Ecological implications of personality in elk

by

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ABSTRACT

Personality has been documented in diverse taxa and growing attention is being directed towards the ecological implications of consistent variation in individual behaviour. These implications include the rise in habituation behaviour by wildlife living in human-disturbed areas, which has resulted in trophic disruptions, risks to human safety, and environmental damage. For ungulates, habituation behaviour may also contribute to global declines in migratory behaviour. The purpose of this thesis was to explore the sources of variation in the behaviour of elk (*Cervus canadensis*) and determine their relevance to changing migratory patterns. I had three specific objectives to: 1) quantify personality (also known as behavioural syndromes) in both wild and captive elk and determine whether personality can predict variations in migratory choices; 2) determine whether aversive conditioning designed to increase the wariness of elk was affected by personality type and the nature of the aversive stimulus; and 3) quantify cerebral lateralization as a potential measure of behavioural plasticity and determine its relationship to personality. I conducted research on wild elk in each of Banff and Jasper National Parks, Alberta, Canada, and on captive elk near Leduc, Alberta, from 2010 to 2013. I demonstrated the presence of behavioural syndromes in elk by identifying seven covarying behavioural traits that together delineated a gradient of shy to bold personality types. Aversive conditioning was more effective at increasing wariness in bolder elk, but extinction of this learned wariness behaviour (or recidivism) was also greater in these individuals when the aversive stimulus was removed. These patterns of responsiveness were similar whether targeted elk were subjected to conditioning chases as part of a group or when conditioning also included isolation of the target from all conspecifics. However, the isolation method significantly reduced recidivistic behaviour during the extinction period, particularly for bolder elk. Measures of laterality, determined by observing the front limb biases of elk foraging in snow, revealed that less lateralized individuals were also more plastic in their responses to both aversive and benign stimuli by people. The combination of laterality and personality best predicted the migratory choices of individual elk. Together, my results suggest that personality and laterality contribute to the responses of individuals to changing environments in diverse contexts, both natural and anthropogenic. Better methods for measuring these attributes in wild animals will make it possible for wildlife managers, conservationists, and planners to foster greater rates of coexistence between people and wildlife in an increasingly urbanized world.

PREFACE

This thesis is an original work by Rob Found. This research project received ethics approval under University of Alberta Ethics for Animal Use Protocol # 7121112.

"A devil, a born devil, on whose nature nurture can never stick."
— W. Shakespeare in *The Tempest*

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My project involved nearly 800 individual elk that often unwillingly formed the basis of my research, and while it is unlikely that any of them are ever going to read this, I want to acknowledge each one of them for never letting me forget that wild animals are individuals, and not just "things" to be used for my own purposes.

My research would have been impossible if not for the tremendous support of Parks Canada. I lack the space to thank all the resource conservation members (Banff and Jasper) that helped me over the course of this project, but I am particularly grateful to Tom Hurd, Steve Malcolm, Geoff Skinner, and John Wilmshurst, for their help with the planning and implementation of the project. Simon Ham and Blair Fyten were both incredibly helpful with my project's field logistics, but I also greatly appreciate how generous they both were with sharing their knowledge of my study site, and my study animals.

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Wildlife research is expensive, and my project would have gone nowhere if not for generous financial support from: The Alberta Conservation Association, Alberta Sports, Parks, Recreation & Wildlife Foundation, Animal Behaviour Society, Canadian Circumpolar Institute, and the Northern Alberta Chapter of Safari Club International. I was personally supported by a scholarship from the Alberta Ingenuity Fund, and NSERC Alexander Graham Bell and Canada Vanier scholarships. Also, elk tend to ignore private property boundaries, so my thanks to Banff Spring Golf Course, CP and CN rail, Jasper Park Lodge, and Pine Bungalows for allowing me access to so many non-public areas.

I want to thank all my friends and family for their enduring support, including my parents Lynn and Bob, and sister, Christine, who continues to help her little brother follow in her biologist footsteps. I also want to thank all those members of St. Clair lab that have been taking graduate student footsteps along with me, but also those "honorary lab members" Rich Moses and Jan Murie, who have helped guide us along the way.

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I can't shake the feeling I'm forgetting someone, so both thanks *and* sorry to them.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Chapter 1

Introduction

"Individuals are moved by only two levers: fear and self interest" – Napoleon Bonaparte

Napoleon may not have been referring to wildlife, but these same two levers underpin optimality models that interpret animal decision-making processes as a balance between costs and benefits, where the relative weights of fear and self-interest govern individual behavioural strategies (*sensu* MacArthur & Pianka, 1966). These balances are rarely static, particularly in stochastic environments, where risk can fluctuate (reviewed by Lima & Dill, 1990), and forage quality can be subject to environmental extremes (e.g. Gaidet & Lecomte, 2013). Humans are having a growing influence on these costs and benefits for other species, for as we move the levers of our own fear and self-interest, we often unwittingly and unpredictably do the same for other species (*sensu* Messmer, 2009). Expansion and spread of human-disturbed habitats force wildlife to either adapt or be displaced (Mysterud, 2010). Where neither displacement nor adaption is possible, the result can be individual death, and even long-term population decline. However, even successful adaptation can result in conservation complications. These can include the adoption of new and often unwelcome behaviours such as habituation (Bejder et al., 2009), or the abandonment of important behavioural processes like migration (Mysterud, 2013).

In areas where humans do not hunt animals, wildlife can pursue their self-interests in close proximity to humans (Conover, 2002). When human stimuli are mostly benign excessive fear can be costly, and there can be selection against stress responses such as vigilance (Shannon et al., 2014), or energetically expensive escape (Gates & Hudson, 1978). Habituation is the process by which animals gradually desensitize to stimuli, but also learn to discriminate between aversive and benign stimuli (Bejder et al., 2009). Habituation to humans and human-disturbed areas has been recorded in a wide diversity of species including carnivores (e.g. brown bears (*Ursus arctos*); Ohta et al., 2012), birds (e.g. Egyptian geese (*Alopochen aegyptiaca*); Mackay et al., 2014), and even insects (e.g. Madagascar hissing cockroach (*Gromphadorhina portentosa)*; Davis & Heslop, 2004).

Prey species can be particularly vulnerable to habituation because if predators show greater avoidance of humans than their prey do, predation refugia can be created in and around human-disturbed areas (Thompson & Henderson, 1998). The development of predation refugia may result in a positive feedback loop whereby refugia select for individuals that can more easily habituate, and this habituation behaviour in turn results in even greater exploitation of the refugia. Through this process, anthropogenic disturbance can result in the adoption of life history strategies involving high fidelity to human-use areas (Atwell et al., 2012), which since localized, can lead to more sedentary behaviour. This represents a dramatic shift in ecosystem function where such animals had previously exhibited more variable habitat usage in response to more stochastic environmental change, such as with season migration (Mysterud 2010).

Most ungulates have evolved to be at least partly migratory, yet migration has been declining in ungulates around the world including wildebeest (*Conochaetes spp.*; Morrison & Bolger, 2012), Mongolian gazelles (*Procapra gutturosa*; Ito, 2005), moose (*Alces alces*; Singh, 2012), and elk (*Cervus canadensis*; Hebblewhite et al., 2006). Ungulates migrate to capitalize on seasonal variation in fear and self-interest, where optimality is achieved through seasonal habitat exploitation (Albon & Langvatn, 1992). Anthropogenic disturbance may change these costs and benefits to the extent that it selects against migration. As ungulates adopt a more sedentary lifestyle they may locally overpopulate areas and begin to over-browse vegetation, disentangle from evolved predator-prey cycles, and otherwise damage ecological integrity (reviewed by White & Ward, 2010). These problems are often exacerbated in protected areas, where humans present little risk, but often-ample reward in the form of anthropogenic food (Thompson & Henderson, 1998).

Despite the apparent adaptive advantages of habituation and exploitation of human-disturbed areas, not all individuals within a given population adopt either of these behaviours (Ensminger & Westneat, 2012). Such individual variation may be the result of behavioural syndromes, which are correlated suites of behaviours defining consistent individual variation, and which have been found widely across taxa (Sih et. al., 2004). Temperament traits have previously been documented in wild ungulates (e.g. Reale et al., 2000), and comprehensive behavioural syndromes have been described in domesticated ungulates (e.g. Wesley et al., 2012). Personality traits can place evolutionary constraints on individuals (Biro & Stamps, 2008), but the impact of personality on ungulate migration and habituation behaviour remains unknown.

Personality may also be implicated in variable responses to management designed to mitigate habituation behaviour. Aversive conditioning can reverse or reduce habituation by imposing evolutionarily-relevant negative consequences on individuals exhibiting habituation behaviour (Domjan, 2010), and has been used to restore wariness in bears (Raur et al., 2003) and elk (Kloppers et al., 2005), but its overall effectiveness has been subject to substantial individual variation in responses. Habituation and responses to aversive conditioning are converse processes that both require an individual to exhibit behavioural flexibility in order to adapt to new and changing disturbance regimes (Geist, 1982).

Variation in behavioural flexibility may thus contribute to both the cause and solution to the problem of wildlife habituation.

Cerebral lateralization describes a hemispherical component to brain structure that can relate to behavioural flexibility, and so may place further constraints on life-history strategies (Vallortigara & Rogers, 2005). Lateral asymmetries in the brain are often overtly displayed through lateralized behaviours, such as handedness in humans, and have been recorded in a diversity of species including domestic dogs (Sinischalchi et al., 2010), octopi (*Octopoda* spp.; Byrne et al., 2004), and lizards (*Podarcis muralis*; Bonati et al., 2010). Lateral compartmentalization of the brain has allowed for evolutionary improvements in cognitive speed and efficiency, but selection for both strong and weak connections between the hemispheres has resulted in individual variation in the degree of this laterality (Bisazza et al., 1998). Strong laterality (i.e. weak connections between hemispheres) has been correlated with quicker responses to stimuli provided by predators (Brown et al., 2007) or prey (Siniscalchi et al., 2014), and increased physical coordination and autoimmunity (Porac and Searleman, 2006). Weak laterality, on the other hand, has been correlated with increased learning ability (Searleman, 1984; Carlier et al. 2012) and creativity (Flaherty, 2011; Lindell, 2011).

The cognitive advantages of weak laterality may be representative of increased behavioural flexibility (Guilford, 1967) or plasticity. This may predispose certain individuals to habituation behaviour, but more generally influence an individual's ability to adapt to the evolutionary novel stimuli present in human-disturbed areas, and exhibit the flexibility in wariness responses common of urban adaptors (e.g. Moller, 2010). The direction and intensity of lateralization exhibited by an individual has also been correlated with personality traits such as aggression and exploratory behaviour in other animals (e.g. Guo et al., 2009; Rogers, 2009; Reddon & Hurd, 2009). Laterality and personality scores may both be useful as predictors of habituation, migratory, and other behaviours.

I studied the implications of gradients of personality and laterality on habituation and migratory choices by wild elk in both Banff and Jasper National Parks, AB, Canada. These two large protected areas each contain central townsite areas with high-human disturbance that reduce predatory activity (Paquet et. al., 1996; John Wilmshurst, personal communication, March 10, 2010) and can provide attractive foraging opportunities (e.g. Mackenzie, 2001). Elk in Banff form a large over-wintering herd comprised of both migrant and resident elk using a winter range centered on the townsite (Figure 1-1). Elk in Jasper form three separate herds that did not mix during our study, and of which only one used the townsite area (Figure 1-2). I augmented the research of these wild populations with supplemental study of a captive born and raised population in central Alberta.

My first set of objectives was to measure a suite of personality traits that could describe an ecologically relevant behavioural syndrome in elk. I predicted that these personality traits would be correlated and consistent across contexts, and would describe a gradient of "shy" to "bold" personality types that would be further correlated with individual migratory choices. I further predicted that behavioural syndromes would also be present in captive elk, despite their more homogenous and risk free habitat, and thus indicate that personality constrains migratory choice more than migratory choices shapes personality.

My second set of objectives was to conduct aversive conditioning chases of known individual elk in order to quantify personality-dependent responses both during and after conditioning trials. I predicted that because the lower initial wariness of bold elk may indicate an inclination towards habituation, bold elk would be most responsive both during and after conditioning, with large increases in wariness offset by subsequently large recidivistic losses. Secondary to this major objective I tested two different types of conditioning treatments: in "Group" AC targeted individuals were allowed to escape along with conspecifics; in "Isolation" AC targeted individuals were isolated then driven away from conspecifics. This latter method was a novel application of modern horse training techniques that exploit ungulate social behaviour (McGreeby, 2007), which I predicted would provide a more aversive stimulus then traditional AC.

My third set of objectives was to quantify behavioural lateralization by measuring front-limb biases expressed by individual elk. I evaluated the potential contribution of laterality to models of migration by determining whether laterality was correlated with individual variation behavioural flexibility. I quantified this flexibility by measuring individual wariness changes in response to consecutive benign human approaches, and in response to aversive stimuli. I predicted the most weakly lateralized individuals would exhibit the largest changes in wariness, regardless of whether the stimuli were benign or aversive, and identify these individuals as having the greatest behavioural flexibility or plasticity. I hypothesized that individuals that were both weakly lateralized and had bolder personality types would be more likely to abandon migration.

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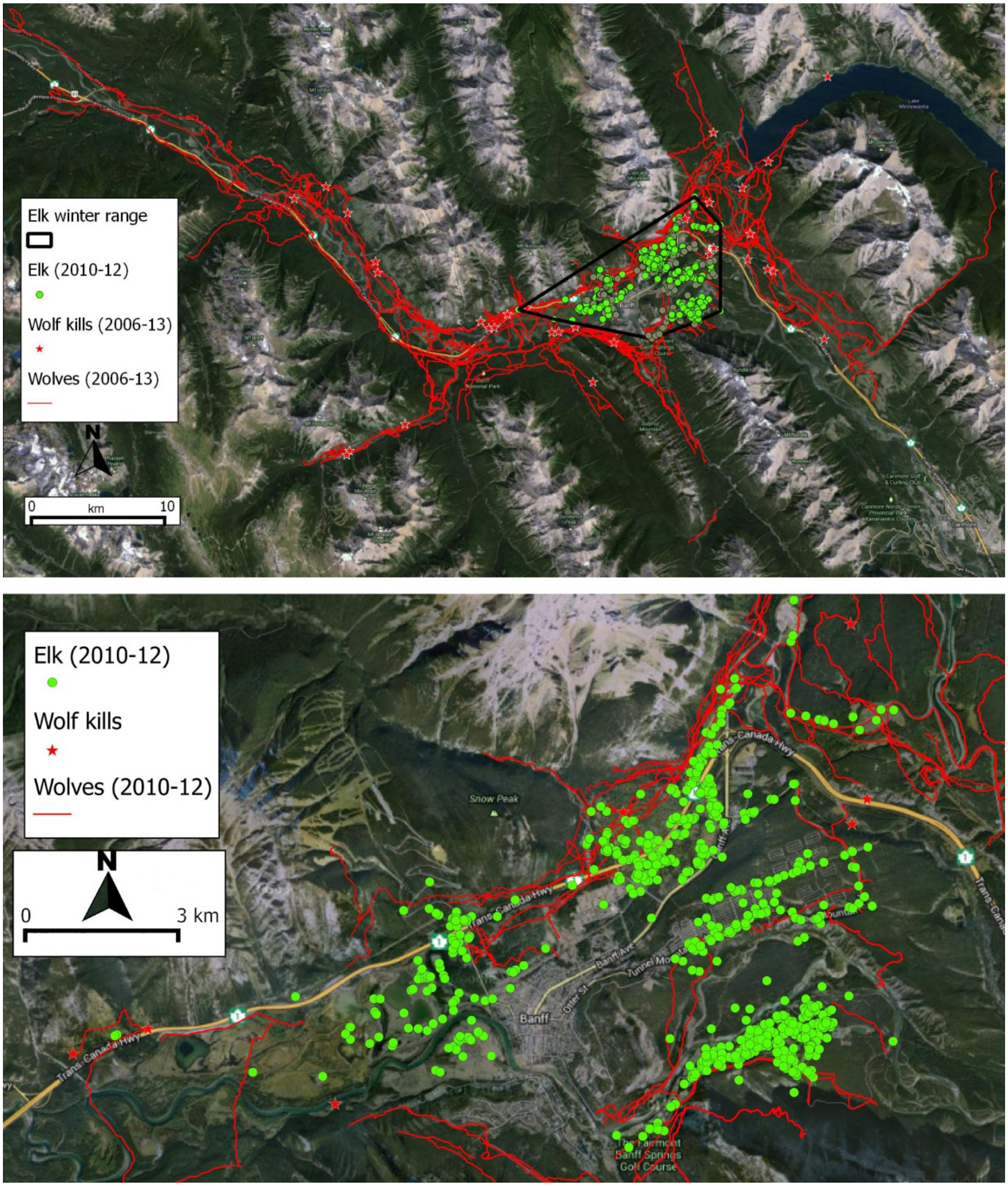

Figure 1-1. (top) Wolf tracks, locations of wolf-killed elk and deer, and daily winter locations of elk, in Banff National Park. Winter range boundary is defined by the extent of elk winter locations. **(bottom)** Close-up of elk winter range of 2010-12, showing only those wolf movements and elk/deer kills during this same time period.

