distance of 1,184 m (± 44.7 m SE), while the control group elk drifted an average of 49 m (± 13.7 m SE) during the sham treatment. I found no significant difference in trial distance between the human and dog conditioned groups ($F_{1,88} = 0.624$, $P = 0.432$), but both the human and dog treatments moved elk significantly farther than the control group ($F_{1,80} \geq 229.4$, $P \leq 0.0001$). The association analysis examined the proportion of time that elk spent with elk of their own treatment group (40.2 % average, ± 2.1 % SE) in comparison with the time spent with elk of the other treatment groups (35.5 % average, ± 1.7 % SE). Five of the six two-way comparisons did not significantly differ ($P \geq 0.367$), but the human treatment group spent a lower proportion of time with elk of the control group than with themselves ($P = 0.001$). Average elk MCP home range size was 2857.5 ha, and there was no significant difference in home range size among treatment groups ($F_{2,23} = 0.042$, $P = 0.959$). The MCP home ranges of the 24 individual research elk overlapped an average of 81.3 % (± 2.9 % SE), and there was no significant difference between the proportions of home range overlap within and among treatment groups ($F_{5,551} = 0.381$, $P = 0.862$). Elk were conditioned at an average frequency of one treatment every 9.8 days (± 1.2 days SE) over the winter field season.

Overall, elk flight response distance increased significantly following treatment application ($F_{1,28} = 23.120$, $P < 0.0001$), and there was a significant difference in that increase among the treatments, as shown by the significant treatment times phase interaction (Fig. 2-1; $F_{2,22} = 10.862$, $P = 0.001$). As I had predicted, the human and dog conditioned groups both differed significantly from the control group ($F_{1,14} \geq 5.631$, $P \leq 0.037$). However, there was no significant difference between the human and dog conditioned groups ($F_{1,14} = 1.101$, $P = 0.312$). On average, elk in the human and dog conditioned groups increased their flight response distance from an approaching human by 22.1 m (± 5.5 m SE), an increase of 47.4%. The flight response of elk in the control group negligibly increased by 6.4 m (± 5.5 m SE). The variables group size, distance to cover, nearest neighbour, location in the group, snow depth and wolf presence were tested for significant univariate correlations. Snow depth was correlated with the time factor (Pearson's $r = 0.60$) and excluded from the model. To test for possible inclusion as covariates in the model, each remaining variable was entered as a fixed effect covariate, singly and in combination with other covariates, but only wolf activity significantly and negatively affected flight response distance ($F_{1,17} = 4.874$, $P = 0.041$). This meant that elk exhibited shorter flight response distances when recent wolf activity was high. There was also a significant interaction between wolf activity and time (Fig 2; $F_{1,22} = 5.788$, $P = 0.025$), showing that flight responses declined with increasing wolf activity disproportionately in the post-conditioning period.

Contrary to my expectation, vigilance declined for all treatment groups during the time that conditioning was applied (Fig. 2-3; $F_{1,21} = 10.113$, $P = 0.005$), and there was no significant difference in the relative decline among treatments (conditioning phase times treatment; $F_{2,21} = 0.183$, $P = 0.834$). There was, however, a trend for the conditioned animals' vigilance to decline less (42%) than the control animals (62 %). The same variables were tested for correlations and inclusion as in the flight response model. Snow depth was a significant covariate but excluded from the model due to strong correlation with my time variable (Pearson's $r = 0.77$).

During the conditioning period, there was a significant increase for all treatment groups in the distance from the daily position of each elk to the town boundary (Fig. 2-4; $F_{1,31} = 11.505$, $P = 0.002$) and a significant conditioning phase by treatment interaction ($F_{4,27} = 2.970$, $P = 0.037$). The human treatment group differed significantly from both the dog and control treatments ($F_{2,19} > 4.124$, $P < 0.034$), with no significant difference between the dog and control treatments ($F_{2,18} = 0.402$, $P = 0.675$). Snow depth and wolf activity were tested for univariate correlations and possible inclusion in the model, but snow depth was highly correlated with my time variable (Pearson's $r = 0.934$) and thus excluded. Wolf activity was not significant once entered with the other variables and so was excluded from the final model. However, there was a significant interaction between wolf activity and treatment (Fig. 2-5; $F_{3,37} = 3.348$, $P = 0.029$), showing that elk occurred at greater distances from town in the human treatment when wolf activity was low.

DISCUSSION

My results suggest that aversive conditioning is capable of modifying some aspects of elk behaviour towards humans and human-use areas. They also suggest that dog and human conditioning treatments can achieve similar levels of success for my primary measure of habituation, flight response distance. This variable, which showed a significant increase to both conditioning treatments, upheld my predictions that elk would be more wary of humans following aversive conditioning. The similarity in response to both treatments for this variable may stem from the magnitude and consistency of their conditioning effort. In particular, both treatments involved chases with sufficient distance (1,215 m), frequency (1/9.8 days) and duration (15 minutes) to emulate or exceed natural predation events by wolves. Prior research in Riding Mountain National Park (Carbyn 1983) showed lethal wolf chase sequence lengths ranged from 20 to 260 m in distance. Lethal wolf chase sequence lengths in Banff averaged 180 m (range 10 to 1,700 m) (M. Hebblewhite, *unpublished data*; Parks Canada, *unpublished data*), though both studies acknowledged potential sample bias towards shorter sequences. Neither of those studies included non-lethal (unsuccessful) chase sequence lengths, which would presumably be much longer (M. Hebblewhite, *personal communication*). My average chase sequence length (1,215 m) therefore exceeded that of recorded natural predation events, but was perhaps comparable in length to non-lethal wolf chase sequences.

The average conditioning frequency of my treatments (1/9.8 days) may also have contributed to their efficacy because it also exceeded the average frequency of visitation by wolves to an elk herd (1/13.4 days, Weaver 1994). While my conditioning treatments did not emulate all aspects of hunting by wolves, the energy loss and stress from my longer and more frequent conditioning events appeared to be severe enough to trigger elk escape and avoidance responses. Longer hunting sequences by humans generated extraordinary large volumes of the stress hormone cortisol in red deer (also *Cervus* *elaphus*) particularly when the animals dashed away only to be repeatedly found and chased again by hunters (Bateson and Bradshaw 1997). Therefore, although our aversive conditioning chase sequences using humans and dogs did not present any direct mortality risk for elk, the procedure may have emulated enough aspects of wolf or human hunting for elk to perceive us as *potential* predators, and display typical antipredator responses (e.g., Beale and Monaghan 2004).

My interpretation that our chase sequences emulated predation events is consistent with the theory that human-caused disturbance stimuli can be considered a form of predation risk (Frid and Dill 2002, Beale and Monaghan 2004), causing animals to modify their behaviour to maximize their security, decrease stress, and maintain their reproductive fitness (Geist 1982, Lima and Dill 1990, Frid and Dill 2002). The predator-resembling nature of the chase sequence in my human and dog conditioning treatments may also explain why elk in my experiment showed no signs of habituating to the conditioning stimuli, whereas in other studies wildlife quickly habituated to the use of auditory (Bomford and O'Brien 1990, Belant et al. 1996, Bender 2003) or visual stimuli (Espmark and Langvatn 1985, Beringer et al. 2003, VerCauteren et al. 2003). A lack of perceived predation risk in those contexts offers a potential explanation for the minimal increase in flight response for control elk in my study. This missing stimulus may also explain increased signs of habituation and aggression by some control group elk to researchers during the four-month treatment period. The rapidity of the changes in the treated elk and the apparent change in the other direction by some control elk suggests that elk can habituate to human presence in a non-threatening environment quickly, which has management implications for Banff and other areas where large numbers of tourists, golfers and residents have benign encounters with elk almost daily (see also Geist 1982).

The decrease in the vigilance behaviour of all elk during my treatment period is inconsistent with my predictions, but perhaps consistent with predictable seasonal changes in elk energy budgets related to snow depth (e.g., Goodson et al. 1991). My baseline data were collected in fall when elk have higher energy reserves that may support greater vigilance investment and flight response distances (Parker et al. 1984). By contrast, my conditioning period data collection partially coincided with the late-winter period when elk typically begin catabolism of body reserves (DelGiudice et. al 1991, DelGiudice et al. 2000). At that time, they may sacrifice their security (particularly with decreased vigilance) in order to increase feeding time (e.g., Moen 1976, Gates and Hudson 1979, Lima and Dill 1990, Parker et al. 1996). The strength of these seasonal effects on vigilance relative to treatment effects could conceivably have diminished my ability to detect real differences among the treatment groups (Type II error). To avoid these sources of potential error for this type of research in the future, one would ideally collect all vigilance data within the same season. While I could not detect a significant difference among treatments, control animals exhibited a 20 % greater decline in vigilance than treated animals (Fig. 2-2). This implies that elk maintained higher vigilance levels under human and dog conditioning than they did without it, offering qualified support for the utility of aversive conditioning for modifying habituated elk behaviour. Unfortunately, the necessity to use vigilance data between the fifth and tenth conditioning treatment of each elk, rather than data following the tenth treatment may have contributed to the non-significant difference among treatment groups.

My final result, that the human-conditioned elk increased the distance between their daily positions and the Banff townsite boundary, further supports my initial prediction that aversive conditioning can modify elk behaviour by teaching avoidance of human-use areas, corroborating the results of Nolte et al. (2003). My result recommends human over dog conditioning and corroborates Frid and Dill's (2002) hypothesis that human disturbance is a form of predation risk. My human-conditioned elk subsequently avoided those areas where conditioning had occurred, suggesting some memory of those aversive stimuli and behaviour to avoid them. An alternative, but not mutually exclusive, explanation for the subsequent avoidance of town by the conditioned elk might reflect the energetic cost of conditioning to the animal, particularly when applied in winter. During the late-winter period with lower temperatures and deeper snow, elk could normally be expected to conserve energy by reducing their movement and staying in areas with the highest relative nutritional quality (Gates and Hudson 1979, Parker et al. 1984, Sweeney and Sweeney 1984, McCorquodale 1993), such as is offered in the town site (McKenzie 2001). When we persistently conditioned the elk more than a kilometre away during that critical period, the energetic cost of moving to and from the town site may have outweighed the travel costs of returning to it (see also Bunnell and Gillingham 1985, Bradshaw et al. 1998). These results suggest that aversive conditioning can potentially reduce the urban 'refuge effect', through both increased perceived predation risk and reduced energetic benefit.

Despite the significant treatment effect I detected for proximity to the town boundary, association analysis showed some evidence that all treatment groups responded to my conditioning, indicating some herd-level influences (see also Galef 1995, Ralphs and Provenza 1999). Because elk receive both energetic and security benefits by herding into larger groups, particularly in late winter (Moen 1976, Geist 1982, Hebblewhite and Pletscher 2002), it is likely that this phenomenon reduced some of the variation I might otherwise have detected among treatments. An additional explanation for herd-level effects could relate to emphatic learning (e.g., Klopfer 1957) or social facilitation (e.g., Griffin 2004), whereby individuals not exposed to the conditioning treatment learn from the behaviour of other conditioned herd members. Yet regardless of the potential for herd level effects to influence this research, the high variation I documented among individuals encourages further individual-based research, and strengthens the apparent success of my human-based aversive conditioning protocols for managing hyper-abundant wildlife in areas with high human use.

An important covariate that was apparent in my analyses of both flight response distance and proximity to town was the activity of wolves. In both cases, wolf activity appeared to reduce the efficacy of my conditioning treatments, as might be expected when elk had the option of challenging us *versus* real predators. Flight responses decreased when wolf activity was high, suggesting that elk were reluctant to flee from us in the vicinity of predators. This effect was much stronger in the post-conditioning period, effectively acting in opposition to my treatment effects. Proximity to town also responded to wolf activity, this time exhibited as an interaction with treatment. This meant that the strong effect of human conditioning was sharply reduced by high wolf activity. Dog and control treatments, which did not show significant post-conditioning effects, were not similarly affected by wolf activity. Again, this result indicates that my effective (human) conditioning would have been even more effective were it not for the counteracting effects of wolves. Banff and other jurisdictions may, thus, bear in mind that more conditioning effort will likely be needed when it pushes animals in the direction of predators relative to comparable situations without predators.

In summary, my results show that aversive conditioning by human and dog treatments can modify aspects of elk behaviour to prevent and manage their habituation. Human and dog treatments performed equally well in increasing elk flight response distance from an approaching human, and this may be the most important variable describing wariness to humans and a decline in habituation. Neither treatment significantly affected elk vigilance. Proximity to the town boundary was significantly increased by human conditioning, but this variable was less responsive when wolf activity was high. Dog conditioning did not significantly affect elk proximity to town.

These results have two main implications for managers. First, because the dog and human aversive conditioning treatments achieved relatively similar levels of success at modifying elk flight responses, the choice of which treatment to apply might be based on economic efficiency and local logistics for jurisdictions contending only with the behaviour, and not the location, of urban wildlife. Presumably, professional dog handlers who are willing to use their highly trained border collies for wild elk management are both scarce and expensive. Human conditioning in many jurisdictions can be done without hiring additional staff, provided they are familiar with elk-conditioning techniques. In my system, I calculated the monthly cost of conditioning with dogs to be $4300 CAD, 15 % higher than the cost of conditioning with humans. For these reasons, I chose to use humans for a second season in which I sought to identify the optimal frequency of conditioning for elk with differing levels of initial habituation (Chapter 3). A second aspect of the choice of conditioning medium for managers of national parks and urban areas is the nature of public perception. For us, the public response towards the quiet, friendly appearance of the dog treatment was generally positive, but I received some noise complaints about the cracker and screamer shells associated with the human treatment. Since the chase sequence appears to be the critical component of conditioning, and the method employed (i.e. cracker shells or dogs) is secondary, managers could also choose a variety of other methods to complement the chase sequence and suit their situation. For example, Banff wardens sometimes use raised hockey sticks with bags tied to one end to condition elk (e.g., emulating antler displays common among sparring elk; Geist 1982, Jennings et al. 2002), and observing Canadians are generally quite accepting of this form of threat display. Ultimately, budgets, the local situation and associated management priorities will dictate whether human or dog aversive conditioning treatment is the most appropriate choice for a given jurisdiction.

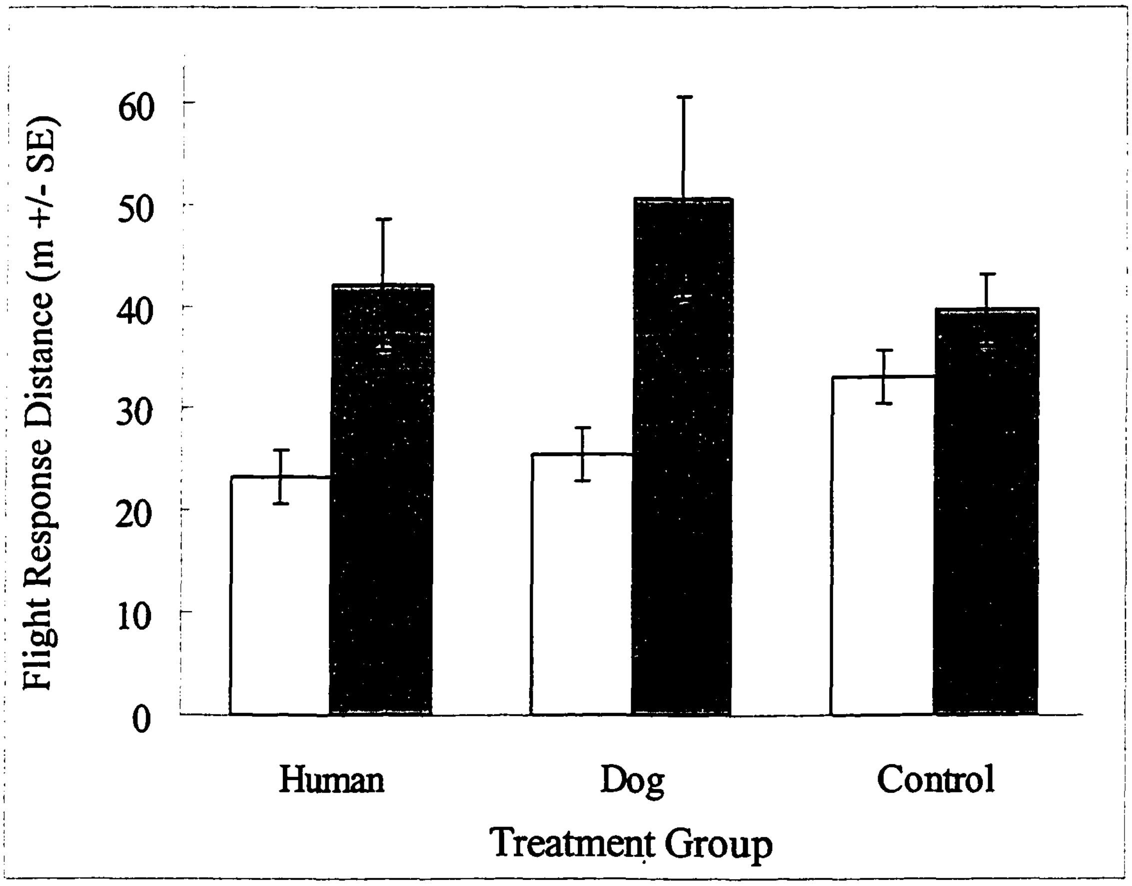

Figure 2-1. Elk flight response distance (m ± SE) before (□) and after (■) aversive conditioning treatments were applied to the three treatment groups in Banff National Park.

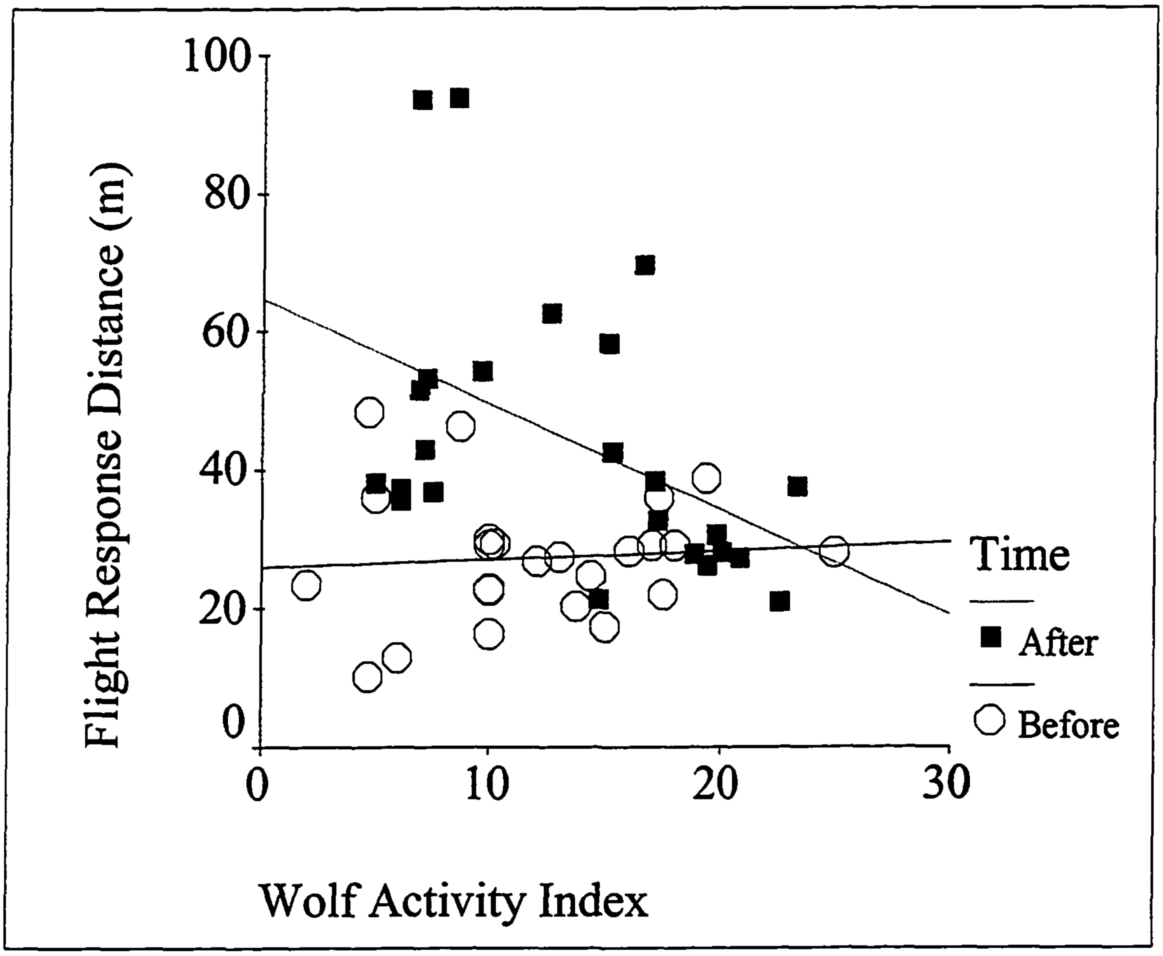

Figure 2-2. Relationship between flight response distance and nearby wolf activity for elk before (○) and after (■) aversive conditioning in Banff National Park.