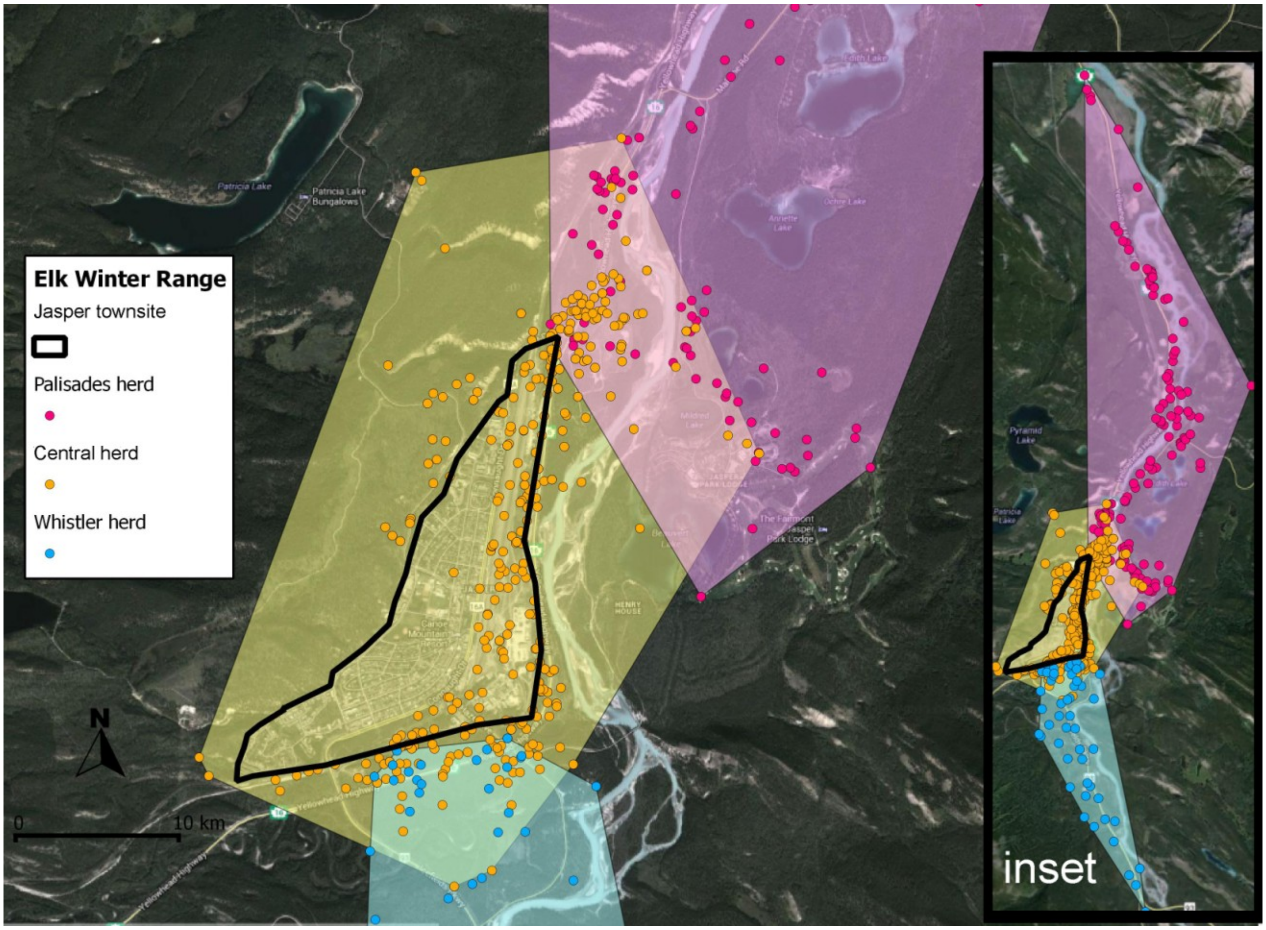

Figure 1-2. Elk locations in Jasper townsite region of Jasper National Park, AB, from December 2011 through April 2012. Inset shows full recorded extent of Palisades and Whistlers herds. Spatial overlap between herds did not coincide with temporal overlap.

Chapter 2

Behavioural Syndromes influence migratory strategies in elk.

ABSTRACT

Global declines in ungulate migratory behaviour are generating conservation problems ranging from excessive herbivory of fragile ecosystems, disrupted predator-prey relationships, to human-wildlife conflict. Many ungulate populations exhibit individual variation in the propensity to migrate, which suggests involvement of behavioural syndromes, which are sometimes referred to as personality or temperament. We identified the presence of behavioural syndromes in wild elk (*Cervus canadensis*) in Banff and Jasper National Parks and captive elk farmed near Leduc, AB, Canada. In each population, we quantified individual variation in up to seven behavioural traits with presumed ecological relevance, using a combination of passive observation, automated cameras, and exposure to novel stimuli. We used multivariate techniques to identify a behavioural syndrome in each population, from which synthesized a single but comprehensive shy-bold gradient. Bold elk had shorter flight response distances, reduced responses to novel sounds, decreased vigilance behaviour, greater exploration of novel objects, social dominance over shyer elk, and preference for peripheral positions within the herd. Among wild elk, migratory individuals exhibited the shy personality type at a 3:1 ratio, whereas resident elk (those that remained in predation refugia all year round) exhibited bold personality types at a similar 3:1 ratio. Our results suggest that behavioural syndromes interact with expanding human populations and infrastructure to contribute to the global declines in ungulate migration, potentially via the refugia people offer from predators and with concomitant damage to ecosystems. By acknowledging behavioural syndromes and targeting particular personality types, wildlife managers may be able to alter current trends in the loss of migratory behaviour in ungulate populations.

INTRODUCTION

Migration is an adaptation to environments with spatial or temporal variation in fitness costs and benefits, and has been reported in a wide variety of vertebrate species (Swingland & Greenwood, 1983). Most ungulates species are partially migratory, in which a proportion of any given population migrates seasonally, while the remainder adopt a resident strategy (Geist, 1971; Albon & Langvatn, 1992). Despite this history of variation, the proportion of migratory individuals within populations has been declining globally in ungulates species including wildebeest (*Connochaetes taurinus*; Morrison & Bolger, 2012), Mongolian gazelles (*Procapra gutterosa*; Ito, 2005), moose (*Alces alces*; Singh, 2012) and buffalo (*Syncerus caffer*; Naidoo et al., 2012), and many others. Some authors have attributed the cause of these declines to habitat destruction and fragmentation (e.g., Fynn & Bonyongo, 2010), while others attribute it to changes in patterns of predation (e.g. Middleton et al., 2013).

Migration by elk (*Cervus canadensis*) is believed to be driven primarily by seasonal changes in access to forage (Boyce, 1991). Elk that migrate to higher elevations in summer gain the advantage of richer forage and lower risk of predation, which appears to offset the energetic costs of migration (Gates & Hudson, 1978) or higher risk of predation during the migratory movement (Hebblewhite & Merrill 2011). However, the net benefits of migration are almost entirely lost where resident elk are able to exploit refugia from predators afforded by areas with high levels of human use (Thompson & Henderson, 1998; Hebblewhite & Merrill, 2009; Goldberg et al., 2014). This problem is particularly acute in human settlements within protected areas, where a lack of hunting by humans, and either the absence or greater wariness of natural predators is known to create large predation refugia (Conover, 2002). Residents in these refugia may reap further rewards through access to anthropogenic forage such as lawns, gardens, crops, and refuse (Mackenzie, 2001).

A declining proportion of migratory individuals in ungulate populations might suggest that a migratory strategy provides diminishing fitness returns in modern environments. On the other hand, the prevalence of partial migration across ungulate species implies that the advantages of migration are variable and context-dependent. This context may include the nature of individuals, which is determined by unique combinations of genes, environment, and gene-environment interactions (*sensu* Davies et al., 2012). Recently, behaviourists have paid tremendous attention to categorizing individual nature as suites of behavioural tendencies that vary consistently within individuals and across contexts (reviewed by Sih et al., 2004, Dingemanse et al., 2012).

Behavioural syndromes are presumed to develop through the co-evolution of complementary behaviours, which result from context-specific advantages that maintain multiple behavioural types, or temperaments, within populations (Dingemanse et al., 2007). Behavioural syndromes are expected to occur most often in stochastic and changing environments, where a particular suite of behaviours might be favoured in some contexts, but not others. A common way to categorize behavioural types within a single syndrome places individuals along a gradient of behavioural types, often labeled "shy" to "bold" (reviewed by Wilson et al., 1994). Recently, some authors have applied continuums of personality traits to predator avoidance and migration in wild populations. Among birds, shy individuals returned to nest sites more slowly after being threatened by a novel object (Cole & Quinn, 2014) whereas bold individuals appeared to compensate for risky behaviour by making greater use of vigilance and alarm calls (Pascual & Senar, 2014). In one fish species with facultative migration, bold individuals were more likely to migrate (Chapman et al., 2011) and those individuals were even more likely to migrate when they were in good body condition (Brodersen et al., 2014). This continuum has been shown to influence individual responses to predation and disturbance regimes in great tits (*Parus major*; Quinn et al. 2012) and migratory tendencies in roaches (*Rutilus rutilus*; Brodersen et al., 2012).

The purpose of this study was to determine the existence of behavioural syndromes in elk and to assess their potential implications for migratory behaviour. We addressed these purposes with two specific objectives, each supported by one or more predictions. First, we sought to identify a suite of behaviours that were ecologically relevant for elk fitness in environments with variation in human disturbance, forage, and predation risk. We predicted these behaviours would be correlated and consistent across varying disturbance contexts, and that there would be less variation within individuals than within populations of both wild and captive elk. Our second objective was to determine if particular behavioural types were correlated with individual migratory choices by wild elk. We predicted that bolder behavioural types would be more prevalent among animals that were resident in areas with high human use and reduced predation, and that shyer types would be more prevalent among migrants.

METHODS

Study Areas and Focal Elk Herds

Banff and Jasper National Parks (BNP, JNP): BNP and JNP are large, neighbouring protected areas within the Canadian Rocky Mountains. We conducted fieldwork in BNP from January-April of both 2010 and 2011, and in JNP from December-April 2012. Our study areas encompassed the townsites of Banff, AB (pop. 7000) and Jasper, AB (pop. 4500). These areas of high human disturbance created areas of reduced occurrence of the two main major predators of elk; wolves (*Canis lupus*) and cougars (*Puma concolor),* in both Banff (Paquet et al., 1996; Goldberg et al., 2014; Ham, 2010) and Jasper (Beschta & Ripple, 2007; John Wilmshurst, personal communication, March 10, 2010). Excluding groups of elk comprised only by males, the total population of elk overwintering in the Bow Valley during this study was 200-240 each year. This population is composed of adult females and sub-adults of both sexes, and is a mix of elk that migrate to higher elevations each spring, and those that remain in the winter range year-round. Elk using the Jasper townsite region numbered 90-100 adult females and sub-adults, and formed three discrete herds we labelled "Palisades", "Whistlers", and "Central".

Captive Population: Studies of captive-born elk were conducted on an elk ranch near Leduc, AB, Canada, during May-September, 2011, and January-March, 2013. The elk enclosures separated groups of adult females and their calves into three adjacent pens averaging 2.7 ha, with 20-40 elk in each). Coyote (*Canis latrans*) presence was detected adjacent and occasionally inside the pens, but there were no incidences of predation during the study period.

Elk Locations

We used radio telemetry and snowtracking to record the locations of wild elk each morning and used minimum convex polygons around the pooled 2010-12 locations to define winter ranges for the Banff elk herd (Figure 1-1) and three Jasper herds (Figure 1-2). Based on aerial and ground telemetry and visual identifications, individuals that were detected outside their winter ranges in July-August were labelled "migrants", while those found within the winter range were labelled "residents". The proportion of migrants to residents was stable throughout the study, although up to 9 residents were culled from the Banff population each winter. Of the three herds in JNP only the "central" herd entered the townsite, and was almost entirely non-migratory, while the two non-town herds were almost entirely migratory.

Predation

We obtained predator activity data post-hoc from snow-tracking surveys that were conducted each winter by Parks Canada in BNP, which recorded unique track detections of both wolves and cougars, along linear transects throughout the Bow Valley (methodology described by Ham, 2010). Tracking methods tended to detect tracks made within the past 24 hours, though the exact time period between predator occurrence and detection could not be known. Based on the number of snow-track detections, wolf and cougar occurrence was low along transects bisecting most areas used by elk in the winter of 2010, and declined even further in 2011. There were just three depredated elk in 2010, and none in 2011. We used the predator occurrence data from 2010 to compare the mean elk flight responses we had recorded in areas on or adjacent to predator-monitoring transects when wolf or cougar tracks were either present or absent, using a time series of means for up to three days after the most recent predator detection.

Behavioural Assays

Our assays focused on adult female elk that were individually marked with ear-tags, VHF radio collars, or both. We assayed 35 individuals in BNP in 2010, and 33 of these individuals along with 18 additional individuals in 2011. We assayed 22 elk in JNP, and 47 captive elk on the elk farm. We observed elk opportunistically throughout the day, but locations and types of data collected during each observation session were chosen non-randomly to ensure all individuals were assayed in a wide diversity of temporal and spatial contexts. We collected non-invasive data before conducting necessarily disruptive stimulus testing, and targeted no elk more than once per day. All observations and stimulus testing of elk were conducted under the approval of the University of Alberta Ethics for Animal Use Protocol # 7121112.

Individual Position Within Herd. At the start each observation session, we recorded the location of focal individuals relative to other elk in its discrete group, which was most typically only a fragment of the entire herd. We rank-ordered and assigned a numerical score for "peripheral", "intermediate" and "interior" positions. Elk that were alone or otherwise not part of an identifiable group were considered peripheral, and elk in groups of 6 or less individuals were considered peripheral or intermediate only. Using these criteria, we calculated a mean "position" score for each individual that was not dependent on group size, with higher values indicating more peripheral positioning.

Flight Response Distance. Starting from between 75 m and 125 m away an observer approached individual elk at a normal walking speed and recorded the distance at which the elk responded by moving at least 5 m. A single observer conducted all flight response trials in order to minimize the potential influence of speed, body size, or gait of an approaching human. We conducted multiple flight trials on each elk to account for seasonal, spatial, and temporal variation, and calculated mean individual values for "flight".