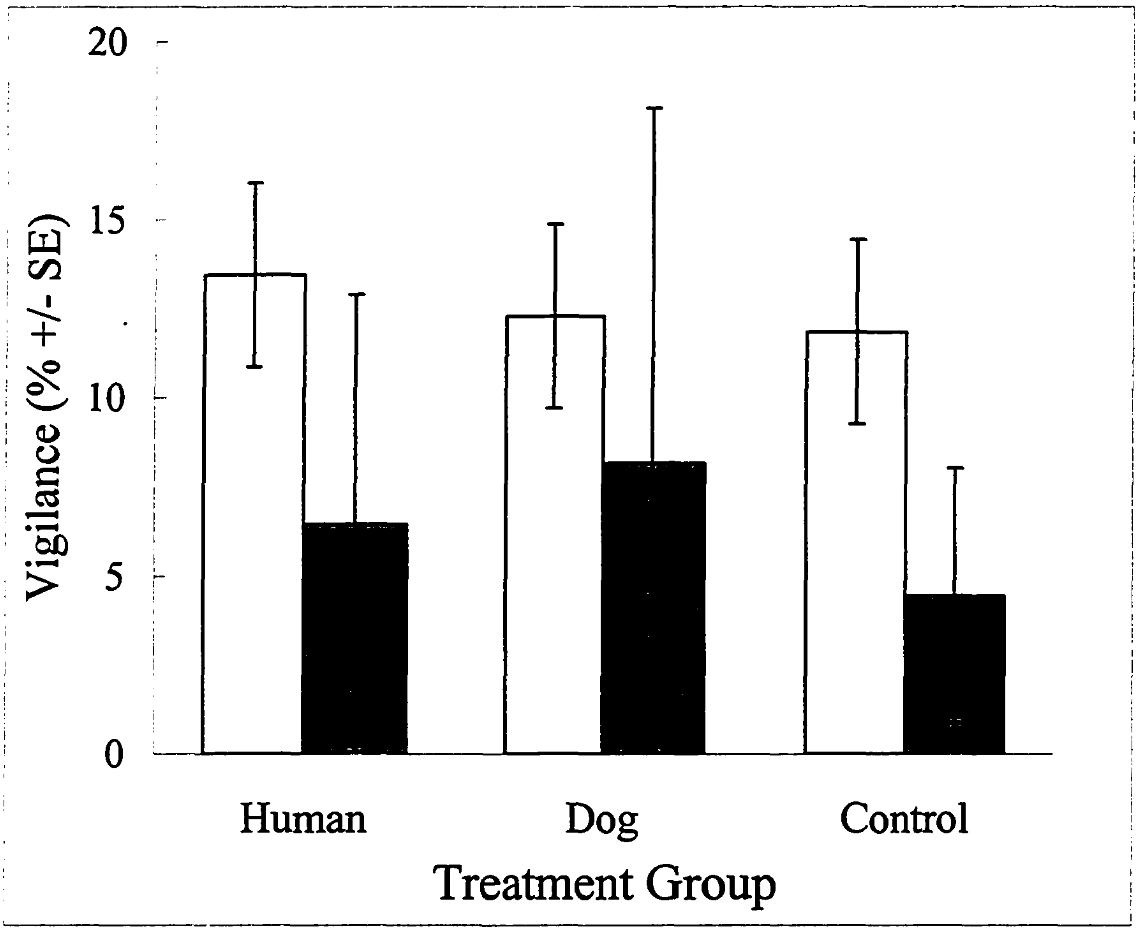

Figure 2-3. Proportion of time elk spent vigilant (% ± SE), before (□) and after (■) aversive conditioning treatments were applied to the three treatment groups in Banff National Park.

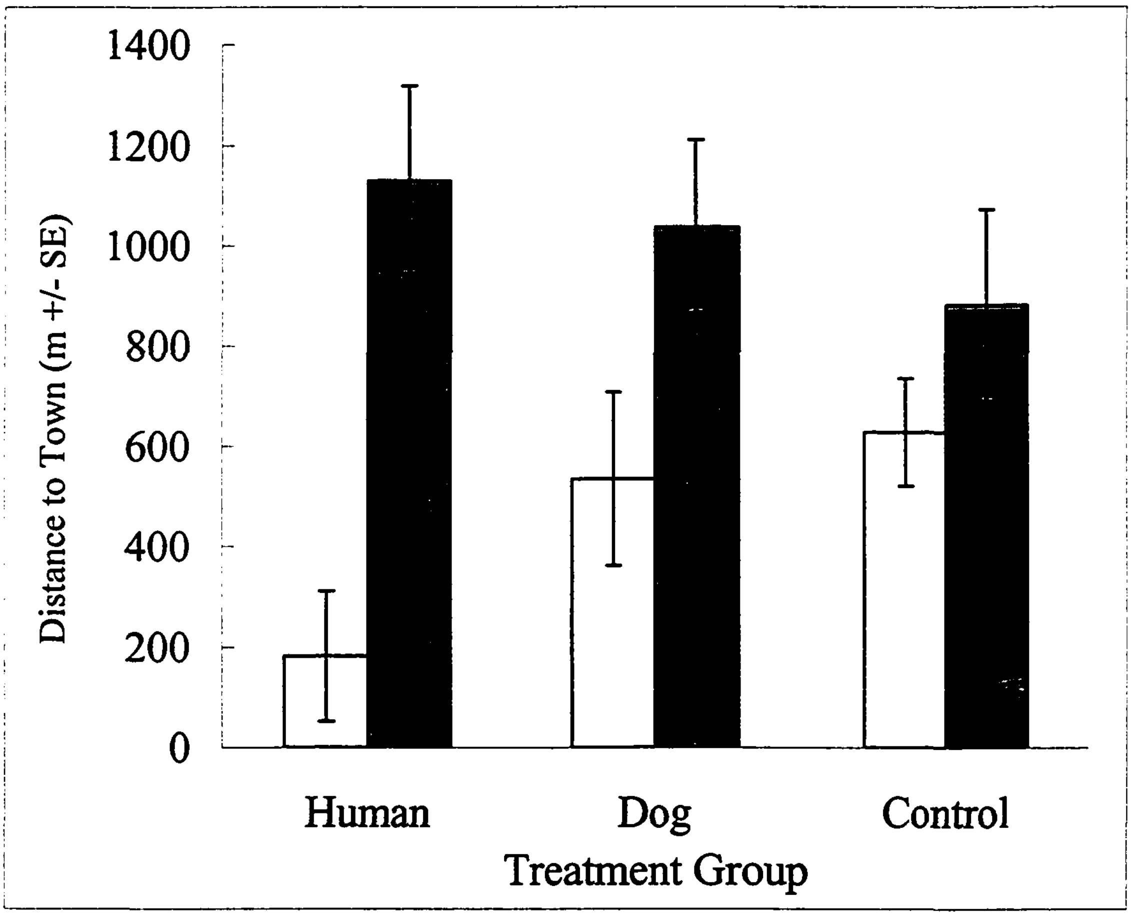

Figure 2-4. Average elk daily distance (m ± SE) to the closest point on the town boundary before (□) and after (■) aversive conditioning treatments were applied to the three treatment groups in Banff National Park.

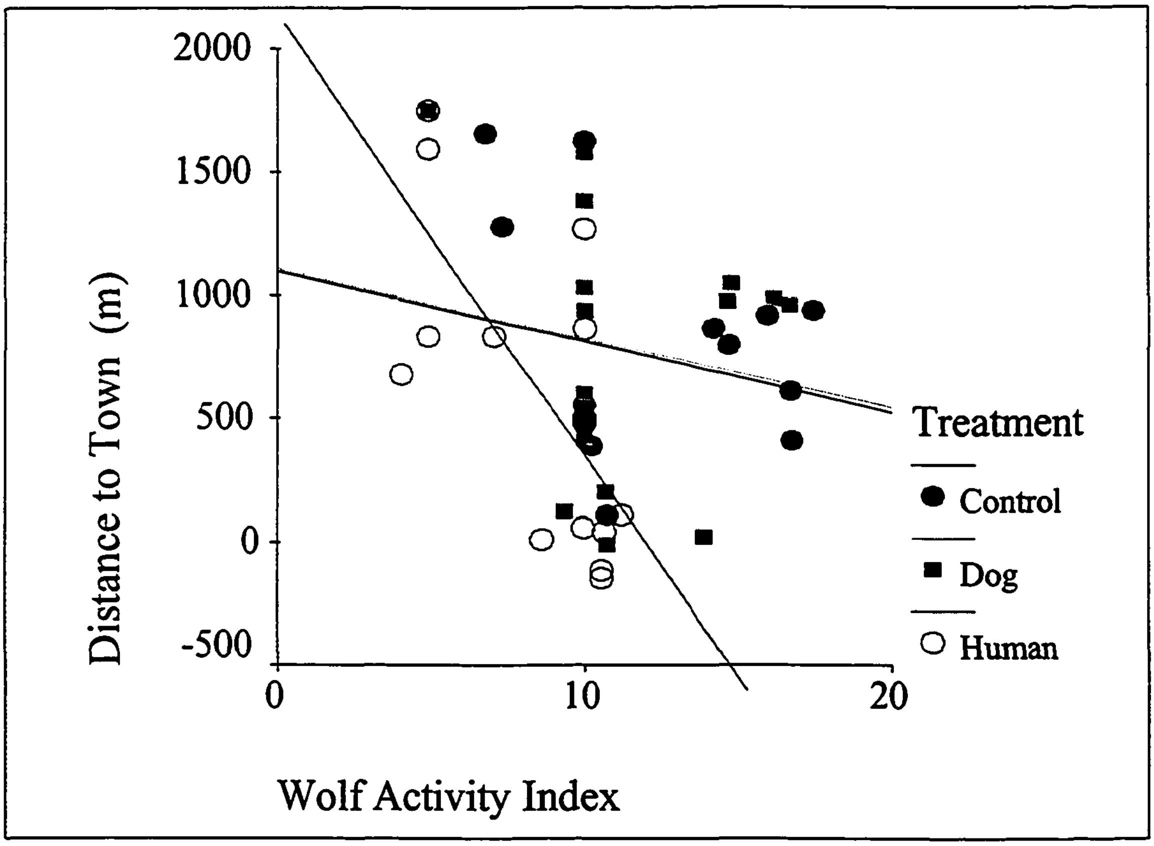

Figure 2-5. Relationship between the proximity of elk to the town boundary and nearby wolf activity for elk that were subjected to human (○), dog (■) and control (●) aversive conditioning treatments in Banff National Park.

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CHAPTER THREE – ELK BEHAVIOURAL RESPONSE TO AVERSIVE CONDITIONING AT DIFFERENT FREQUENCIES

Worldwide, wildlife-human conflict is increasing as expanding human populations consume native wildlife habitat and create attractive alternatives to it (Fall and Jackson 2002). Typically, this conflict causes property damage, crop loss and nuisance effects, and confers costs that are both high and rising (Conover et al. 1995, Wagner et al. 1997, Ward et al. 2004). Some of this conflict concerns ungulate species, which may pose additional threats to human life and safety through vehicle collisions and direct contact. Ten years ago, the annual costs of ungulate damage in the United States was estimated at $1.1 billion combined for car repairs and damage to timber, in addition to 211 human deaths and 29,000 injuries from collisions with cars (Conover et. al 1995). Elk (*Cervus elaphus*) is a species of particular concern because these herding animals can be locally abundant and are large enough to inflict considerable damage and injury (DeCalesta and Witmer 1994). They are also prone to habituation to humans, which challenges traditional expectations for wildlife avoidance of humans and human-use areas (Thompson and Henderson 1998). The presence of habituated elk is a widespread and growing problem in the protected areas of the Rocky Mountain region of North America (Thompson and Henderson 1998) and occurs in Yellowstone National Park (P. White, *personal communication*), Rocky Mountain Park, Colorado (T. Johnston, *personal communication*), and within Banff and Jasper National Parks, Alberta (G. Peers, *personal communication*).