Response to Novel Sound Playback. To measure the responses of elk to novel sounds, we hid a speaker in vegetation and waited until groups of marked elk were in its vicinity while facing towards the sound source, and approximately equidistant from it. Sound stimuli were chosen from a wide variety of novel alarming sounds (e.g., machine gun, drum solo, power saw) and generated by a hidden observer. We recorded the order that individuals were displaced in response to the sound, considering the first to be displaced as being more responsive than the next elk to be displaced, and so on. We ranked all individuals by the order of their departure relative to all other individuals in that measured group, and combined the results from all trials to infer the relative responsiveness of all individuals. Where we could not directly compare two individuals, we inferred the rank of their responsiveness using results from trials where each individual was compared to common individuals. If all individuals responded simultaneously, or not at all, the trial was eliminated from further analyses. These data were collected in BNP only.

Exploration of Novel Objects. We selected as novel objects items that were foreign to wild elk habitat, and were expected to elicit a range of individual behavioural responses from neophobia to neophilia (for examples see Appendix, Figure A-1). We placed these objects throughout our study area, each positioned 7 m away from a motion-activated camera and changed both the camera site and novel object after each visit by any group of elk. We categorized each individual elk visit along a gradient of exploratory behaviour: 1 = visited the site and looked at but did not approach the object; 2 = approached object; 3 = investigated object to within head-length of object; 4 = physically interacted with the object. We used the means of these scores to calculate an "exploration" value for each individual.

Social Hierarchy. We recorded the results of all dyadic encounters between marked adult females where overt aggression resulted in the displacement of one elk. We categorized the displacing elk as "dominant" and the displaced animals as "submissive", and used the collective results to delineate a dominance hierarchy for all marked elk. We decided ties between marked elk by using their respective dyadic outcomes with unmarked elk. If direct encounters between two elk had opposite outcomes, we assigned the same rank to both individuals.

Vigilance Behaviour. We used a high-definition video camera to film groups of grazing elk for focal samples of 10 minutes, and then watched the videos to determine precise time budgets for individuals. We differentiated multiple forms of vigilant or potentially vigilant behaviour, such as "pseudo-vigilance" (Fortin et al., 2004), and apparently vigilant behaviour that video analysis ultimately revealed to be social or rumination behaviour. Analysis later showed vigilance and pseudo-vigilance were correlated, and so our vigilance metric was a combination of the two. We were not able to collect vigilance data in our captive population.

Lead Elk. In BNP (2010 only), when large enough groups of elk moved from one discrete habitat patch to another the herd typically formed in single or double file with clear leaders at the heads of these lines. Each time we observed such movement we recorded the identity of the lead elk, and used the sum of occurrences as that individual's value for "leading".

Data Analysis.

We used principal component analysis (PCA) to quantify elk behavioural syndromes, using eigenvectors to demonstrate the relationships between each of the personality traits we measured, and reducing this information to two orthogonal axes upon which we could plot the relative positions of each individual elk within two dimensions of any existing behavioural syndromes. Because some behavioural metrics were inherently non-normal, and thus discouraged the use of the PCA axes as independent variables for further analysis, we employed NMDS to create a single dimension defining a gradient of personality types. We derived separate gradients for each population and year. We used this metric of "personality" as an independent variable to determine the effect of elk age on personality, using captive elk aged 3 to 14 years old. We also regressed the personality values from the Banff population in 2010 values against 2011 values, using only those elk assayed in both years, in order to quantify the interannual consistency of personality within the same individual elk (for trait-trait comparisons, see Appendix, table A-1). We also used logistic regression to determine if this personality gradient was correlated with the subsequent choice to either migrate or not. We used two-tailed t-tests to compare the mean personality scores and individual behavioural means of both migrants and residents, and to compare mean elk flight responses in the absence or presence of predators. Because all possible comparisons are reported in the results, we did not make any corrections to *P*-values for multiple comparisons (following Saville, 1990; Rothman, 1990). We used $\alpha = 0.05$, and performed all statistics were with Stata 11.1 (Statacorp).

RESULTS

Behavioural Correlations

In BNP (2010) we recorded 5 to 18 flight response trials per elk ($\bar{x} = 9.4$), 239 total sound stimulus dyads, 158 dominance interactions, 51 incidents of leading behaviour, 5 to 16 time budgets and positions-in-herd per elk ($\bar{x} = 9.6$), and presented 66 unique novel objects that were visited by at least one elk. In BNP (2011) we recorded 4 to 19 flight response trials per elk ($\bar{x} = 13.1$), 333 total sound stimulus dyads, 334 dominance interactions, 4 to 20 time budgets and individual positions ($\bar{x}$ = 10.6), and presented 144 novel objects. In JNP we recorded 6 to 15 flight trials per elk ($\bar{x}$ = 11.1), 90 dominance interactions, 4 to 30 time budgets and individual positions ($\bar{x}$ = 21.3), and presented 61 novel objects. On the elk farm, we recorded 6 to 16 flight response trials and positions-in-herd per elk ($\bar{x}$ = 11.9), 101 dominance interactions, and presented 27 novel objects.

We found PCA reduced the data orthogonally to axes that accounted for 72.0% (BNP 2010), 80.2% (BNP 2011), 83.4% (JNP), and 91.5% (captive) of the variation within the dataset (Figure 2-1). In BNP and JNP all behaviours loaded most heavily onto the first factor (F1, horizontal axis) except for vigilance, which loaded most heavily onto F2. Correlations between behaviours are presented in Table 2-1. The correlations between these behaviours thus elucidate a behavioural syndrome in which a single dimension (F1) can be interpreted as personality gradient from what we have labelled "shy" to "bold", from negative to positive values along F1, with vigilance as part of a secondary personality dimension. Eigenvalues depicting the relationships between each behaviour show that for each population, elk with the higher scores on the boldness axis more dominant, more exploratory, adopted more peripheral positions within the herd, had lower flight response distance, were less responsive to novel sounds, and were more likely to lead groups of elk (Figure 2-1).

Consistency of Personality Across Contexts

The second part of our first objective was to demonstrate that these behavioural correlations are consistent across contexts, and thus constituted a true behavioural syndrome gradient. To conduct further analysis on a personality gradient less vulnerable to non-normal data we used NMDS to reduce the data to a single dimension we termed "personality" (BNP 2010; n = 35, loss criterion = 0.011: BNP 2011; n = 50, loss criterion = 0.0075: JNP; n = 22, loss criterion = 0.0076: Captive; n = 70, loss criterion = 0.0071), and used these personality gradients as variables in the following two analyses. Individual age at the time of assay did not have an effect on personality in captive elk 3 to 14 years old ($r^2 = 0.006$, $F_{69} = 0.43$, $P = 0.52$; Figure 2-2). In BNP elk values from the 2010 personality gradient did not differ from their respective values on the 2011 personality gradient ($F_{32} = 2633$, $R^2 = 0.99$, $P < 0.0001$; Figure 2-2).

We could not compared predator activity to our gradient of personality types, but found that individual elk flight response distances increased from 40.4 m to 46.3 m in areas and on days where wolf tracks were detected (SE = ± 8.7 m, $t_{1,50}= 2.75$, $P < 0.01$), but only to 42.5 m if the detected predator was a cougar ($t_{1,28} = 0.69$, $P = 0.49$). This effect of wolf activity diminished over time, and elk flight responses were greater but not significantly so one day after (± 5.1 m, $t_{1,40} = 1.73$, $P = 0.092$), two days after (±3.9 m, $t_{1,37} = 1.45$, $P = 0.16$) or three days after (± 0.6 m, $t_{1,35} = 0.31$, df = 35, $P = 0.76$) a wolf track was detected.

Personality and Migratory Strategies

In the Banff population migrant elk (n=29) had 40% higher mean flight responses ($P < 0.001$), 67% higher mean ranking in response to novel sounds ($P < 0.01$) compared to resident elk (n=21). Resident elk had 50% higher exploration scores ($P < 0.01$), 9% higher position scores ($P < 0.01$), and a mean dominance ranking that was 61% higher than migrant elk ($P < 0.01$). Vigilance was 36% higher in migrants and residents, but this was not significant ($P = 0.10$). A comparison of separate PCA and factor loadings for migrants versus residents showed that behaviours relating to anthropogenic and novel stimuli (i.e. flight from humans, novel objects and sounds) made larger contributions to describing the personality in migrants, while those relating to non-anthropogenic and non-novel stimuli (i.e. vigilance, position in herd, social hierarchy) made larger contributions to the personality in residents (Table 2-2).

Mean positions along the F1 personality gradient were significantly higher for residents than migrants in all populations: BNP 2010 (Res. = 1.10, Mig.= -0.73; $t_{1,33} = 3.03$, $P = 0.005$); BNP 2011 (Res. = 1.16, Mig. = -0.84; $t_{1,48} = 3.89$, $P < 0.001$); JNP (Res. = 0.68, Mig. = -1.46; $t_{1,20} = 3.08$, $P < 0.01$). However, there was no difference between the mean values for F2 in BNP 2010 ($t_{1,33} = 0.97$, $P = 0.39$), BNP 2011 ($t_{1,48} = -0.41$, $P = 0.68$) or JNP ($t_{1,20} = 1.51$, $P = 0.15$). In BNP we found that personality values were correlated with individual migratory choices in the summer following data collection in both 2010 (LL = -18.54, χ^2= 7.17, n = 33, $P < 0.01$) and 2011 (LL = -28.95, χ^2= 10.13.30, n = 50 $P < 0.01$. We use the median personality value along the F1 shy-bold gradient to halve the population into "bold" versus "shy" personality types, and found migrant elk were shy:bold at approximately a 3:1 ratio in both 2010 and 2011, while resident elk were shy:bold at a 1:3 ratio (Figure 2-4).

DISCUSSION

Our first objective was to determine if elk had a covarying suite of behaviours that were consistent across contexts, which thus would constitute a behavioural syndrome. We found that 7 separate elk personality traits were correlated and consistent within individuals, between years, and independent of individual age. While these individual personality traits do not all necessarily describe separate gradients of "boldness", we used multivariate techniques to delineate this behavioural syndrome into a gradient of personality types best described along a shy to bold axis. Bolder elk were characterized by lower flight distances, reduced responsiveness to sounds, occupancy of more peripheral positions within groups, greater exploration of novel objects, social dominance over shyer conspecifics, and were most likely to lead other elk to new habitat patches.

Our second objective was to examine the relationship between personality and individual migratory choices. The behavioural syndromes we quantified were evident in two partially migratory populations, but also a captive population devoid of migration and any of the selective pressures of predation and forage variability. Regardless of whether the migrants and residents within wild herds were seasonally mixed (Banff) or permanently separate (Jasper), individuals that migrated each spring to allopatric ranges had lower mean scores on the shy-bold personality gradient than resident elk. This indicates an increased likelihood that migrants have shy personality types, whereas individuals that did not migrate and instead resided in and around townsite predation refugia year round were more likely to have bold personality types.

Individual personality scores in Banff elk did not change between 2010 and 2011, indicating a consistency of behavioural expression despite seasonal and yearly fluctuations in disturbance, weather, predation, and forage availability. While we found that wolf activity increased average elk flight response distance measured within a day of the wolf detection, the mean flight response for all elk actually increased in 2011 despite a decrease in predation over all (Ham, 2011). The persistence of personality in habitat with homogenous disturbance and forage, and no predation, may be a further indication of a permanence and thus heritability of personality type that is similar to what has been found with personality traits in bighorn sheep (Reale et al. 2009), and also in humans (Penney et al. 2011). While we had no age data for wild elk, age had no effect on personality in captive elk. This resembles studies in humans (Caspi 2005), and suggests personality development may be a less adaptive process than previously thought (see Sih et al. 2012). Personality in elk may thus influence future migratory choices more than past migratory choices shape personality.

A resident strategy may favour bolder individuals because their reduced responsiveness to anthropogenic stimuli, such as to human approaches and novel sounds and objects, allows them to reap the benefits of proactive exploration and opportunistic edge positions within the herd. The converse situation arises outside of refugia, where there is little novelty to encounter and exploit, human disturbance is low, but predators are more frequently encountered (Muhly et al. 2011). These types of areas, as would be found along migratory routes (Hebblewhite & Merrill, 2009) and at migration destinations far from the valley bottoms where human disturbance is typically highest (Thompson & Henderson 1998), may favour shy elk, whose personalities tend towards greater risk aversion, higher sensitivity to disturbance, and quicker responses to stimuli. Declines in ungulate migration have been linked to broad changes in habitat that appear to tip the balance of costs and benefits in favour of a resident strategy for many ungulate species (Middleton et al. 2013).

The existence of behavioural syndromes in elk can have wide reaching importance for the conservation and management of other ungulates and megaherbivores. Personality-based management may improve the efficacy of captive-reared reintroductions of endangered species such as woodland caribou and black rhino (suggested by Watters & Meehan, 2007). For example, elk translocated from the Banff townsite had poor survival when introduced into predator-risky habitats, compared to elk translocated from other risky habitats (Frair et al., 2007). While the authors attributed their results to experience vs.

predator naïveté, if those Banff townsite elk were predominantly bold, as our study suggests, it may have been their own personalities that limited their translocation success. Because a wide range of behavioural types exist even in captive populations, we could use behavioural syndromes to predict and choose which individuals will have the greatest success in areas of high human disturbance, or those areas where the limiting factor is high predation (Bolger et al., 2008).

Because behavioural traits have co-evolved to create different personality types where different and changing risk and disturbance regimes favour different suites of characteristics (Smith & Blumstein, 2008) selection against migratory behaviour may also constitute an unintentional selection for bolder personality types, and against shyer personality types. Anthropogenic selection for or against specific behaviours can have unintended management consequences when co-evolutionary relationships between behaviours are unknown, or poorly understood. For example, artificial selection for a lack of fear of humans in captive junglefowl unintentionally increased the prevalence of co-evolved behaviours such as neofilia (Agnvall et al., 2012). While exploration can clearly be to the benefit of herbivores, such behaviour near farms could lead to crop damage that is at the expense of humans (Brook, 2009), or when on roadways may result in increases in wildlife collisions that are to the detriment of both elk and humans (Conover, 2002). Perhaps more seriously, habituated wildlife may begin to consider humans as competitors, and selection for social dominance can result in aggression towards humans that presents a serious risk to public safety (Geist, 1982). For example, one elk in our study was involved in a number of public safety incidents, one that required hospitalization, and this elk was later identified as the boldest and most dominant in the population. However, very dominant and lead elk were also found amongst migrants, so the extension of social competition from elk to humans may be a further characteristic of resident elk, and possibly develop through repeated experience with humans.

The link between personality and selection for particular life-history strategies has been made in other species (Reale et al., 2007). Much like the exploratory behaviour shown by resident elk in our study, other researchers have found resident warblers (*Sylvia melanocephala*) exhibited more exploratory behaviour than migratory warblers (*S. borin*; Mettke-Hoffman 2005). Boldness traits have also been correlated with migratory choices in another species with facultative migration, the roach (*Rutilus rutilus;* Chapman et al., 2011). Seemingly contrary to our results, it was the "shy" roaches that were resident and the "bold" roaches migratory, but the roach's migration is used to escape the higher levels of predation that resident roaches experience. In both roaches and elk it is the individuals with more risk-averse personalities that, unsurprisingly, adopt the strategy with the least risk.

Distinct personality types develop in environments with heterogeneity in resources and risk, where different suites of correlated behaviours are favoured in different contexts (Sih et al., 2012), but this is not necessarily always at the expense of other personality types. During our study residents were bold:shy at a 3:1 ratio, while in migrants the ratio was 1:3, suggesting personality may be implicated in frequency-dependent selection of migratory strategies. Theoretical models in behavioural ecology predict the presence of so-called mixed evolutionarily stable strategies that exist in populations with comparable fitness only at specific proportions of individuals, such as between co-operators and defectors (Franz et al. 2013), and between migratory and non-migratory birds (Lundberg, 2013). In this vein, our results may outline a conceptual model of the frequency-dependent complementarity of shy and bold personality types in which variations in optimality depend not only on one's own migratory choice, but those of conspecifics.

Understanding this frequency dependence and the concept of personality variation as a potentially evolutionary stable strategy (e.g. Patrick et al., 2013; Brodersen et al., 2014) will lead to even greater insights into the individual weighing of costs:benefits that make personality-targeted management such a promising concept. This could lead us away from coarse management strategies that select for or against whole personality types – often unwittingly – and towards refined techniques that target only the specifically undesired behaviours, and thus maintain the personality diversity inherently important for the longterm survival of populations (reviewed by Wolf & Weissing, 2012). Aesop once taught that persuasion is better than force (translated by William Caxton, 1484), but conventional management continues to try to force wildlife to behave in certain ways they do not want to. Perhaps greater success might be achieved by exploiting personality differences to consistently disadvantage resident ungulates, and thus persuade an increasing proportion of them to make their own choices to migrate.

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Table 2-1. Correlation matrix for behavioural traits comprising elk behavioural syndromes, in wild (Banff and Jasper) and captive elk. *P*-values below 0.050 are bolded.

Banff National Park (2010)

	flight	**vigilance**	**position**	**exploration**	**sound**	**dominance**
flight	**1**	0.151	**-0.522**	**-0.415**	**0.867**	**-0.757**
vigilance	0.151	**1**	-0.221	-0.100	**0.344**	-0.003
position	**-0.522**	-0.221	**1**	**0.452**	**-0.436**	**0.617**
exploration	**-0.415**	-0.100	**0.452**	**1**	-0.281	**0.583**
sound	**0.867**	**0.344**	**-0.436**	-0.281	**1**	**-0.693**
dominance	**-0.757**	**-0.003**	**0.617**	**0.583**	**-0.693**	**1**

Banff National Park (2011)

	flight	**vigilance**	**position**	**exploration**	**sound**	**dominance**
flight	**1**	**0.423**	**-0.716**	**-0.666**	**0.920**	**-0.832**
vigilance	**0.423**	**1**	**-0.440**	**-0.408**	**0.414**	**-0.437**
position	**-0.716**	**-0.440**	**1**	**0.422**	**-0.783**	**0.597**
exploration	**-0.666**	**-0.408**	**0.422**	**1**	**-0.576**	**0.625**
sound	**0.920**	**0.414**	**-0.783**	**-0.576**	**1**	**-0.765**
dominance	**-0.832**	**-0.437**	**0.597**	**0.625**	**-0.765**	**1**

Jasper National Park (2012)

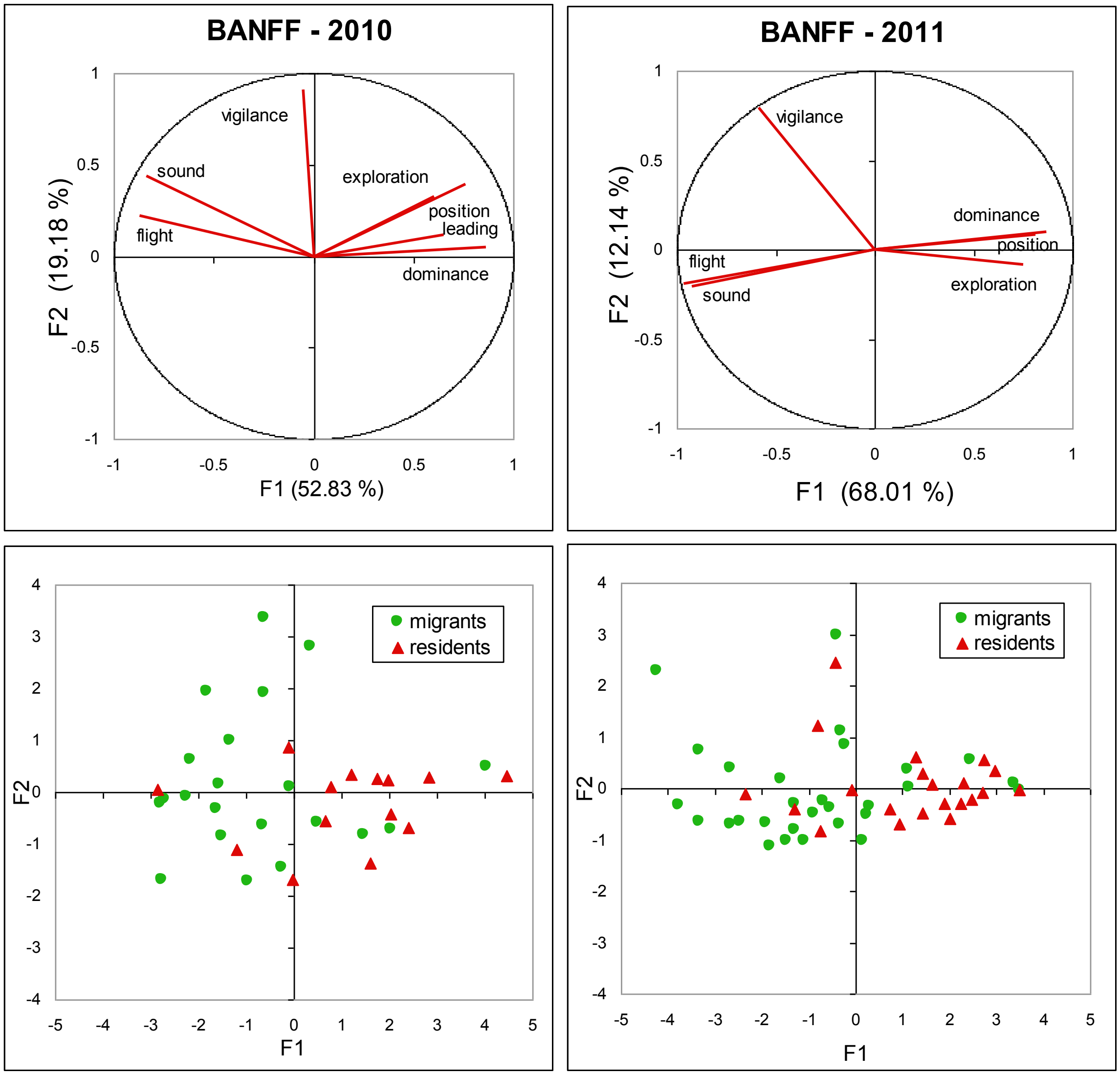
	flight	**dominance**	**position**	**exploration**	**vigilance**
flight	**1**	**-0.722**	**-0.567**	**-0.579**	**0.534**
vigilance	**0.534**	**-0.399**	-0.102	-0.049	**1**
position	**-0.567**	**0.710**	1	**0.551**	**-0.102**
exploration	**-0.579**	**0.757**	**0.551**	1	**-0.049**
dominance	**-0.722**	1	**0.710**	**0.757**	**-0.399**

Amberlane (Captive)

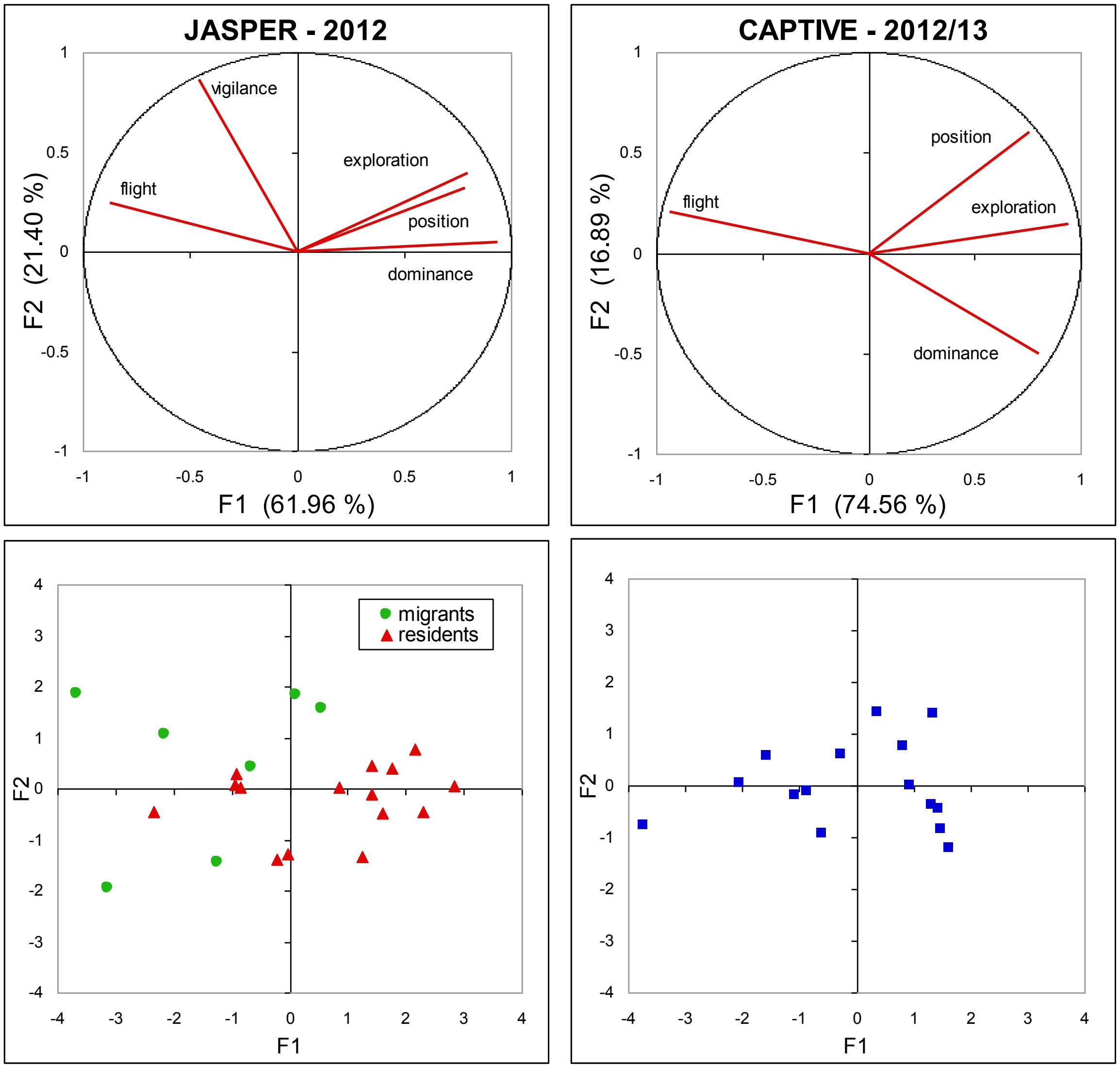
	flight	**dominance**	**position**	**exploration**
flight	1	**-0.777**	-0.541	**-0.878**
position	-0.541	0.383	1	**0.726**
exploration	**-0.878**	**0.612**	**0.726**	1
dominance	**-0.777**	1	0.383	**0.612**

Table 2-2. Percentage contribution of each variable to F1 and F2 PCA axes, for migrant and resident elk. Individual behaviours composing elk behavioural syndromes are grouped by relation to (i) anthropogenic and novel stimuli and (ii) non-anthropogenic and non-novel stimuli, including predation detection and social interactions. Bolded values show personality factors that have (i) greater influence on migrants than residents, and (ii) greater influence on residents than migrants.

		Migrants		**Residents**	
		F1	**F2**	**F1**	**F2**
(i)	**flight**	***23.489***	3.894	21.965	1.600
	exploration	***14.744***	2.178	7.158	58.298
	sound	***22.485***	1.520	20.957	8.332
(ii)	**vigilance**	6.460	84.770	***11.107***	23.485
	position	14.775	3.080	***17.286***	5.610
	dominance	18.047	4.558	***21.527***	2.676


BANFF - 2010
vigilance
sound
exploration
position
leading
flight
dominance
F2 (19.18 %)
F1 (52.83 %)
1
0.5
0
-0.5
-1
-1
-0.5
0
0.5
1
BANFF - 2011
vigilance
dominance
position
flight
sound
exploration
F2 (12.14 %)
F1 (68.01 %)
1
0.5
0
-0.5
-1
-1
-0.5
0
0.5
1
● migrants
▲ residents
F2
F1
4
3
2
1
0
-1
-2
-3
-4
-5
-4
-3
-2
-1
0
1
2
3
4
5
● migrants
▲ residents
F2
F1
4
3
2
1
0
-1
-2
-3
-4
-5
-4
-3
-2
-1
0
1
2
3
4
5

a)



b)

Figure 2-1. PCA results for personality traits composing behavioural syndromes in elk in (a) Banff and (b) Jasper and a captive population near Wetaskiwin, AB, showing **(top panels)** eigenvectors for each personality trait and **(bottom panels)** positions of individual elk along factor axes. Individuals remaining in winter range all year are "residents" (red) compared to "migrants" (green).

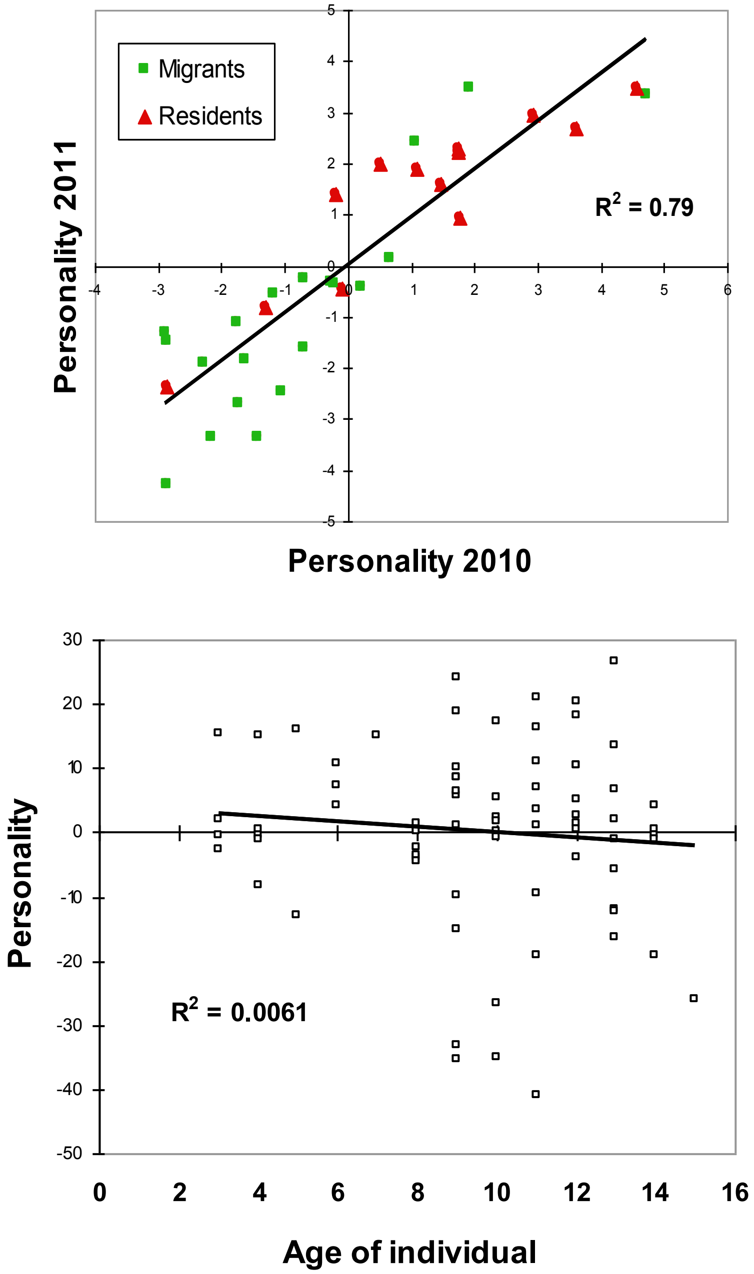


Figure 2-2. (a) Comparison of elk (wild) personality in 2010 and those same individuals in 2011 and **(b)** effect of age (X-axis) on personality (Y-axis) in captive elk. Personality gradients are dimension 1 from NMDS analysis.