Several techniques to limit conflict between habituated elk and humans in National Parks and other protected areas have been examined. One approach is to remove habituated animals from the system by translocation. Unfortunately, this approach is expensive, removes a prey base from the ecosystem, and frequently fails because translocated animals simply return to their capture locations (Craven et al. 1998). Limiting attractants has been helpful in some jurisdictions (e.g., Nolte 1999), but requires legislative obligations with high proportions of enforcement and compliance (H. Dempsey, *personal communication*). A limitation of both approaches is that they do not address the root problem of habituation that brings the animals in close proximity to human-use areas in the first place. Habituation results from exposure to stimuli that are irrelevant to fitness (Taylor and Knight 2003), whereas animals may be expected to show avoidance of stimuli that previously conferred negative consequences (e.g., Nolte et al. 2003) and attraction to stimuli that provided positive reinforcement (Domjan 2003). Because humans within protected areas are harmless to elk, these animals soon lose their wariness of them (Geist 1982). Subsequent human-elk conflict is likely whenever human-habituated elk perceive humans as competitors (e.g., in an attractive foraging site), predators (e.g., during calving season; Geist 1982), or as subordinate within their dominance hierarchy (e.g., Wirtu et al. 2004). In addition to elk-human conflict, habituated elk typically cease to migrate (Geist 1982, Berger 2004) and thus cause significant ecological damage by overgrazing (White et al. 1998).

The basis of habituation to elk habituation to humans suggests that it would be possible to reduce elk-human conflicts if wariness to humans could be reinstated with predator-resembling aversive conditioning. This technique, which is a form of operant conditioning, is intended to pair the stimulus of human presence with a negative, evolutionarily-relevant consequence. Previously, I showed that it was possible to condition habituated elk in Banff National Park with a predator-resembling chase sequence (Chapter 2). Whether enacted by humans or dogs, this aversive conditioning appeared to increase two measures of wariness; the distance at which elk approached by humans turned and moved away (flight response distance) and the daily proximity to the town site boundary (see also Nolte et al. 2003). These techniques showed much promise for reducing habituated elk behaviour, but they were labour-intensive and costly to apply. Thus, managers need to know what minimum conditioning effort is needed to elicit the desired changes in elk behaviour. Although disturbance frequency and magnitude are known to impact wildlife behaviour in general (Knight and Cole 1995), the specific effect of different aversive conditioning frequencies on wildlife behaviour has not to my knowledge been experimentally evaluated.

The objectives of this research were to determine: (1) the minimum aversive conditioning frequency required to increase elk wariness enough to improve public safety (currently defined in Banff as a 45 m elk flight response distance); (2) whether different levels of elk habituation generate different responses to the frequency of aversive conditioning; and (3) the duration of conditioned responses following treatment (i.e., behavioural extinction). I measured two response variables to assess these behavioural changes: elk flight response distance from an approaching human (e.g., Altmann 1958, Stuwe 1986, Recarte et al. 1998, Taylor and Knight 2003); and elk daily proximity (by radio-telemetry) to the town site boundary.

METHODS

Study area and schedule

Fieldwork was conducted in the townsite and surrounding area of Banff, AB (51°15'N, 116°30'W), within Banff National Park, Canada. Banff townsite is situated at an elevation of 1383 m, in the Bow Valley within the central Canadian Rockies. The lower Bow Valley bottomlands typically have modest snowfall combined with occasional warm periods, creating important winter habitat for ungulates (Woods 1991). Our study area consisted of the urban land-use area of Banff in addition to adjacent montane wetlands, forests, shrublands and a golf course within 2 km of the town boundary, for a total area of 466.5 ha. A thorough description of the vegetation of this area was provided by Holland and Coen (1983). The Banff townsite has a permanent human population of 7135 people, but temporary park visitation approaching five million people per year (Banff-Lake Louise Tourism Bureau, *personal communication*). The elk population in the town site area numbered 137 animals in the spring of 2002, showing a continuing decline in response to management actions and increased predation by wolves since a high of 533 animals in 1994 (Banff National Park, *unpublished data*). During the 2002-03 field season only 8 wolves (*Canis lupus*) used the area surrounding the Banff town site, and spent the majority of time well away, contrasting sharply with the number of wolves that frequented the town site during two previous winters (13 and 18 wolves respectively; Banff National Park, *unpublished data*).

Data were collected through the winter of 2002-2003. We collected pre-conditioning 'before' data during the months of September and October, 'conditioning' data between November and February, and post-conditioning 'after' data during the months of March and April. We conducted our conditioning between November and February because Banff's partially-migratory elk are typically concentrated in the lower-elevation urban areas then and this behaviour is believed to facilitate habituation to humans and their infrastructure (McKenzie 2001, see also Kilpatrick and Spohr 2000).

Radio-collaring and treatment assignment

We radio-collared 8 moderately-habituated elk in September and October of 2002 using ground-darting immobilization. In addition to 17 animals that were previously collared, this provided a total sample size of 25 adult (> 2 years) moderately-habituated female elk that were without calves from the previous spring. We defined 'moderately' habituated elk as those that had no known histories of year-round townsite residency, yet allowed human approach that was close enough for ground-darting (< 40 m). These 25 study elk associated in large mixed herds that moved freely throughout the Banff townsite and periphery throughout the winter research (see Chapter 2). Thus, I expected that elk from the different treatment groups were subjected to relatively similar forage availability, habitat, predation pressure and other environmental factors that could influence my dependant variables.

The 25 elk were divided into five treatment groups of five elk, with the goal of evenly spaced conditioning frequencies ranging on average from one treatment every 10 days to one treatment every 30 days. I chose a frequency of 10 days as one end of my conditioning continuum because my previous work had shown this frequency (average = 9.8 days; Chapter 2) to be effective in increasing both flight response and proximity to the town site boundary. I called the frequencies: 'high' (1 treatment every 10 days); 'medium-high' (1 /15 days); 'medium' (1 / 20 days); 'medium-low' (1 / 25 days); and 'low' (1 / 30 days). I haphazardly assigned elk to the five frequency groups, but I suspected that initial habituation level might impact subsequent elk response to aversive conditioning. To enable testing of habituation as a covariate, prior to the start of treatment application, I reassigned elk ensuring that average 'before'-conditioning flight response distance (which I subsequently call 'habituation level') was equal between the five treatment groups. We attempted to condition elk according to their assigned frequencies, but if we were unable to meet individual frequency targets for any reason, I reassigned those elk to the frequency group closest to their actual frequency, while still maintaining similar average habituation level among the treatment groups. Throughout this paper, I refer to 'habituated' elk as having a 'before' flight response distance of ≤ 25 m, 'moderately habituated' elk between 26 m and 34 m, and 'wilder' elk ≥ 35 m. These groupings are for ease of description, but analyses of habituation effects were based on the continuous variable of actual flight distances before conditioning.

Aversive Conditioning

We applied 15-minute aversive conditioning treatments (below) to each elk according to their designated frequency schedule between November 2002 and February 2003. Elk were only conditioned when they were found within or on peripheral entry points to the town site. Because elk of different treatment groups were generally interspersed within the same herds, a treatment was only applied if the scheduled treatment animals could be gently split away from the others by researchers walking slowly among them, directing them apart by subtle body movements and herding principles (Smith 1998, Chapter 2). If the whole herd reacted to this splitting, we abandoned the conditioning trail. When we succeeded in splitting treatment animals from the rest of the herd, they were conditioned in a direction away from the remaining herd and the town site, and towards suitable grazing habitat. While this splitting could be considered another form of conditioning, it was done consistently for all treatment groups and should have the same relative impact on elk behaviour.

The aversive conditioning treatments followed the same 'human conditioning' protocols within the predator-resembling chase sequence found to be effective in the 2001-02 research (Chapter 2). Treatments were applied by two people chasing the elk for 15-minutes while firing five pyrotechnic screamers and five cracker shells over their heads using starter pistols (RG 300 Clip Launcher; Margo Supplies, High River, Alberta, Canada). Screamer shells were fired first to start the elk running and control their direction of travel, followed by cracker shells towards the end of the treatment to best maintain their sense of fear, anxiety and confusion. During some trials, traffic, facilities or extraneous people compromised elk or human safety. In these cases the elk were slowly herded towards the edge of town before shells were fired, or the trial was abandoned if necessary. During the conditioning trials, we moved the animals as far and as quickly as possible, and typically at a running pace if it was deemed to be safe for animal, human and property safety. I considered this 'chase sequence' component of the treatment to be particularly important for maximizing elk energy loss and stress, and reducing the likelihood of habituation to our stimuli (see Chapter 2). Additionally, if elk moved into dense hiding cover and we lost sight of them, we snow-tracked and continued the pursuit and application of noise and visual stimuli to best emulate predator hunting and stalking (e.g., Bateson and Bradshaw 1997). All trials were tracked with a handheld global positioning system (GPS; Trimble GeoExplorer3; Trimble, Sunnyvale, California, USA) to accurately measure the distance elk were displaced.

Flight response distance

Flight response trials were conducted opportunistically throughout the winter, but at a minimum of 24 hours following application of conditioning treatment on a given elk. Flight response was measured only when the elk was neither bedded down nor travelling (moving purposefully at a steady pace without stopping to engage in other activities), and was > 25 m away from vegetation cover (visually determined to be of sufficient density and height to conceal an adult elk). When these conditions were met, one person approached the focal elk from a start distance of > 75 m, measuring the alert distance, flight response distance (closest distance the elk could be approached before reacting by moving > 5 m), reaction type and distance moved. All distances were measured with a digital range finder (Bushnell Yardage Pro 500; Bushnell Corporation, Overland Park, Kansas, USA), accurate to within 0.5 m. For analysis purposes, the pre-conditioning flight response data for each elk was averaged into a 'before value', the trials during the conditioning period were averaged into a 'during value', and the post-conditioning trials were averaged into an 'after value' per elk.

I anticipated that several uncontrolled variables might also influence flight response (e.g., LaGory 1987). Thus, for each trial I recorded herd size, nearest neighbour distance, distance to cover, and relative location within the herd (solitary, on herd periphery, or central). Snow depth at the time of each flight response trial was calculated *post hoc* from an average of snow transect measurements around the town site (H. Breniser, *unpublished data*). Because the proximity of wolves was likely to influence the behaviour of elk (e.g. Lima and Dill 1990 and Chapter 2), a relative index of wolf pressure was calculated post hoc using trackpad data from town site-area wildlife underpasses (A. Clevenger, *unpublished data*). Wolves and other animals concentrate their movements toward the town in these underpasses because a 2.4 m wildlife exclusion fence borders the highway that parallels the Bow Valley through Banff National Park (McGuire and Morrall 2000, Clevenger et al. 2001). To index wolf activity with this information, I averaged the number of wolf southbound passages (towards the town site) for the week preceding each flight response trial.

Identifying the conditioning frequency needed to achieve typical management objectives (i.e., to increase flight distance by some percentage or to some absolute value), requires knowledge of the shape of the curve by which elk respond to variation in conditioning frequencies. Using the frequent conditioning results of my first season (Chapter 2) as one end point, and monthly conditioning as the other, I imagined that elk might respond to intervening frequencies in two distinct ways (Fig 3-1): they might exhibit a linear response, increasing flight distance gradually with increasing conditioning frequency (A), or they might exhibit a threshold response whereby flight distance increases rapidly after some threshold of conditioning frequency is reached. That threshold might occur quickly (B), at a moderate frequency (C), or slowly (D). I hoped to derive the shape of this flight response increase curve as a function of these treatment applications.

Proximity to town site

To assess displacement from the urban area following conditioning, I recorded one morning visual sighting or radio-telemetry location per elk daily between September 2002 and April 2003. These locations were recorded prior to measurement of flight response or the application of conditioning treatments. From those locations, elk distance to the closest point on the town site boundary was calculated using ArcGIS Spatial Analyst (Environmental Systems Research Institute, Redlands, California, USA; McCoy and Johnston 2000). The town site boundary was an arbitrary and imaginary line surrounding the town, roughly corresponding to the location of human infrastructure and within which the conditioning was conducted. Snow depth and wolf pressure values for the time of each elk location were calculated as per flight response (above). For analysis purposes, the pre-conditioning distances for each elk were averaged into a 'before' value, distances during the conditioning period were averaged into a 'during' value, and the post-conditioning distances were averaged into an 'after' value per elk.

Statistical analyses

Because of the relatively small sample size in this study (five animals per group), we set *alpha* = 0.10 in all analyses to balance Type I and II errors. All analyses were conducted using SPSS 11.5 (Norusis 2002). As preliminary analyses, one-way ANOVA was used to compare the average distance moved in each trial among treatments, as well as the arc-sine transformed proportion of time each elk associated with elk of the same and other treatment groups (i.e., an association analysis). Analyses of both response variables, change in flight response between conditioning phases and proximity to the town site boundary, were conducted using repeated measures linear mixed models. In the flight response model, the variables group size, nearest neighbour, distance to cover, location in the group, snow depth and wolf presence were tested for significant univariate correlations and inclusion as possible covariates. The variables wolf presence and snow depth were tested for use in the model describing proximity to town site. All biologically plausible two-way interactions were also tested by adding them, one at a time, to the final main effects models and assessing their significance.

RESULTS

Elk received a range of three to nine conditioning treatments (average = 4.8 treatments ± 0.4 SE) over the winter season. Vagaries of elk availability and position created some variance within the intended frequency categories, so the conditioning frequencies we actually applied to the elk ranged from a high of one treatment every 12.8 days to a low of one treatment every 30.3 days (average = 1 / 21.9 days ± 1.4 SE). The resulting five frequency treatment groups were: high (1 / 12.8 days), medium-high (1 / 18.0 days), medium (1 / 21.8 days), medium-low (1 / 26.6 days) and low (1 / 30.3 days). During the 15-minute conditioning trials we moved elk an average distance of 918 m (± 42.5 m SE). The distance that elk of each frequency group was moved during the trials differed significantly, but unintentionally ($F_{4,75} = 2.269$, $P = 0.070$); *post-hoc* analyses indicated that we moved elk conditioned at the medium-low frequency an average of 359 m further per trial than those conditioned at the high frequency. Measured by association analysis, there was no significant difference ($F_{1,71} = 0.622$, $P = 0.433$) between the proportion of time that elk spent with elk of their same conditioning frequency group (65.7 % ± 8.9 % SE) compared with proportion spent with elk of other frequency groups (61.7 % ± 4.3 % SE). This confirms that elk of our different frequency groups mixed and associated with each other sufficiently to avoid bias related to potential behavioural differences between separate cohorts.

Flight response during conditioning

Elk flight response distance increased significantly during conditioning treatment application (Fig. 3-2; $F_{1,23} = 47.573$, $P \leq 0.001$), with an average increase of 13.0 m (± 1.5 m SE), or 31.9 %. There were no significant differences among the five frequency groups ($F_{4,9} = 0.383$, $P = 0.816$) when analyzed by ANOVA, but there was a significant and positive correlation between conditioning frequency and flight distance (Fig. 3-3; $F_{1,23} = 3.704$, $P = 0.067$). By contrast, habituation level (as represented by pre-conditioning flight distance) had a strongly negative effect on the increase in flight distances (Fig. 3-4 (a); $F_{1,4} = 19.452$, $P = 0.012$), indicating that more habituated animals responded to conditioning with greater increases in flight distance than did wilder elk. A significant interaction between conditioning frequency and habituation level (Fig. 3-4 (b); $F_{1,4} = 15.048$, $P = 0.018$) further revealed that the lack of response to conditioning by the wilder elk was constant across all frequencies of conditioning, whereas the more habituated elk increased flight response distance with application of greater than medium-low conditioning frequencies. In essence, elk conditioned at the low frequency showed the same minimal response to conditioning across all habituation levels. Although the flight increase by habituated elk was greater than for wilder elk, the resulting flight response distances achieved during conditioning did not significantly differ by habituation level (Fig. 3-5; $F_{1,23} = 0.895$, $P = 0.354$), with an overall average 40.6 m (± 1.5 m SE).

In addition to the conditioning frequency and habituation effects, flight response increase was affected by a significant interaction between nearest-neighbour distance and conditioning frequency ($F_{5,13} = 9.036$, $P = 0.001$). Compared with elk conditioned at lower frequencies, elk conditioned at greater than medium-high frequencies exhibited higher flight increase in response to conditioning when they were at greater distances from their nearest neighbours. Other covariates were not significant singly or in combination with other variables ($F_{1,17} \leq 1.499$, $P \geq 0.238$).

Flight response post-conditioning

During the 8 weeks after conditioning, elk flight response distance did not significantly change (Fig. 3-2; $F_{1,21} = 2.242$, $P = 0.229$), declining an average of 4.2 m (± 1.7 m SE) or 11.2 %. This resulted in average flight response distances ranging between 22.5 m and 55.2 m (average = 36.4 m (± 1.8 m SE)), which were significantly higher than pre-conditioning flight response distances (average = 36.3 m (± 1.7 m SE); $F_{1,23} = 10.584$, $P = 0.001$).

Proximity to town site during conditioning

Elk distance from the Banff town site boundary significantly increased by 224.9 m (± 72.3 m SE) or 27.5 % (Fig. 3-6; $F_{1,23} = 9.668$, $P = 0.002$) during aversive conditioning application, resulting in an average distance of 817.3 m (± 27.0 m SE) from the town boundary. Frequency of conditioning did not significantly affect this increase in distance, and neither did the covariates habituation level, wolf activity or snow depth, singly or in combination with the other variables ($F_{1,16} \leq 0.657$, $P \geq 0.430$).

Proximity to town site post-conditioning

During the 8 weeks following the end of aversive conditioning application, elk distance from the town boundary did not significantly change (Fig. 3-6; $F_{1,23} = 4.050$, $P = 0.138$), although it did decline by 125.4 m (± 20.2 m SE), or 15.3 %. Elk remained an average of 690.4 m (± 14.5 m SE) from the town site, which did not significantly differ from their pre-conditioning distance to town (average = 592.4m (± 72.1 m SE); $F_{1,21} = 1.744$, $P =$ 0.291)

DISCUSSION

The results of this research show that aversive conditioning can significantly modify elk behaviour towards humans and human-use areas, offering additional support for the results presented in Chapter 2. They also give insight into elk behavioural response to aversive conditioning at different frequencies and reveal that initial habituation level can affect subsequent elk response to conditioning treatments.

Conditioning frequency can play an important role in modifying animal behaviour (e.g., Van Haaren 1984, Knight and Cole 1995, Davison and Baum 2000). Frequency of conditioning in this research significantly affected flight response during conditioning, but did not affect town proximity. The sample sizes in this study likely were too small (n = 5) to mathematically determine finer-scale differences among conditioning frequencies, but the frequency response curve generated (e.g., Fig. 3-3) reflects a general pattern of elk behavioural response to aversive conditioning, that may permit some extrapolation to other contexts. The flight response curve for elk in Banff (Fig. 3-3) resembles the slow threshold curve (see Fig. 3-1, D), and suggests that fairly high frequencies of conditioning are needed to reach the threshold where behaviour modification begins to occur more rapidly.

Another significant predictor of flight response increase in our study was the prior level of human-habituation by the study elk, as measured by initial flight response distances. Other researchers have also reported that wildlife response to humans varies dramatically with previous exposure to similar stimuli (e.g. Knight and Temple 1995, Whittaker and Knight 1998, Hojo and Ono 2004). In our study, habituated animals exhibited larger increases in flight distance than wilder elk, and this is somewhat counterintuitive, because by definition, habituated animals should react less to the presence of humans than wilder conspecifics (Whittaker and Knight 1998). This might indicate a switch from 'habituated' behaviour to 'sensitization', which indicates an increase in response to stimuli (effectively the opposite of habituation; see Whittaker and Knight, 1998). It might also be explained in more relative terms: I defined habituated elk loosely as having initial flight response distances of less than 25 m, which is substantially lower than the minimum 35 m pre-conditioning flight distance I defined wilder elk with. Therefore, the greater relative increases in flight distance by habituated elk only raised their flight response distance to the same average flight distance that wilder elk were already at. This may indicate the existence of an upper threshold in flight response, above which animals do not increase their flight response distance given the current set of environmental variables. The interaction between conditioning frequency and habituation level further shows that wilder elk responded equally to all frequency levels of conditioning (offering further support for the existence of an upper threshold), whereas more habituated elk required at least medium-low frequencies to modify their behaviour to reach that same behavioural response as wilder elk.

The significant interaction between nearest neighbour and conditioning frequency suggests that more solitary elk perceived our chases to be more threatening when they were applied at higher conditioning frequencies. Many animals derive anti-predator benefits from living in groups (Krause and Ruxton 2002), some of which apply to the context of anti-predatory flight behaviour (e.g., Stuwe 1986, Recarte et al. 1998). This offers support for our theory (see Chapter 2) that aversive conditioning can, at appropriate frequencies, emulate aspects of predatory events.

As in our first year's research (Chapter 2), elk distance from the town site increased during conditioning again corroborating the results of Nolte et al. (2003), but was neither affected by conditioning frequency nor habituation level. This suggests the possibility of herd-level effects exerting the predominant influences on elk location (see Chapter 2). In our research, most of the elk occurred in a single large herd by late winter (e.g., for protection and energy conservation; see Geist 1982), possibly swamping individual differences in proximity to the town site boundary in response to variation in conditioning.