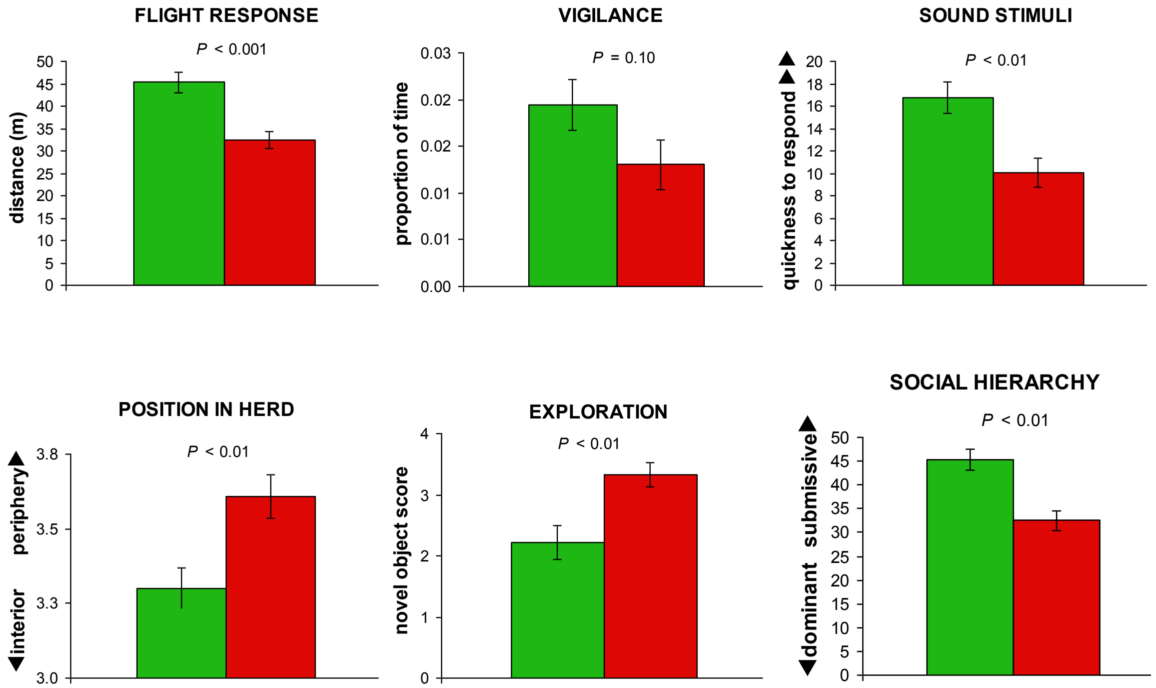


Figure 2-3. Mean scores for correlated individual behavioural traits composing elk behavioural syndromes, for each of migrant (green) and resident (red) adult female elk in Banff, AB. All measures were taken when residents and migrants form a single overwintering herd. Y-axes for Sound Stimuli and Social Hierarchy represent rank ordination. Y-axes for Position-In-Herd and Exploration represent average scored values for those behaviours. P-values are for two-tailed *t*-test results with df = 48. Error bars are SE.

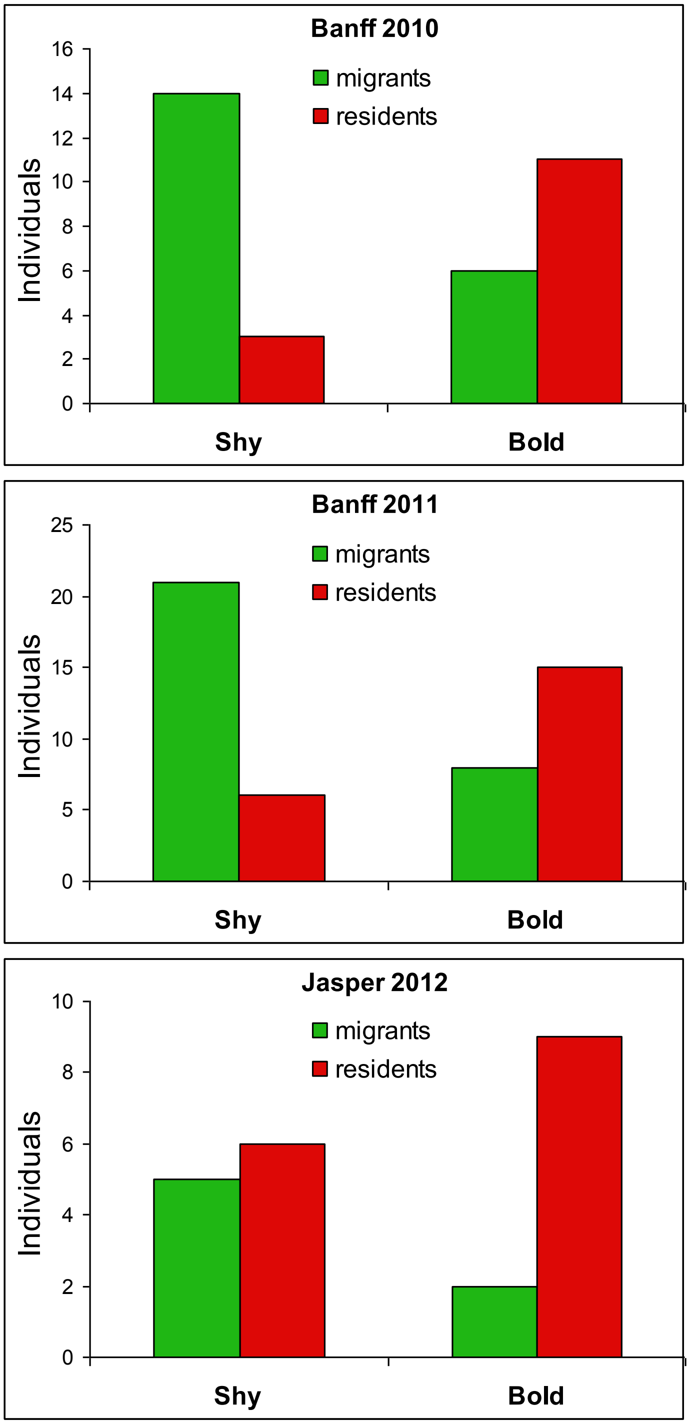


Figure 2-4. Population proportions of migrant and resident elk with shy or bold personality types, in Banff National Park, AB in 2010 and 2011, and Jasper National Park, AB in 2012. Global medians of personality scores for each population were used to divide each population in shy and bold halves.

Chapter 3

Elk (*Cervus canadensis*) personality influences responsiveness to aversive conditioning

ABSTRACT

Wildlife that habituate to humans can damage ecosystems by becoming locally hyper-abundant, which may be further associated with the loss of wariness of people to result in human-wildlife conflict. These problems can sometimes be mitigated via aversive conditioning (AC) by creating negative associations between people and undesired experiences, such as pain or fright. However, high variability in the responsiveness of animals to conditioning limits its application as a management technique. We determined the effects of two potential contributors to this variation, stimulus specificity (as group vs. isolation-based AC) and our measurement of a personality dimension (bold vs. shy types), by subjecting 20 wild elk (*Cervus canadensis*) to repeated conditioning events and measuring changes in their wariness over time via flight response distances when approached by a person. Bolder elk had significantly greater increases in wariness during conditioning, but they also had greater decreases in wariness during the extinction period. The specificity of treatment did not affect responsiveness to AC during the conditioning period, but isolated animals retained more wariness once conditioning had ended. These results suggest that personality is an important contributor to the responsiveness of animals to AC, and perhaps other experiences, and may explain why individuals with bolder personality types are more likely to habituate to people and abandon migration. More generally, our results suggest that wildlife managers could benefit by identifying and targeting specific personality types in the context of modifying habituated behaviour.

INTRODUCTION

Human population growth and an expanding footprint of human disturbance are increasing rates of human-wildlife conflict around the world (Conover, 2002). Whenever the positive consequences of encountering humans and using human-disturbed areas outweigh the negative consequences, wildlife desensitize to stimuli that would formerly elicit an aversive response (Thompson & Henderson, 1998), and become habituated to human presence and infrastructure (Messmer, 2009). Habituated animals – particularly if they are large – can become aggressive towards humans and pose direct threats to public safety (Bounds & Shaw, 1994). Habituated prey can also exploit human-disturbed areas as refugia from predators (Laundre et al., 2001), which results in local hyperabundance, and trophic disruptions through excess herbivory and spatial separation from predators (Beschta & Ripple, 2009; Goldberg et al., 2014).

For ungulates, a further consequence of habituation may be the abandonment of migratory behaviour (Berger, 2004). The proportions of migratory individuals have been declining in ungulate populations worldwide, including wildebeest (*Conochaetes spp.)* in Africa (Morrison & Bolger, 2012), gazelles (*Procapra gutturosa)* in Asia (Ito, 2005), and moose (*Alces alces*) in Europe (Singh, 2012). This situation also characterizes elk (*Cervus canadensis*) across North America, where the proportion of non-migratory residents (Morgantini & Hudson, 1988) is increasing (Hebblewhite et al., 2006; Middleton et al., 2013). While the proportion of migrating elk can be increased through selective culling of resident individuals (Tom Hurd, Parks Canada, personal communication), this is a temporary measure (see Chapter 2), but this type of lethal management remains unpalatable to the public (e.g. Koval & Mertig, 2004). A more promising strategy might be to tip the balance of costs and benefits to favour migration, such as by increasing the benefits of migration through supplementary feeding along migratory routes (Gundersen et al., 2004), or using aversive conditioning to increase the costs of living near humans, and thus reduce habituation behaviour directly (Kloppers et al., 2005).

Aversive conditioning (AC) is a form of instrumental conditioning that can reduce or reverse a given behaviour by subjecting individuals to negative consequences when they exhibit it (Domjan, 2010). This approach has been used to restore wariness in species such as wolves (*Canis lupus*; Hawley et al., 2009), bears (*Ursus americanus*; Rauer et al., 2003; Mazur, 2010) and elk (Kloppers et al., 2005), but it has two important limitations. First, substantial variation can occur among individuals. For example, some grizzly bears (*Ursus arctos*) conditioned to avoid human-disturbed areas permanently avoided the areas after just one treatment, but others actually increased their use of the areas despite multiple years of conditioning treatments (Honeyman, 2008). There is no universal explanation for individual variation in responses to AC, but comparable differences in other behaviours are routinely attributed to behavioural syndromes, or personality (Sih et al., 2004; Bell, 2007; Biro & Stamps, 2008). Habituation behaviour has previously been correlated with personality in mice (*Mus musculus*; Light et al., 2011), and we recently found that elk with bolder personality types were less likely to undertake migration compared to shyer elk (Chapter 2). We speculated that bold elk obtain greater benefits by adopting year-round residency in town sites mainly because they are better at habituating to humans and exploiting novel infrastructure and more unpredictable disturbance patterns; in other words, they are more flexible.

A second limitation of AC is that ongoing reinforcement is needed to prevent extinction of most behaviours learned by association, once the association is removed (Domjan, 2010). Even perpetual and consistent application of AC does not prevent this recidivistic behaviour because animals can even desensitize and habituate to the aversive stimuli (Lattal & Lattal, 2012). In general, higher initial intensity of aversive stimuli can be maintained with lower treatment frequency to minimize desensitization (Domjan, 2010). In the context of wildlife management, AC intensity is usually expressed as the frequency of events (e.g., Kloppers, 2005), or the intensity of pain stimuli (e.g., Honeyman, 2008), but intensity might be increased in other ways. For example, many social animals are assumed to dislike isolation (Franz et al., 2013), which makes isolation an effective AC method for managing human prisoners (i.e. solitary confinement; Arrigo & Bullock, 2008) and training domestic horses (Fureix et al., 2009). Isolation is likely to be an unconditioned aversive stimulus because solitary individuals have much higher risks of predation (Foster & Trehurne, 1981), which also characterizes smaller groups of elk (Hebblewhite & Pletscher, 2002). The efficacy of isolation as an AC method for treating habituated elk is likely to interact with personality. For example, personality traits of shy-type elk appear more suited for anti-predation strategies, while bold-type elk appear more dependent on larger group sizes (Chapter 2).

In this study, we examined the separate and combined effects of personality and isolation-based AC on the wariness of habituated elk in two mountain parks. Specifically, we categorized elk along a continuum of personality types and then measured their changes in flight response distance (a measure of wariness of humans) between the periods before, during, and after being subjected to repeated AC events. All events consisted of chases by humans on foot that targeted individual animals, but treatments either permitted them to remain within a group or isolated them from all conspecifics as much as possible. Based on our earlier findings that suggest bold-type animals may be more adaptable to human stimuli (Chapter 2), we predicted bold elk would be more responsive to both the application of conditioning (greater increases in flight responses) and its removal (greater subsequent losses of those gains during the extinction period). We further predicted that Isolation AC would increase wariness gains and reduce recidivistic losses, and that this difference would be more apparent in bold than shy elk.

METHODS

Study Area

We collected all behavioural data and conducted all aversive conditioning trials in Jasper National Park (JNP), AB, in the winters of 2011-12 and 2012-13. JNP is 10,880 km^2, and receives nearly 2 million annual visitors. Our focus was on the three valley confluence area in the center of the park, within which is found the townsite of Jasper (52°52′N, 118°04′W, pop. est. 4,500), and a nearby village system of Jasper Park Lodge. Both of these highly human-disturbed sites attract elk, presumably to reduce the risk of predation by wolves (*Canis lupus*) and cougars (*Felis concolor*). Excluding groups composed only of adult males, elk in this region formed three large herds composed of 90-100 total adult females and sub-adults. Our research focused on 20 adult females that were individually marked with ear tags and/or VHF radio collars. Post-hoc we used summer location events to label each individual as a "resident" (found within the winter range in the summer) or "migrant" (found outside the winter range in summer). All data were collected under the University of Alberta Ethics for Animal Use Protocol # 7121112.

Dependent Variable: Flight Response Distance (i.e. wariness)

Our response variables were wariness changes, measured as changes in mean flight response distance between experimental phases (before, during, and after aversive conditioning). Each mean was based on a minimum of five separate flight response trials on each elk, during each of the three phases. To record each flight response distance a single observer approached the target elk at a regular walking speed and posture, and used a laser range finder to record the distance at which the elk responded with a displacement of at least 5 m. We did not conduct multiple trials on any elk on any single day, nor any trials at all on elk that were bedded, obviously sick or injured, physically interacting with another elk, or where a strong escape response was deemed too dangerous (e.g. running onto a roadway). On occasions when the elk did not move when approached to within 1m, or when the elk's response was to charge the observer, we recorded its flight response as 0 m.

We collected "before" conditioning flight response measures from December 2011 to early January 2012. To minimize the potential desensitization effect of these flight trials we waited a full week before commencing the aversive conditioning treatments. Flight response measures "during" the conditioning period were taken immediately prior to each aversive conditioning chase of that same target elk. Flight response measures "after" the conditioning period were taken in April 2012, and "1 year" post-conditioning measures were taken from December 2012 to January 2013.

Aversive Conditioning (AC)

We could not quantify a personality gradient until after the AC treatments, but because un-conditioned mean flight response may be correlated with personality type (Chapter 2) we used the before-AC flight response distance means to rank-order each elk, then alternately assigned each individual to one of two AC treatment categories ("Group" or "Isolation"). In this way, we increased the likelihood that gradients of personality type were equally represented in each AC treatment group.