Overall treatment effects did not significantly decrease during the 8-week post-conditioning period but trends suggest that treatment effects may decline after some longer period of time. To managers, this indicates that aversive conditioning is capable of temporarily modifying the flight response behaviour of habituated elk, but that longer-term research is needed to determine the persistence of post-treatment aversive conditioning effects.

Wolf activity did not significantly affect elk flight response or distance to town during this winter's research. This result appears to contradict the strong effects of wolf activity observed in Chapter 2 for both response variables, but can be explained by the extremely low levels of wolf activity recorded in the Banff town site area this winter (69 % decline since last year, and the lowest level in four years).

There are two management implications for this research. First, it suggests that at least medium-low conditioning frequencies are required to begin modification of flight response in the Banff elk herd, which is readily transferable to management action. Fitting a curve to a scatter plot of my data (Fig. 3-7) suggests that a conditioning event each 13.7 days could achieve a public safety objective predicated on a minimum flight response distance of 45 m (T. Hurd, *personal communication*). Combined with regulations that prohibit people from approaching elk closely (e.g., no closer than 30 m in

Yellowstone National Park (2000)), a conditioned flight response distance of this magnitude is likely to prevent daily incidences of human-elk overlap, and reduce benign reinforcement leading to habituation (e.g. Domjan 2003).

A second implication of this research is that aversive conditioning needs to achieve much larger changes to flight distances to achieve public safety goals with more habituated elk. In other words, it may be more cost-effective to aversive condition elk before they have become highly habituated. This finding has particular significance for areas where there are no existing programs to manage ungulate behaviour. In many of these places, elk or other ungulates are encroaching on human-use areas and displaying behaviours indicative of habituation to humans (i.e. year-round residence near human-use areas, tolerance of close human approach; see also Thompson and Henderson 1998). My research showed that significantly higher gains in flight distance (suggesting greater time and cost) were required to manage highly and moderately habituated elk compared to those yet at wilder levels. I therefore strongly recommend that managers critically evaluate the habituation potential of ungulates in their jurisdiction, and proactively implement programs such as aversive conditioning as early as possible in the habituation cycle to prevent elk from reaching higher levels of habituation. Anecdotal evidence from extremely aggressive elk in the Banff area (outside the scope of this study) suggested that once elk passed beyond high habituation (defined as a lack of response to humans; see Whittaker and Knight 1998) and displayed aggression towards humans, no amount of aversive conditioning (i.e. > 200 total conditioning events per individual at a daily conditioning frequency) could reverse their behaviour, to the point where the only management options left were translocation or destruction (G. Peers, *unpublished data*). Proactive application of aversive conditioning to prevent habituation of ungulates offers both an ethically appealing and efficient solution to managers. It ensures that only the minimum amount of management intervention need be applied to wildlife to meet simultaneous objectives to maintain ecological integrity while ensuring public safety and providing opportunities for enjoyment of wildlife.

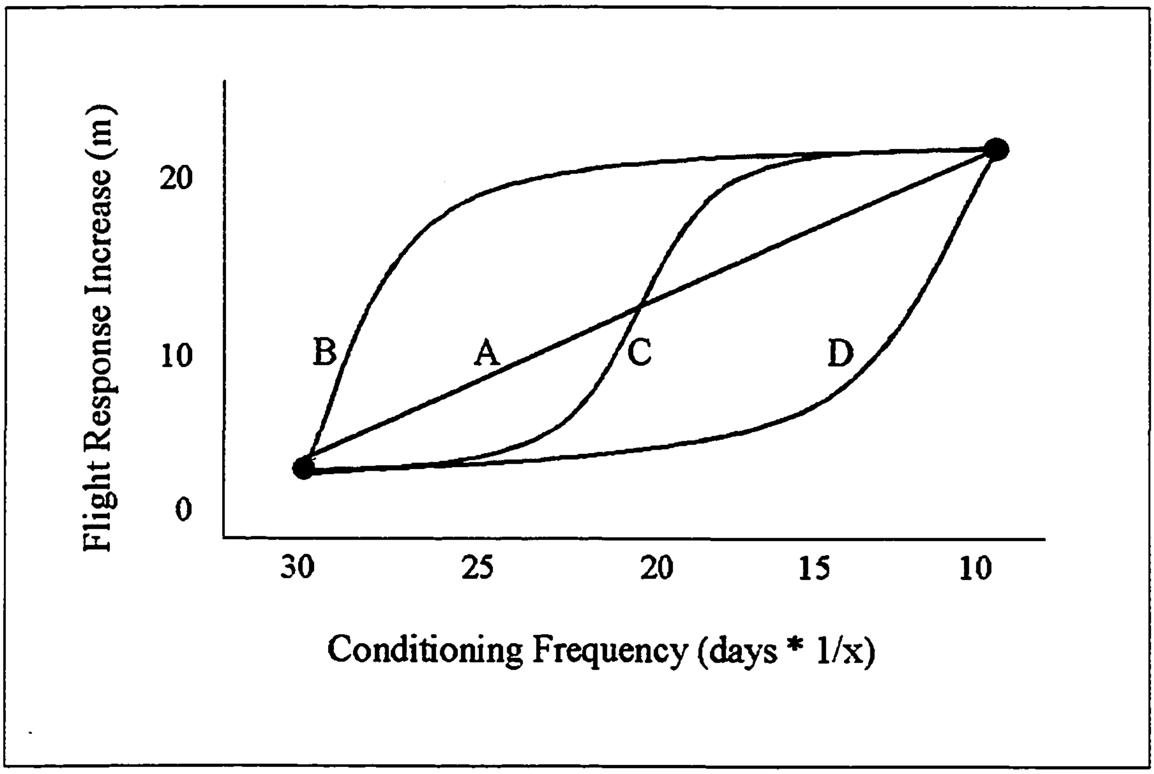


Figure 3-1. Hypothetical response curves for elk flight distance increase across a range of aversive conditioning frequencies. These four hypothetical curves represent: A) a linear response where flight distance gradually increases with increasing conditioning frequency; or a type of threshold response, where flight distance will rapidly increase after some conditioning frequency threshold is reached, i.e. B) the threshold might occur rapidly, C) at moderate frequency, D) or slowly.

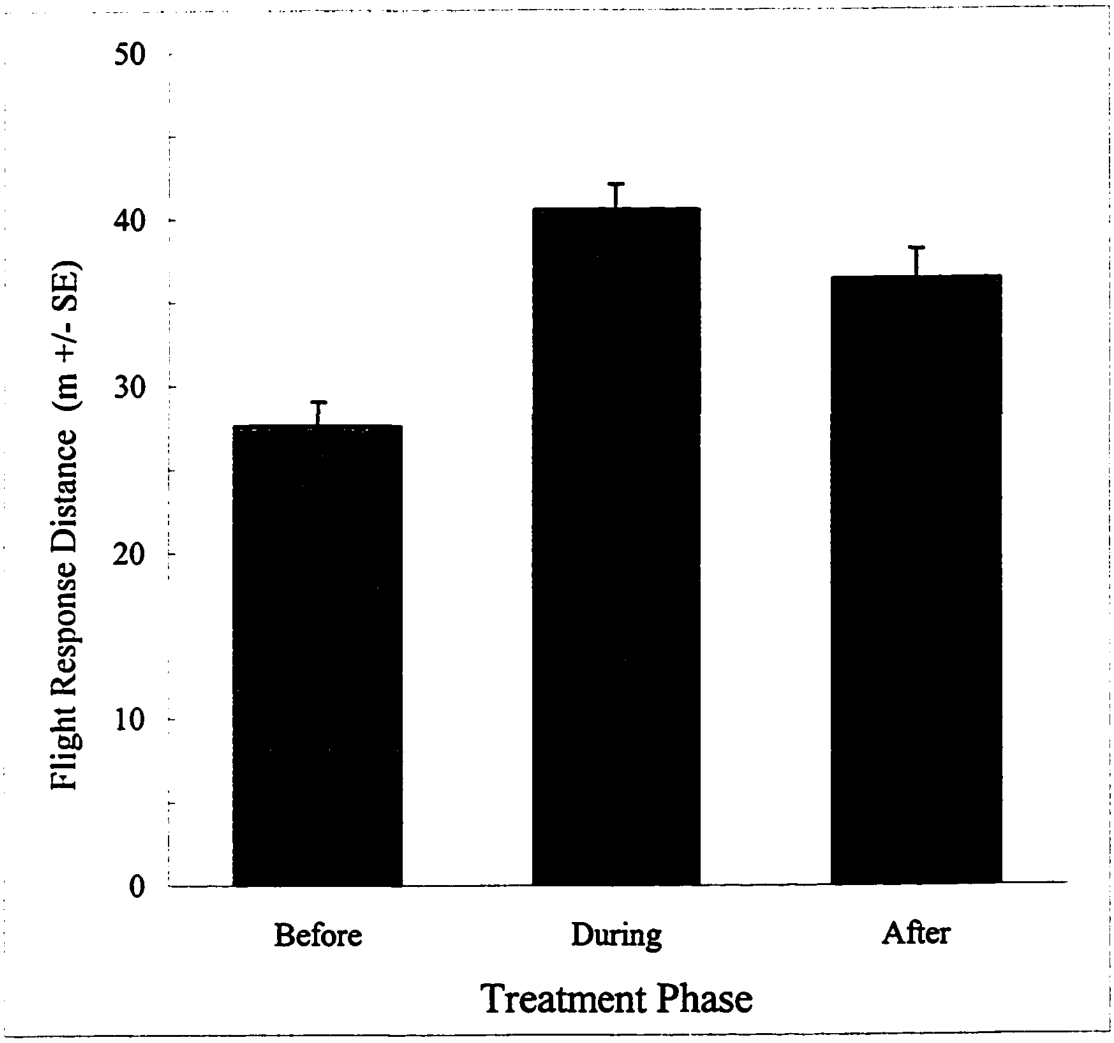


Figure 3-2. Elk flight response distance (m) before, during and after aversive conditioning application in Banff National Park.

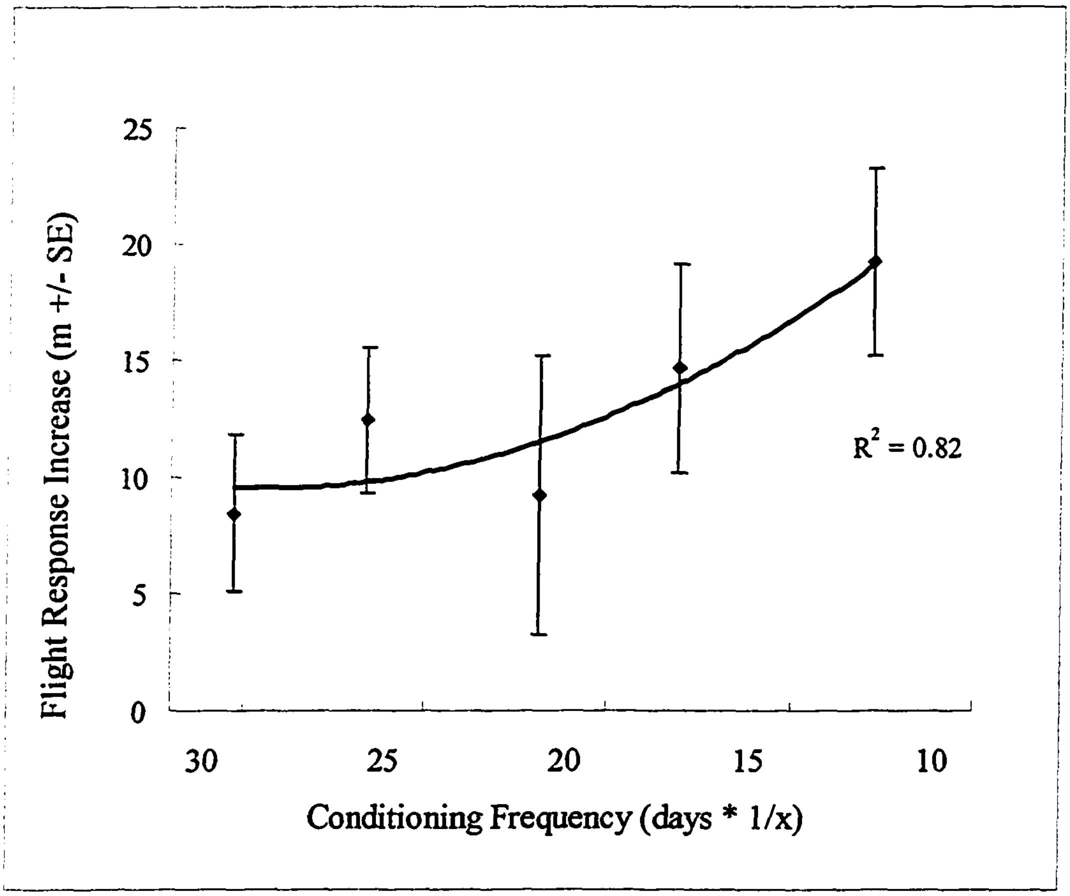
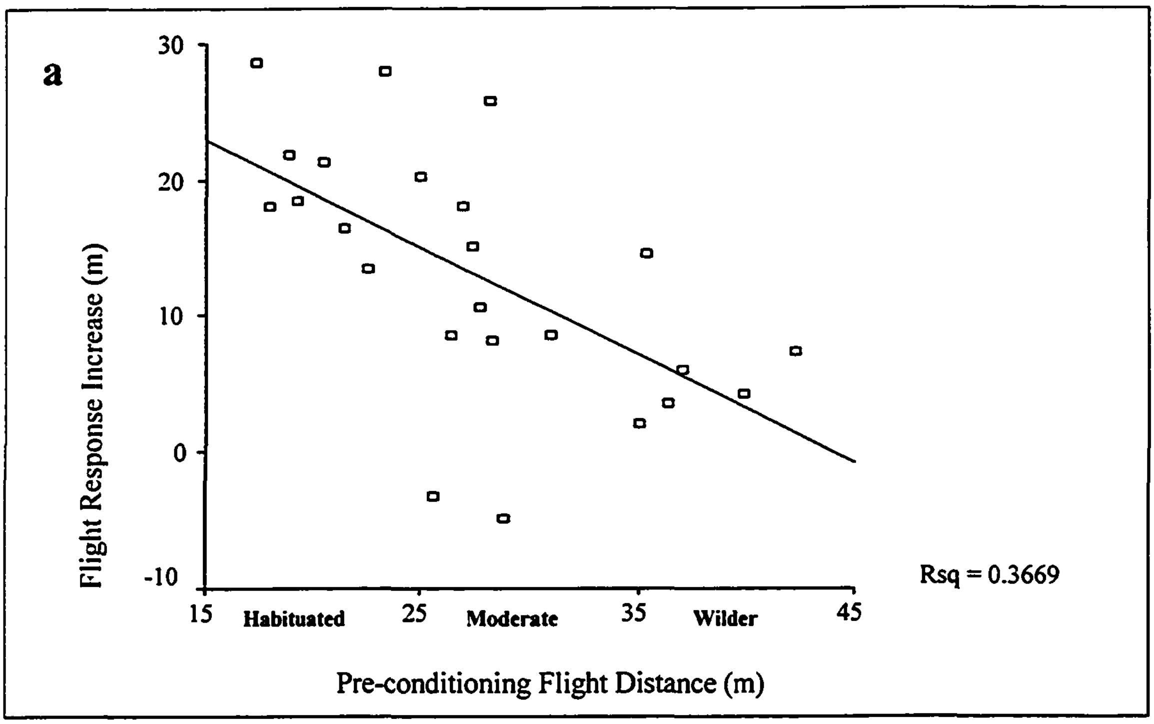


Figure 3-3. Elk flight response distance increase (m) during aversive conditioning application across a range of conditioning frequencies in Banff National Park.



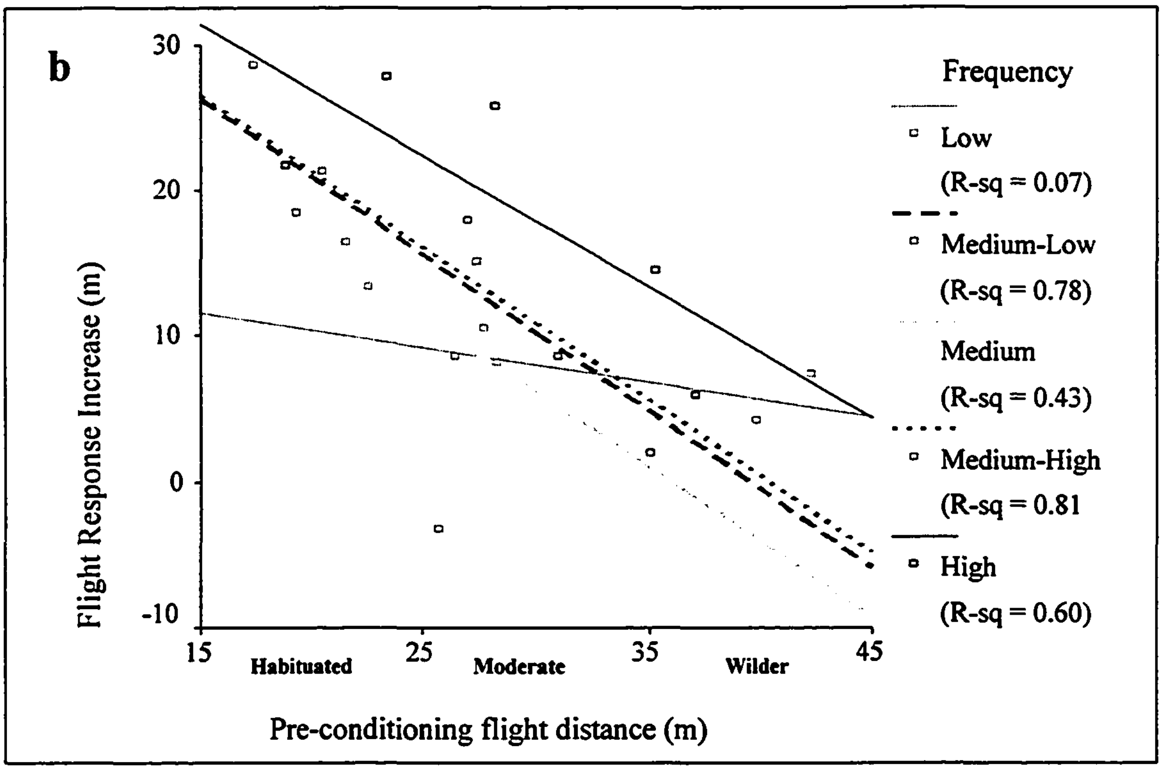


Figure 3-4. Elk flight response distance increase (m) during aversive conditioning application in Banff National Park, as a function of **(a)** elk habituation level; and **(b)** the interaction between elk habituation level and conditioning frequency.

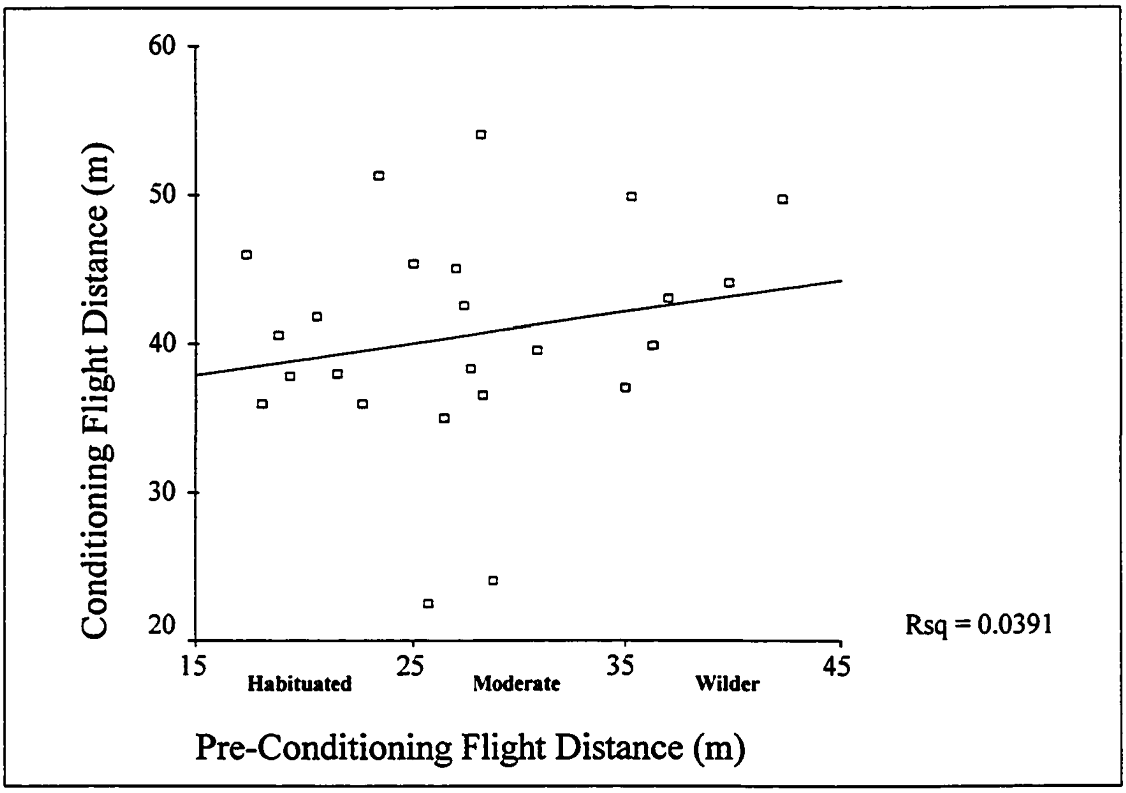


Figure 3-5. Elk flight response distance (m) as a function of elk habituation level, during aversive conditioning application in Banff National Park.