All AC trials were conducted from January through March 2012. Each target elk was subjected to six separate conditioning trials over a 76-day period, for an average of one trial each 12.7 days. This approximated the successful 1 trial/10 day frequency used on a similar sample size of elk by Kloppers et al. (2005), which itself approximated the average rate elk encounter wolves (once every 13.4 days; Weaver, 1994). No individual elk was involved in more than one AC chase in a single day, either as the target or collaterally as part of a group. We achieved this by selecting targets from the different herds, but also by exploiting the regular fragmentation of single herds into smaller groups. Daily choice of target elk was partly opportunistic based on which elk could be located, but also on site safety for any prospective chase. We maintained a balanced schedule so that the total amount of AC accumulated equally for each elk (i.e. an elk would not receive its 6th trial before every other elk had received its 5th).

A fundamental aspect of both AC regimens was that chases were not dependent on the area the target elk was using, so that conditioning would be associated with humans in general, and not location. For both Group and Isolation AC pursuits were 10 minutes duration, and conducted by two people making noise and waving flagging on hockey sticks to start and sustain the pursuit (also following Kloppers et al.). A GPS unit was used to record chase trajectories, and a range finder and backtracking of elk footprints were used to determine the relative position of the target elk to the GPS unit. Pursuits were coordinated with Parks Canada, who provided traffic control where vehicles presented a potential risk to elk or human safety. We did not pursue elk across roads on days with high traffic volume or poor driving conditions.

During Group AC chases both observers followed the target elk at as high a running speed as could be sustained over the terrain, for the full 10 minutes. If the target elk broke off into a subgroup, we chased only that subgroup. We furthered the aspatial aspect of the AC by allowing elk to choose their own escape routes, except in situations where we intervened to guide elk away from potential hazards. During Isolation AC, the goal of chasing the target elk for 10-minute chase was secondary to goal of isolating it from the herd for as much of the 10-minute trial as possible. The two pursuers would accomplish this by using two-way radios to conduct separate but coordinated manoeuvres to first separate the target from rest of the herd, and then maintain the isolation (see Figure A-2). Once isolated these targeted elk were invariably highly motivated to join the herd, and employed their own strategies to run around, in between, or over their pursuers in an attempt to reach other elk. To extend the range from which we could block or divert these escape routes we used weighted throw-bags which trailed bright pieces of 1 m long flagging, and could be thrown in advance of (but never directly at) escaping elk from up to 15 m away (see Figure A-3).

Personality

To quantify a continuum of elk personality types, we used personality trait data previously collected from this population (see Chapter 2 for more further methodological details), but only for the subset of individuals subjected to aversive conditioning treatments in this experiment. The collected personality traits included: mean flight response distance from an approaching human; individual mean score of relative spatial positions ranked from the less risky positions in the center of the herd, to the more exposed peripheral positions; rank within the adult female social hierarchy, relative only to other marked females within the group; mean individual value for exploratory behaviour as scored on a progressive scale of neofilia towards presented novel objects; and the mean proportion of time budgeted for vigilance behaviour.

Data Analysis

We used Stata 11 (Statacorp) for all statistical analysis, and because we directly measured personality-dependent responses, and this inherently high individual variation increased the chances of failing to detect effects that might be present, we set $\alpha = 0.10$ as our level of statistical significance. Error terms for reported means are standard error. We first correlated the personality traits to demonstrate the ecological relevance of our chosen suite of behaviours for defining elk personality (Table 3-1). We used non-metric dimensional scaling (NMDS) to reduce these five traits to 3, 2 and 1 dimensions, using Kruskel's stress test (i.e. loss criterion) to measure of goodness of fit at each stage. For clarity of illustration, we depicted the five traits as reduced to 2 dimensions (Figure 3-1). We then used a scree diagram to determine that the data could be reduced to a single dimension without substantially increasing the amount of stress ($n = 19$, dimensions = 1, loss criterion = 0.055), and used this gradient as our variable "personality". Compared to shyer individuals, bolder individuals were typified as having lower mean flight response distances and time spent on vigilance behaviours, social dominance over shyer individuals, exhibiting more exploratory behaviour towards novel objects, and choosing more peripheral spatial positions within the herd.

We used t-tests to compare the mean changes in flight responses between conditioning phases for each AC treatment. Because we chose these period-period comparisons *a priori*, they were not independent. For personality-dependent analyses, we converted absolute changes in flight response distance to effect sizes. The change from before to during conditioning was the "conditioning" effect, the change from during to after conditioning was "extinction", the overall change from before to after conditioning was the "net AC" effect, and the overall change from before conditioning to one year later was the "1 year" effect. We used generalized linear mixed models (GLMM) to model these effect sizes as functions of personality and the interaction between personality and AC method. We conducted additional GLMMs to compare the effect of personality and AC treatment type on two spatial response variables: the mean individual displacement from the start to end of AC chases and the mean linear distance each individual was chased.

To determine what factors might be affecting wariness responses, which we necessarily based on means (above), we modeled the responses and available covariates for each singular flight response distance trial. We built separate GLMMs for each of the conditioning phases (before, during, after). We used a model building strategy of purposeful selection of covariates (following Hosmer & Lemeshow, 2000), using $P < 0.25$ for inclusion in the model, $P < 0.10$ for retention, and included all confounding variables, which we defined as those influencing the parameters of any remaining variables by more than 20%. Along with the personality and AC treatment group, we used the following covariates, together with all ecologically-relevant interactions: time of day, snow depth, wind speed and temperature at the time of the trial, day number since start of study period (date), elk group size, and calf:cow ratio of the associated group. Covariates relating to predator activity were not available.

RESULTS

Sample sizes of both individuals and conditioning events deviated slightly from those anticipated by the experimental design. Owing to difficulties finding one individual, the injury of another (unrelated to this study), and depredation by a cougar of a third, trials were completed on only 9 of 10 elk in each of the Group and Isolation AC treatments. One further individual was lost from the Isolation group in the period after AC. For the remaining animals, there was a minimum of 6 and maximum of 16 days between successive trials. The similar distribution of personalities between treatment groups was verified by (a) a strong correlation between the mean flight response of animals before conditioning and their personality scores ($F_{1,17} = 7303.4$, $P < 0.001$, $R^2 = 0.99$) and (b) the similarity in the mean personality scores for animals assigned to Isolation AC ($\bar{x} = 3.48 \pm 3.3$) vs. Group AC ($\bar{x} = 0.24 \pm 2.17$; $t_{18} = 0.82$, $P = 0.42$).

We quantified changes in flight response distances between each period of the experiment as a measure of wariness change. During the conditioning period, overall mean flight response increased by 74% from 20.7 m (± 1.59) to 36.0 m (± 2.02; $t_{18} = -10.28$, $P < 0.0001$). In the 5 week period after AC, mean flight response declined 28% to 25.8 m (± 2.83; $t_{17} = 6.76$, $P < 0.01$). This resulted in a net increase in mean flight response of 28% from pre-conditioned levels ($t_{17} = 1.77$, $P = 0.017$). After 1 year, mean flight response declined only slightly (by 8.4 % to 23.8 m ± 3.24) and non-significantly ($t_{17} = -1.22$, $P = 0.24$).

Conditioned gains in wariness were almost identical between the two groups (4% higher in elk conditioned with Group AC [14.9 ± 2.0 m] than with Isolation AC [14.2 ±2.0 m; $t_{16} = 0.29$, $P = 0.82$; Figure 3-2]). By contrast, recidivistic losses during the post-conditioning period were 67% greater for elk subjected to Group AC (-12.5 ± 1.8 m), compared to Isolation AC (-7.5 ± 2.0 m; $t_{15} = 1.87$, $P = 0.081$). This produced a net wariness change as a result of AC that did not differ significantly between Isolation AC individuals (5.1 ± 1.5 m) or Group AC individuals (2.3 ± 2.0 m; $t_{15} = 1.07$, $P = 0.30$). After one year the net wariness change in elk in Group AC (1.3 ± 1.6m) and Isolation AC (0.30 ± 1.8m) were not different ($t_{15} = 0.43$, $P = 0.68$).

Our measure of responsiveness to AC – individual increases in mean flight response distances – were positively correlated with increasing boldness of personality type (coefficient = 0.057, $z_{16} = 3.47$, $P < 0.001$), but there was no additional effect of AC treatment type (coefficient = -0.018, $z_{16} = -0.76$, $P = 0.45$; Figure 3-3). Similarly, the responsiveness of individuals to the withdrawal of AC, measured as the individual decrease in mean flight response distance during the extinction period, was also higher for bolder animals (coefficient = - 0.016, $z_{15} = - 2.54$, $P = 0.011$), but again with no additional effect of treatment type (coefficient = -0.0020, $z_{15} = -0.23$, $P = 0.82$).

The offsetting patterns of responsiveness during and after the AC period (Figure 3-3) largely neutralized the role of personality on the net effect of AC, whether it was measured as a main effect (coefficient = -0.0022, $z_{16} = -0.15$, $P = 0.88$) or as an interaction between personality and AC method (coefficient = -0.0082, $z_{15} = - 0.32$, $P = 0.75$). Irrespective of AC method the net change in flight response distance one year after the onset of AC was less for bolder elk (coefficient = -0.021, $z_{16} = -1.99$, $P = 0.046$), but there was no interaction between personality and AC method (coefficient = -0.016, $z_{16} = -0.98$, $P = 0.33$). However, separate analyses for each AC type showed that the relationship between personality and one year change in wariness was significant only for those conditioned with Isolation AC (coefficient = -0.021, $z_6 = -3.44$, $P < 0.001$), and not for animals treated with Group AC (coefficient = -0.020, $z_8 = -1.00$, $P = 0.32$). The association between personality and migratory strategy (Chapter 2) meant that resident elk had larger changes in mean warines than migratory elk, both during and after AC (Figure 3-4).

To illustrate what other covariates potentially influenced measures of mean flight responses, and because there were no relevant period wide covariates available to compare to these means, we created models for all singular flight response distance trials during each period of the experiment. In the period before AC flight response distances were positively correlated with shyness (i.e. lower values on the personality axis; $z_{140} = -14.39$, $P < 0.001$) and increasing snow depth ($z_{140} = 2.72$, $P < 0.01$), but decreased with advancing day number ($z_{140} = -1.86$, $P = 0.062$). In the period during conditioning flight responses flight responses were positively correlated with shyness of personality ($z_{108} = - 2.86$, $P < 0.005$), and increased with advancing day number ($z_{108} = 1.77$, $P = 0.077$). In the period after conditioning flight response distances were positively correlated with shyness of personality ($z_{91} = -7.00$, $P < 0.001$).

DISCUSSION

Based on earlier work that suggested elk with bolder personality types might be more adaptable to human stimuli, we predicted that bold animals would exhibit greater changes in wariness in response to both the application and withdrawal of aversive conditioning. Our results supported this prediction. We also predicted that all individuals would be more responsive to isolation-based conditioning, but bold animals would be more responsive. Our results partially supported this prediction. Isolation and Group based AC methods were equally effective at increasing wariness, but while wariness losses during the extinction period were lower after Isolation AC, this was not enough to make a significant difference in net AC effectiveness. One year after conditioning began, bolder animals that were treated with Isolation AC had lost more of the conditioned gains from their initial flight response distances. In other words, the bolder animals managers will likely want to target for aversive conditioning were more responsive, but this responsiveness applied to every stage of the process; the gain in wariness during AC and the loss of that gain during extinctions periods of a few weeks and a year.

Our results have important implications for the use of flight response distances as measurements of wariness. Our initial measures of flight response distances demonstrated a high correlation with subsequent measures of a correlated suite of personality traits quantifying a gradient of bold to shy personality types. This lends support to findings by others that flight response is a useful measure of personality in horses (*Equus caballus*; Birke et al., 2011) and marmots (*Marmot flaviventris*; Petelle et al., 2013), but our study also showed that this metric can change in response to both the application and removal of aversive stimuli. Similar results have been found previously, such as flight response declines in wolves (*Canis lupus*) that are subjected to repeated, but benign, encounters with people (Wam et al., 2014), or flight response increases as an adaptation to aversive stimuli such as hunting or predation (e.g. ungulates; Stankowich, 2008).

Because the metric of flight response distances is determined partly by innate temperament (*sensu* Reale et al. 2007) and partly by ongoing experience, it is likely especially susceptible to changing predation risk. Even indirect encounters with wolves can affect elk behaviour for up to several days (Creel et al., 2008), but a previous study that subjected wild elk to AC found no effect on flight responses of recent wolf activity in the area (Kloppers et al., 2005). Our own previous work in Banff (Chapter 2) determined that wolf presence increased elk flight response distance only on the day or day after the wolf presence was detected (Chapter 2). We rarely detected such recent wolf activity in areas where we were conducting AC chases, and this, coupled with the relative infrequency of elk encounters with wolves in typical wolf-elk system (about every 2 weeks; Weaver, 1994), caused us to attribute the changes in wariness we observed to our own conditioning regimes.

We found no evidence that the specificity of aversive conditioning can entirely overcome the effects of personality or experience, but it may have exaggerated the responsiveness of the bolder animals. Although there were no consistent effects of isolation-based AC on flight response distances, animals subjected to isolation AC appeared, to those conducting the chase, to be more visibly stressed. Stress hormones, such as cortisol, can increase the encoding of behaviours learned during stressful events (Sandi et al., 2007). If Isolation AC was in fact more stressful for elk, the decreased recidivism we found may be the result of greater acquisition of learned wariness. This resembles previous results found with dogs (Demant et al., 2011), but also fear-conditioned humans (Bentz et al., 2013).

Whereas we had predicted that the personality traits of bolder elk would make them more sensitive to isolation, these animals also seemed more aggressive in countering our isolating techniques, which may have dampened the negativity of their experience. Some ungulates readily see humans as competitors (Geist, 1982) and increased aggression towards them is a frequent consequence of urbanization (Galbreath et al., 2014). Thus, and somewhat ironically, animals that were born with bolder personalities may have reinforced that tendency by responding more aggressively and effectively to Isolation AC. In addition, by isolating individuals we aimed to reduce the collateral exposure to stimuli experienced by non-targeted neighbouring elk, but if those neighbourin animals were also relatively bold, they may have actually experienced a form of benign encounter with the chasing humans that contributed to their own recidivism (similar to Bejder et al., 2009). Any animal can desensitize to aversive stimuli that are perceived as less aversive over time (Lattal & Lattal, 2012).

Our combined results have several important implications for wildlife managers challenged to retain habituated wildlife while supporting ecological processes and public safety. First, the subtle and multi-faceted ways by which bolder animals may contribute to their own increased habituation to people may be difficult to counter. They are likely worsened by conventional approaches to AC, which typically begin with occasional hazing with gradually increasing intensity, invariably following repeated transgressions by problem animals we now know are likely to have bold personality types. This process is likely to desensitize animals or may even inoculate them against further aversive stimuli (Domjan, 2010). Our models of singular flight response trials showed that flight response distances gradually decreased with each successive trial during the period before AC. Since this effect was unrelated to personality, or any other covariates, it suggested that elk were gradually desensitizing to the cumulative exposure of the benign approaches we relied on to collect flight response data. This effect was reversed once we began AC, which supported our assertion that once our approaches became aversive, elk began to sensitize to human stimuli.

A second implication of our results is that shy elk may experience relative disadvantages in human-dominated areas because of their reduced responsiveness to changing human stimuli. Optimal escape theory predicts that animals should act to minimize wariness responses (Ydenberg & Dill, 1986), presumably because flight responses are energetically costly (Gates & Hudson, 1978). Shy animals might respond by choosing habitats with more homogenous disturbance and risk, such as those along migratory routes (Hebblewhite et al., 2009), or elsewhere outside of predation refugia (Burger, 2004). Although elk encounters with wolves are infrequent, and predation events unpredictable, (Weaver, 1994) they are invariably aversive. This homogeneity of risk should favour inflexible and conservative wariness responses, whereas the heterogeneity of risk near humans should favour greater flexibility (Ensminger & Westneat, 2012). Through such associations, personality or temperament may constrain individual life history choices (*sensu* Dochtermann & Dingemanse, 2013), though over longer periods of time migration may select for personality traits different than residency does, such as the prevalence of shy migrants and bold residents (Chapter 2). A third implication of our results follows from the other two: reduced wariness is at least partially an innate aspect of temperament (following Linares-Ortiz et al., 2014) that is consistently favoured in human-dominated areas to contribute to the loss of migratory behaviour for elk in this study area and, potentially, for ungulates world wide (reviewed by Berger, 2004).