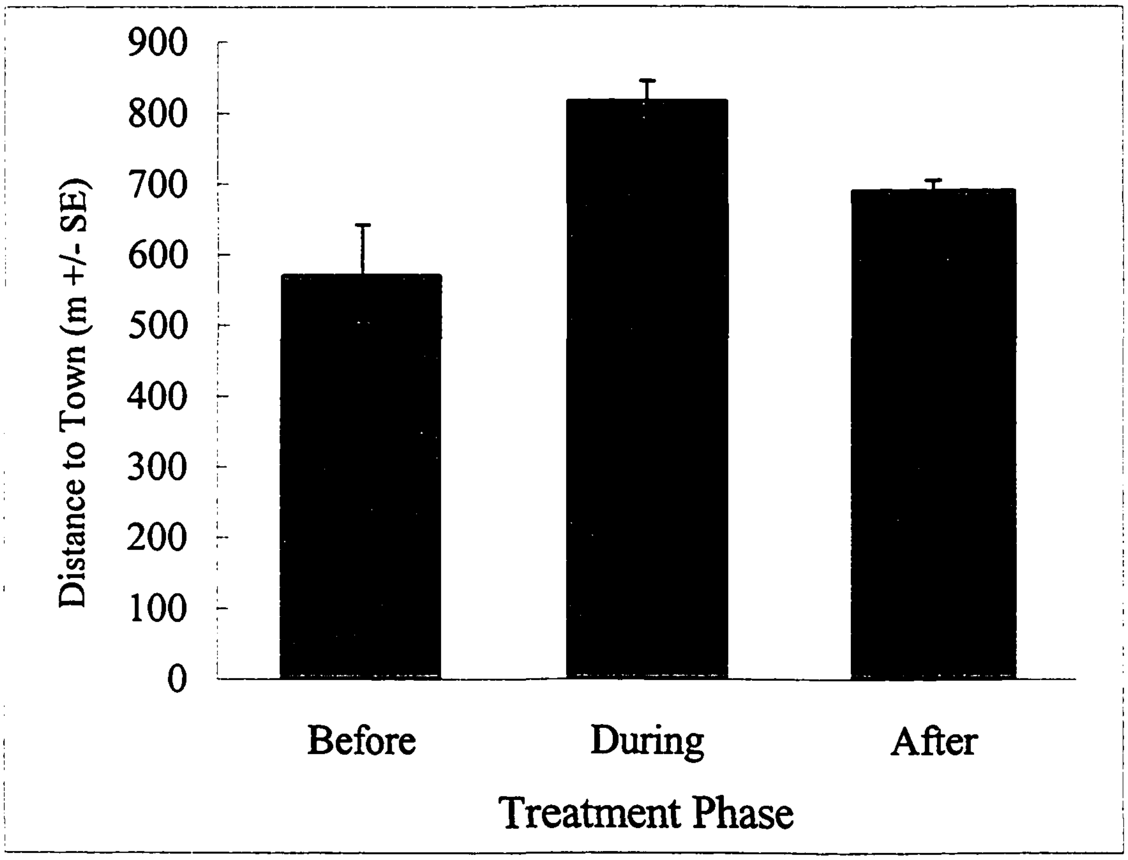


Figure 3-6. Elk distance from the Banff town site boundary (m) before, during and after aversive conditioning application.

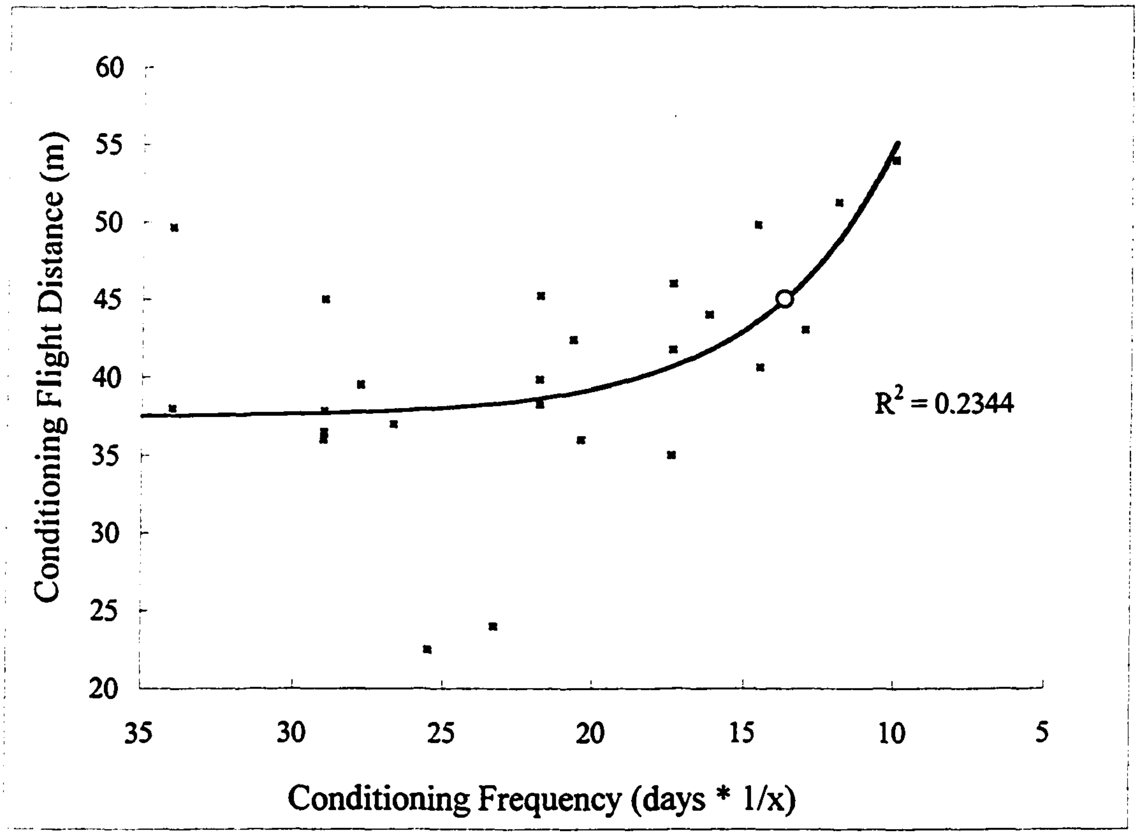


Figure 3-7. Elk flight response distance (m) during aversive conditioning application in Banff National Park across a range of frequencies. The fitted curve suggests the public safety target of 45 m elk flight response distance (O) could be met at a minimum conditioning frequency of one treatment every 13.7 days.

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CHAPTER FOUR – CONCLUSIONS

In summary, the results of my first year's research (Chapter 2) show that aversive conditioning by human and dog treatments can modify aspects of elk behaviour to prevent and manage their habituation, and that human and dog treatments performed equally well in increasing elk flight response distance from an approaching human, which is likely the most important variable describing wariness to humans. I surmise that the predator-resembling chase sequence of sufficient distance and duration is the key common element of aversive conditioning success between those two treatment types, and likely what prevented habituation to our stimuli. Neither treatment significantly affected elk vigilance. Only human conditioning significantly increased proximity to the town boundary, but this variable was less responsive when wolf activity was high. Choice of conditioning technique is therefore more likely to be decided by resource availability, current management priorities, carnivore activity levels, and perhaps public perception within a particular jurisdiction.

My second year's research (Chapter 3) showed that elk flight response distance and distance from town both significantly increased in response to aversive conditioning, supporting the results obtained in Chapter 2. Elk response to aversive conditioning across a range of frequencies is closely linked to initial levels of habituation, as measured by flight distance. Conditioning at higher frequencies generally resulted in greater flight responses, regardless of habituation level, except for the lowest frequency, which showed no response by elk of any habituation level. More habituated elk showed greater flight response increases during aversive conditioning than wilder elk, although the flight distance achieved did not differ by habituation level, suggesting existence of an upper threshold for flight response. The increase in elk distance to the town site was neither affected by conditioning frequency or habituation level, suggesting herd-level influences. In the 8 weeks post-conditioning, both behaviours modified by aversive conditioning (elk flight response distance and distance to the townsite) did not significantly change, although trends indicated that they might wane given a longer monitoring period. Unlike in our first year's research (Chapter 2), nearby wolf activity level was too low to significantly affect conditioning effects.

There are several main management implications of this work. First, I recommend that managers intent on preventing and managing habituated elk intervene in the early stages of habituation when aversive conditioning is most effective. This challenge is prevalent in many jurisdictions in North America (Thompson and Henderson 1998), which may require different aversive conditioning techniques and frequencies to address habituation levels, and meet public safety objectives. Furthermore, I recommend an adaptive management approach that adjusts the applied frequency of aversive conditioning in response to changes in elk habituation and nearby wolf activity levels.

A final important overall management implication of this research (Chapters 2 and 3) concerns the consistency of the applied conditioning treatments. It is important to ensure that conditioned elk are not subsequently given conflicting messages if and when they approach the town site. Indeed, incremental habituation would occur with every benign encounter with a human and act in opposition to the previous aversive conditioning (e.g., Geist 1982, Domjan 2003). If the confusing 'welcoming messages' provided by available forage and benign humans were reduced or prevented, elk would have less incentive to reside in the town site in the first place. The importance of minimizing food attractants in contexts that involve human-wildlife conflict is generally accepted for large carnivores (e.g., Herrero 1985, Ciarniello 1997, Burns and Howard 2003), but is often overlooked for wildlife perceived by the public to be less dangerous (Conover 1999, Orams 2002), such as herbivores (but see Rea 2003) in urban settings. Decreasing attractants would necessarily involve an integrated strategy with stakeholders to reduce use of fertilizers, plant unpalatable species of decorative vegetation, and fence key green spaces (such as playing fields) near peripheral entry points of towns. If localized fencing was used, essential wildlife movement through corridors and large expanses should still be maintained (Duke et al. 2001, Tigas et al. 2002).

The issue of close human approach of elk could be managed using methods ranging from information bulletins and education programs describing habituation risks (e.g., potential for human injury, attraction of carnivores to the town site to hunt habituated elk), to the enactment of regulations prohibiting people from closely approaching elk. Yellowstone National Park, USA is already enforcing a prohibition on approaching elk closer than 25 yards (Yellowstone National Park 2000), presumably nipping the habituation problem in the bud. In combination, these measures could greatly reduce the potential for elk habituation and subsequent conflict, and save considerable future aversive conditioning cost and effort. I believe that it is only when both sides of the habituation equation are addressed, that sustainable coexistence between humans and wildlife in Banff and other areas will be possible in the longer-term.

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