In general, wildlife that can habituate to humans are more likely to enter into human-wildlife conflicts (Linnel et al., 1999), overuse urban areas (Conover, 2002), and abandon migratory behaviour (Middleton et al., 2013) to create numerous challenges for managers. Aversive conditioning may provide a helpful tool to counter these tendencies, but integrating our study with the literature suggests that its efficacy is highly influenced by animal personality. This conclusion is not surprising. Individual variation in learned responses to human behaviour has been documented in both dogs (Hare et al., 2002) and horses (Proops et al., 2010), and is believed to have been instrumental in the process of habituating and then domesticating these species (Driscoll, 2009). The proclivity to habituate likely varies among individuals in all wildlife populations (Ensminger & Westneat, 2012), but human-disturbed landscapes will tend to favour the bolder individuals, with the more flexible behaviour. Consequently, aversive conditioning that targets these behavioural types is likely to increase wariness and reverse the process of habituation, but only if it is designed and implemented using well-described principles of associative learning, to create a net effect that consistently encourages long-term wariness responses.

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Table 3-1. Correlation matrix for 5 personality traits used to describe gradient of elk personality types. Bolded values are statistically significant (Pearson's correlation, two-tailed, alpha = 0.05).

	flight	**position**	**dominance**	**exploration**	**vigilance**
flight	**1**				
position	**-0.456**	**1**			
dominance	**-0.748**	**0.641**	**1**		
exploration	**-0.580**	**0.419**	**0.711**	**1**	
vigilance	**0.611**	**-0.263**	**-0.498**	-0.093	**1**

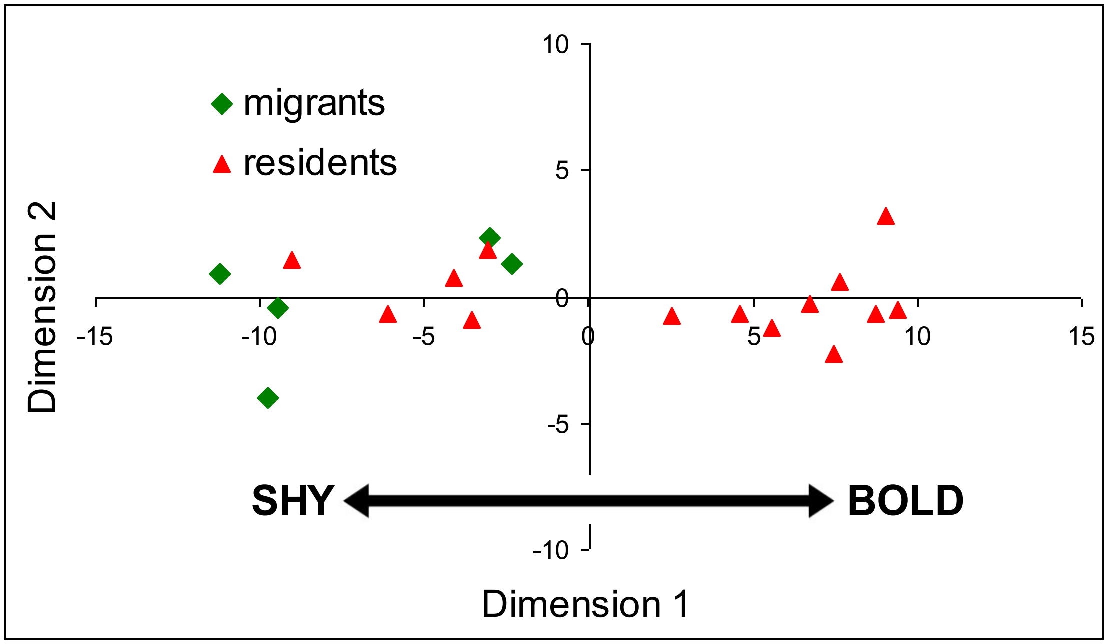

Figure 3-1. Non-metric dimensional scaling of 5 separate personality traits of both migratory and non-migratory elk in Jasper National Park, AB, during 2012-13. First dimension (X-axis) approximates shy-bold gradient of personality types, and was used as variable "personality".

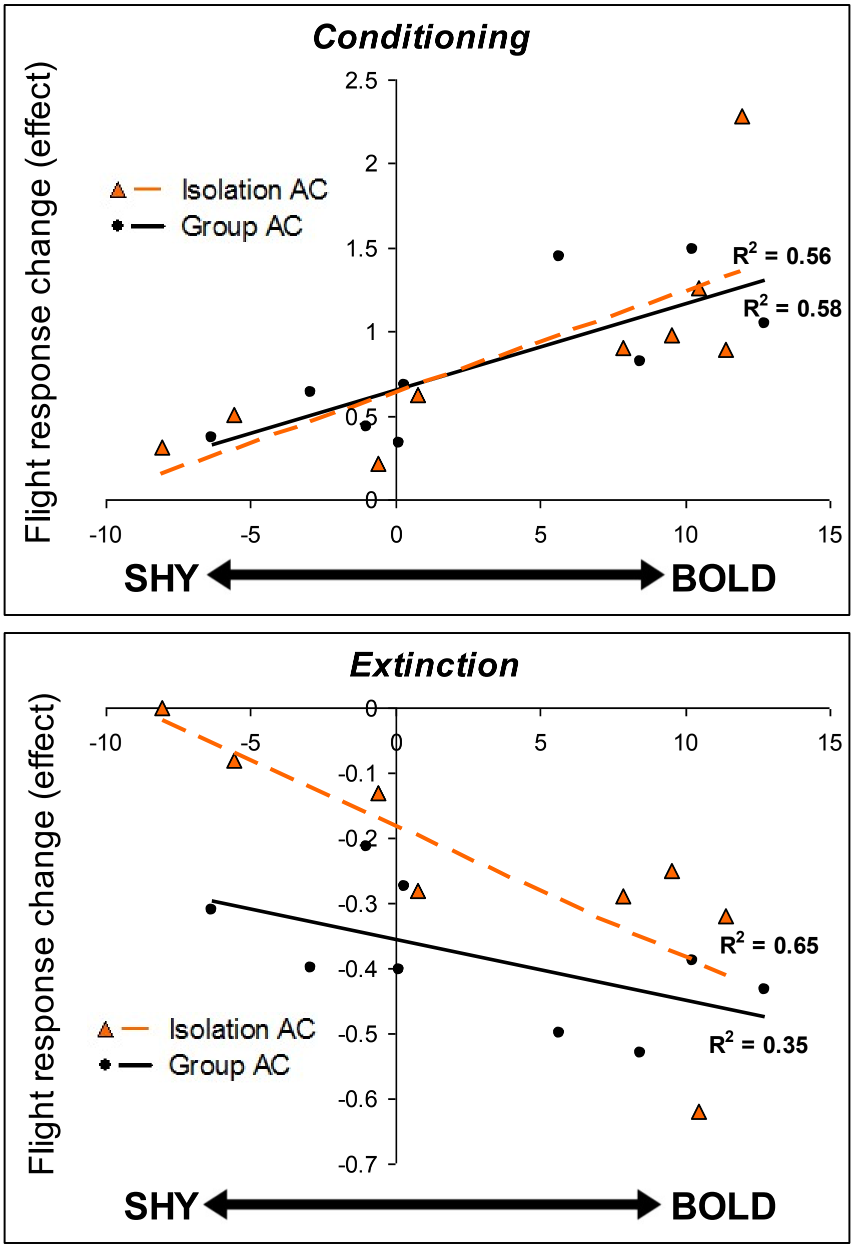

Figure 3-2. Change in mean flight responses (wariness) for elk with personality types ranging from shy to bold (X-axis), and conditioned with either Isolation or Group-based methods. Change is effect size for difference between responses in 1-month long period before aversive conditioning (AC) treatments to 76-day conditioning period **(top)** and from the conditioning period to the 5 week "extinction" period after conditioning had ended **(bottom)**.

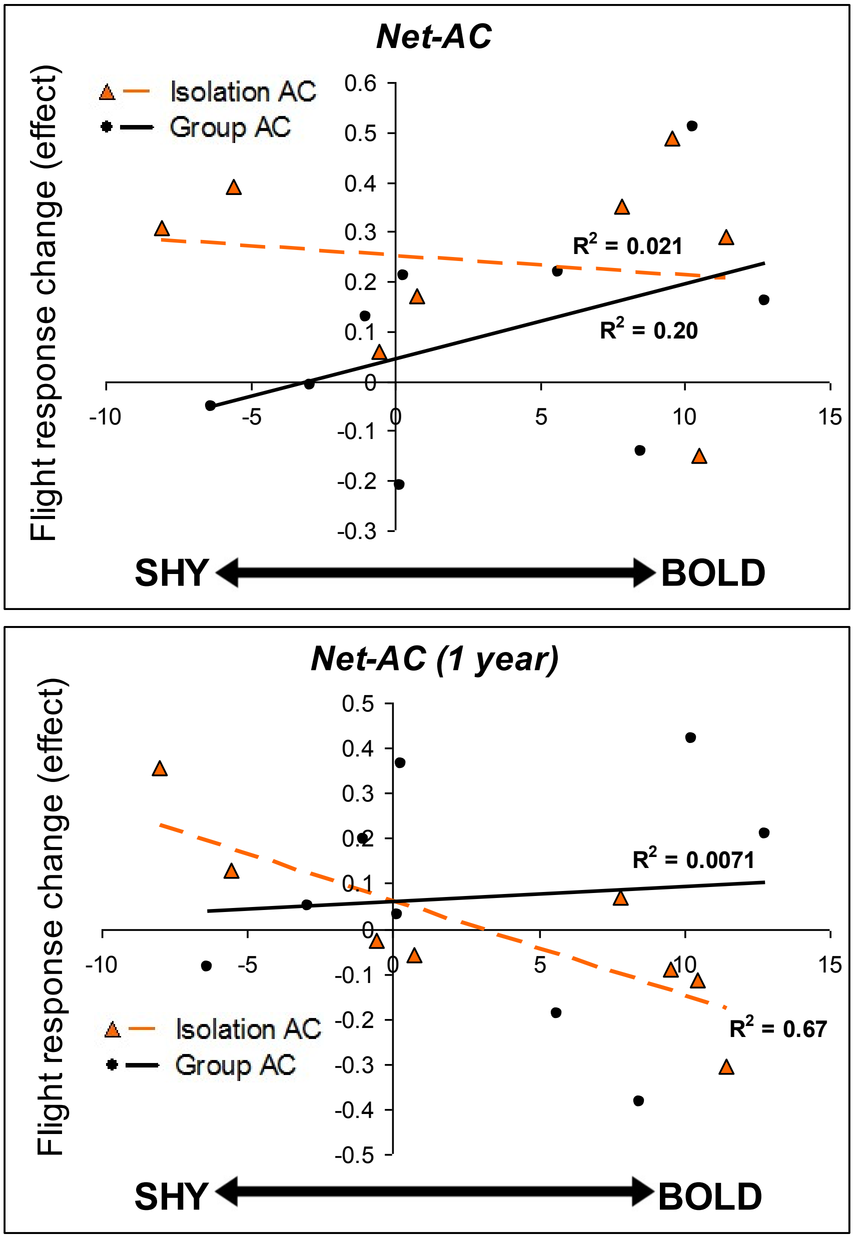

Figure 3-3. Change in mean flight responses (wariness) for elk with personality types ranging from shy to bold (X-axis), and conditioned with either Isolation or Group-based methods. Change is effect size for difference between mean responses in 1-month long period before aversive conditioning (AC) treatments to 5-week long period immediately after AC treatments ended **(top)** or 1-month long period 1 year later **(bottom)**.

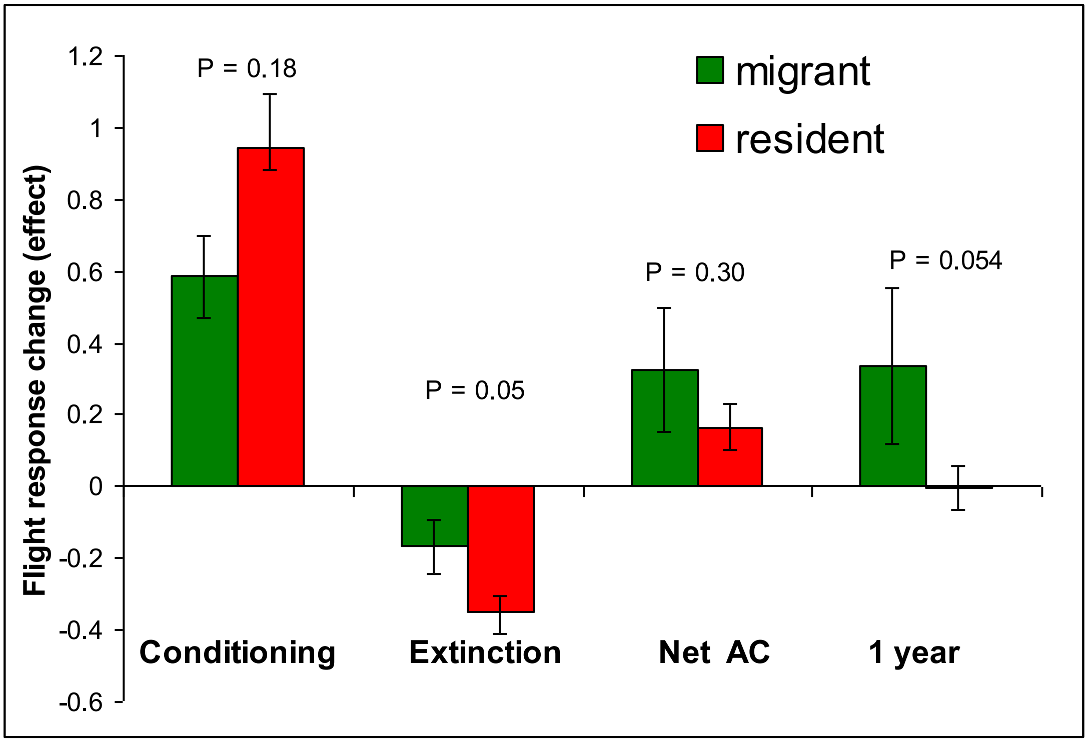

Figure 3-4. Mean flight response (wariness) changes for migratory (n = 5) vs. resident (n = 12) elk in Jasper National Park, AB, in 2012. Changes are mean effect sizes (Y-axis) for the 76 day "conditioning" period, 5 week "extinction" period after AC had ended, overall change as "net AC", and overall net change "1 year" later. Error bars are SE.

Chapter 4

Lateralization predicts individual behavioural plasticity and loss of migratory behaviour by elk.

ABSTRACT

Studies of animal personality have shown that consistent individual variation places evolutionary constraints on behavioural adaptation in species, but our understanding of individual variation in behavioural plasticity itself remains poor. Individuals lacking sufficient plasticity may be unable to adapt to changing disturbance regimes, while those that can may do so by expressing behaviours that are undesirable to humans, such as habituation and conflict behaviour. We examined potential correlates of plasticity in the context of a wild ungulate with facultative migration. Lateralized behaviours, such as eye or limb biases, are overt expressions of variations in cerebral structure that are present at the level of both species and individuals. Laterality may provide an explanatory mechanism for individual variation in the plasticity of behavioural responses. We found that elk that migrated had stronger front-limb biases than the more-habituated resident elk. We also found that the least lateralized individuals exhibited the greatest plasticity in wariness, as measured by flight response distances, when exposed to two contrasting types of human stimuli. The least lateralized elk habituated more rapidly to benign approaches by humans, but they exhibited greater increases in wariness when exposed to aversive chases. The degree of lateralization was weakly correlated with a bold-shy gradient in personality types comprised of 5 correlated personality traits. Laterality and personality are both assumed to influence behaviour, but the nature of their interaction is not yet clear. Behaviourists might find intriguing study systems in the context of wild populations with facultative behaviours, particularly where they contribute to human-wildlife conflict. Managers might use assays of laterality and personality to improve behavioural modification strategies by targeting the individuals that are more likely to exhibit conflict behaviour.

INTRODUCTION

As human-disturbed areas encroach into wildlife habitat, wild species are either displaced, forced to modify their behaviour, or simply die (e.g. Rodriquez-Prieto et al., 2010). Species with higher sensitivity to human disturbance, such as grizzly bears (*Ursus arctos*; Coleman et al., 2013) and woodland caribou (*Rangifer tarandus*; Dyer et al., 2001) are especially likely to experience reductions in habitat availability and declining populations. Conversely, species that readily desensitize and habituate to human disturbance (Messmer, 2009), such as coyotes (*Canis latrans*; Bounds & Shaw, 1994; Murray et al. in press), and elk (*Cervus canadensis*; Geist, 1982) can thrive, but in doing so often disrupt ecosystem function through local overpopulation and disrupted predator-prey dynamics (Conover, 2002). This problem is particularly acute in protected areas where repetitive benign encounters with humans can accelerate habituation behaviour, and prey species may exploit human-disturbed areas as predation refugia (Beschta & Ripple, 2009). Habituated ungulates may also abandon migratory behaviour to use these human-disturbed areas year round, thereby further damaging ecological integrity (Berger, 2004; Laundre et al., 2001).

The rate at which a species tends to accommodate human-induced changes to the environment is associated with the life-history trait of specialization, which human disturbance can select against (e.g. butterfly communities; Kitahara & Fujii, 1994), but similar variation can also exist among individuals within species (e.g. Mettke-Hoffman, 2010; Dingemanse et al., 2012). The persistence of behavioural types within populations is presumed to result from environmental variability, which selects for different suites of co-evolved behavioural traits, also known as personality types, under different disturbance regimes (Sih et al., 2004). If environmental change is rapid enough to occur within generations, selection may favour behavioural plasticity itself, which we define as the ability to have adaptive changes in the same behaviour. Guilford (1957) anticipated the adaptive benefit of this capacity for humans when he described creative and flexible individuals as ones that "respond efficiently and effectively to a constantly changing, and regularly challenging, environment". More recently, this relative ability to adapt to change versus retaining familiar routines has been ascribed to variations in coping style (Janczak et al., 2003), which has been proposed to be a second axis of consistent individual behavioural variation along with personality (Koolhaas et al., 2010).

A potential metric of the underlying neural architecture that accompanies behavioural flexibility appears to be the degree of lateralization of repeated behaviours, such as a preference for using one limb or one eye over the other (Tomasi, 2010). Lateralized behaviours result from compartmentalization of the brain into lateral hemispheres, a process that allows vertebrates – and even some invertebrates – to improve cognitive speed and efficiency (Bisazza et al., 1998). Fitness benefits can accrue from both strong and weak connections between the hemispheres, to produce individual variation in the degree of laterality (Bisazza et al., 1998). Strong laterality (i.e. weak connections between hemispheres) has been correlated with quick responses to stimuli such as predators (Brown et al., 2007) or prey (Siniscalchi et al., 2014), and in humans, increased physical coordination and autoimmune strength (Porac & Searleman, 2006). By contrast, weak laterality has been associated with superior learning ability (Searleman, 1984; Carlier et al., 2012) and creativity (Flaherty, 2011; Lindell, 2011).

The strength of laterality can be inferred by observing behaviours that employ the front limb because these lateralized behaviours are largely independent of species-wide or even vertebrate-wide hemispherical specializations (Rogers, 2009). For example, if a ball is rolled straight towards an infant human, there is no obligate reason for the baby to grab it with one limb instead of the other. Weakly lateralized individuals are expected to choose to use their left and right limbs in similar proportions, while strongly lateralized individuals will consistently favour one limb over the other (Laskowski & Henneberg, 2012). Front-limb biases have been found in laboratory mice (Ribeiro-Carvalho et al., 2010), wallabies (*Macropus refogriseus*; Giljov et al., 2011), and domestic dogs (Poyser et al., 2006).

Although it has not been investigated in this way, lateralization is likely to be relevant to many conservation problems related to adaptation to changing disturbance regimes. These problems may include the issue of wildlife habituation in response to anthropogenic disturbance, which in ungulates may lead to the abandonment of migratory behaviour. Although all ungulates exhibit some degree of variability in their migratory choices (Morgantini & Hudson, 1998), a gradual reduction in the proportion of animals that migrate is occurring in ungulate species around the world, including wildebeest (*Connochaetes taurinus*; Morrison & Bolger, 2012), Mongolian gazelles (*Procapra gutturosa*; Ito, 2005), moose (*Alces alces*; Singh, 2012), and elk (Hebblewhite et al., 2006). Migratory behaviour has been associated with personality in a few diverse species, including a fish (*Rutilus rutilus;* Chapman et al. 2011), a bird (*Junco hyemalis;* Atwell et al., 2012), and, in our own previous work, a mammal (elk; Chapter 2). In that study, we found that most migrating elk had shyer personality types, whereas most resident elk had bolder personality types. However, the presence of a few bold migrants and a few shy residents suggested that another factor pre-disposed individuals to their particular life history choices. Identifying that factor may make it possible for managers to identify the individuals that are most likely to habituate, abandon migration, and contribute to the associated ecological and safety problems. An opportunity to investigate the potential importance of laterality in this context is suggested by the presence of limb biases during grazing behaviour by feral horses (Austin & Rogers, 2012) and a similar need for elk to paw craters in the snow to access forage in winter (Fortin et al., 2005).

Here, we hypothesize that the tendency in elk to abandon migration and exhibit bold-type behaviour is associated with the weaker laterality of more flexible individuals. An association between lateralization and migration might also explain why some elk continue to migrate, even though this can subject them to higher risk of predation compared to elk that reside in human-associated predation refugia (Robinson & Merrill, 2013; Goldberg et al., 2014). Such life history constraints were predicted to be a consequence of heritable variation in behavioural types (Biro & Stamps, 2010), although there have been few demonstrations of this phenomenon. Our specific objectives were to (a) determine whether lateralization was evident in wild populations of elk comprised of both migratory and resident individuals, (b) identify potential correlations within individuals between laterality scores and other metrics of behavioural plasticity and (c) compare the roles of laterality, behavioural plasticity and personality in predicting the migratory strategies of elk. To achieve these objectives, we studied elk in two populations over two winters and quantified front limb laterality when elk pawed at the snow, measured the responses of elk to repeated approaches by humans that were categorized as aversive (via a predator-resembling chase; Kloppers et al. 2005) or benign (below), and applied a previously-derived gradient of personality types.

METHODS

Study areas and focal populations

All data were gathered in Banff (BNP) and Jasper (JNP) national parks, in the Canadian Rocky Mountains of Alberta, Canada, in the winters of 2010-11 to 2012-13. BNP is 6,697 km^2 in size and receives approximately 4 million annual visitors, while northern neighbour JNP is 10,880 km^2 with 1.8 million annual visitors (Parks Canada, 2014). Each protected area has a human-disturbed townsite area exploited by elk for both anthropogenic forage and reduced predation from wolves (*Canis lupus*) and cougars (*Felis concolor*; Paquet et al., 1996; Goldberg et al., 2014; John Wilmshurst, personal communication, March 10, 2010). We used previous classifications from Chapter 2 that identified "migrants" as those individuals that migrated away from an identified winter range each spring, and "residents" as those remaining within the winter range through to the next winter. We focused on large herds of adult females and sub-adults of both sexes that overwinter in the valley bottoms near the townsites within each park. Banff elk comprised a single group of 200-240 individuals each year, of which 36-50 adult females were marked with ear tags and VHF radio collars. Jasper elk divide into three neighbouring but non-mixing herds totalling 90-100 individuals, of which 22 adult females were marked with ear tags and/or radio collars.

Lateralized behaviours

We recorded front limb biases exhibited by elk when they accessed snow-covered grasses and forbs by digging and scraping through the snow with their front hooves. Elk can only use one hoof at a time for this behaviour, so we recorded whether they chose their left or right hoof for any single digging sequence, regardless of whether the sequence was a single strike, or the more usual occurrence of a few consecutive strikes. We only recorded front-limb biases for elk grazing on level terrain because elk on sloping terrain must use the downhill-facing limb for support. We recorded preferences for left vs. right limbs, but then calculated a value for individual "laterality" as the absolute strength of their lateral biases, regardless of side, using: $|(L-R)/(L+R)|$ (Ward & Hopkins, 1993).

Behavioural Plasticity

We measured changes in flight response distance, in response to different modes of stimulus, as metrics indicating plasticity of behaviour. Flight response distance is a measure of wariness that has previously demonstrated the capacity for behavioural change (reviewed by Stankowich, 2008; e.g. Kloppers et al., 2005). To measure flight response distance, we approached a targeted female elk at a steady walking pace from a minimum of 75m away and only when elk were (a) at least 5m from forest cover, (b) not bedded, and (c) not visibly engaged in any social interactions. We used a single observer for all flight response trials and recorded the distance at which elk responded to the approaching by moving at least 5m.

Our first metric of behavioural plasticity was the degree to which flight response distance individual elk changed between two consecutive, benign approaches by humans. For each experimental trial a single observer performed two approaches 7-10 minutes apart, by walking towards the target elk from the same direction and with a similar pace and carriage, and returning to a blind between the approaches. The 7-10 minute interval was chosen to provide an opportunity for elk to return to their previous behaviour, while retaining a high likelihood that an individual would remain in view and within the same social and environmental context for the second approach. We performed at least 3 sets of trials on each of 20 marked elk in Jasper, and 44 marked elk in Banff (2012 population). We recorded the change between each set of trials, then calculated individual mean changes as an effect size for what we termed a "habituation response". We used this habituation response as one of our two metrics of behavioural plasticity.

Our second metric of behavioural plasticity was derived from individual mean changes in flight response distance after elk were subjected to aversive conditioning (AC), from January through April 2012 (JNP). For detailed methodology and personality-based results of conditioning, see Chapter 3. We measured the change between the mean of 5 flight response distance trials per individual in the period before AC began, to the mean of 5 flight response distance trials per individual during the conditioning period. We used this conditioned change in wariness as a measure of behavioural plasticity in response to aversive stimuli. We performed AC on 18 elk, but because of mortality could only collect post-AC data on 17 elk. Eight months elapsed between the last of the AC trials and the first of the habituation trials (above), but we used the same individuals for each experiment.

Personality

We compared the laterality gradient to a personality gradient derived previously (Chapter 2) by using non-metric dimensional scaling (NMDS) to reduce a suite of separate, but correlated personality traits into a single dimension for each elk population and year (BNP; 2010, 2011, and 2012 and JNP; 2012). This suite of separate behaviours included flight response distance, proportion of time spent vigilant, latency to respond to novel sound playbacks, central vs. peripheral positions within the spatial herd structure, social position along a dominance hierarchy, leading behaviour, and exploration of novel objects placed out in natural habitat (for behaviour details see Chapter 2). Leading behaviour was recorded only in BNP (2010), responses to novel sound stimuli only recorded in BNP (2010 and 2011).

Data analysis and ethical note

We used Stata 11.1 (Statacorp) for all statistical analysis, and set $\alpha = 0.05$. We used two-tailed T-tests to compare laterality means, and chi-square tests for all contingency and goodness-of-fit analyses of lateral biases. We used linear regression to compare the gradients of laterality to personality, and applied logistic regression to determine whether migratory behaviour was better predicted by candidate models with the parameters for laterality, personality, or a combination of the two. Because of the small number of parameters, we compared the three possible models and ranked them using Akaike's Information Criterion (AIC). We assessed the fit of laterality and personality to migratory behaviour only for elk in the BNP population because it was a more thorough mix of migrants and residents compared to JNP, and also provided larger sample sizes. When reporting results of logistic regression, we used Nagelkerke's pseudo R^2 values. We used linear mixed models (LMM) to compare the effectiveness of laterality at predicting individual responses to benign (i.e. habituation responses) vs. aversive approaches by people and, for the JNP elk that were more spatially segregated according to migratory strategy, included migration as a random effect. To determine if these results were confounded by the correlation between laterality and migratory strategy, we added migratory strategy as a random effect to the previous models. All behavioural data collection, including aversive conditioning chases, was conducted, reviewed, and approved under University of Alberta Ethics for Animal Use Protocol # 7121112.

RESULTS

Laterality

Elk in both Banff (BNP) and Jasper (JNP) exhibited front limb biases during cratering behaviour, but the direction and magnitude of laterality differed between populations and across years within populations. Including results for unmarked individuals, in BNP we recorded 6130 individual front limb digging sequences in 2011 and 1292 sequences in 2012, and recorded 1469 sequences in JNP (2012). Before converting all limb bias data into an absolute (with direction) value for laterality, we explored the limb biases to determine if there were any directional differences. In BNP there was a herd-wide bias for using the left front limb in 2011 ($\chi^2 = 6.14$, $P = 0.013$), and a contrasting but not statistically significant right front limb bias in 2012 ($\chi^2 = 3.51$, $P = 0.061$). The herd-wide front limb bias for elk in JNP favoured the right foreleg ($\chi^2 = 6.14$, $P = 0.013$). The absolute magnitude of laterality for the marked elk in BNP was 0.15 (SE = 0.015) in 2011, which was significantly lower than in BNP in 2012 (0.29 ± 0.047), and in JNP in 2012 (0.24 ± 0.036; $F_{2,106} = 4.72$, $P = 0.011$).

After using the limb bias data to calculate absolute values for the magnitude of laterality in each elk, we found migrants were more lateralized than residents were, but again with differences between the populations in direction and magnitude. In 2011 and BNP, the absolute values of laterality were almost 88% higher for migrants ($\bar{x} = 0.18$) than residents ($\bar{x} = 0.096$; $t_{1,48} = 2.98$, $P < 0.005$; Figure 4-1). In 2012 and BNP, there was a similar result; migrants ($\bar{x} = 0.38$) were 76% more lateralized than residents ($\bar{x} = 0.22$; $t_{1,40}$

= 1.66, $P = 0.11$). In JNP, migrants ($\overline{x} = 0.41$) were even more lateralized than residents (173%; 0.15; $t_{1,18} = -3.85$, $P < 0.001$). Migrants also expressed a greater directional limb bias than residents in BNP 2011 ($\chi^2 = 7.48$, $P = 0.042$) and JNP 2012 ($\chi^2 = 4.63$, $P = 0.032$). There was no difference in directional limb bias between migrants and residents in BNP 2012 ($\chi^2 = 0.16$, $P = 0.69$).

Behavioural Plasticity

The absolute magnitude of laterality was significantly and negatively correlated with individual mean changes in flight response distance as a result of benign approaches by humans (i.e. habituation responses) in both JNP ($z_{18} = 2.62$, $P = 0.009$) and BNP ($z_{18} = 2.19$, $P = 0.029$; Figure 4-2). To determine if these results were confounded by the correlation between laterality and migratory strategy, we added migratory strategy as a random effect to the previous models, and found laterality was still correlated with habituation responses in BNP ($z_{18} = 2.19$, $P = 0.029$) but not in JNP ($z_{18} = 0.68$, $P = 0.50$). In JNP , the mean net change in flight response distance was negative in residents (- 20.5 ± 4.2%), but positive and significantly smaller in magnitude in migrants (+ 5.0 ± 2.2% ; Figure 4-3; $t_{1,18} = -4.19$, $P < 0.001$). In BNP, habituation to benign approaches was similarly apparent in the decline in flight response distances for both residents (- 20.7 ± 5.9%) and migrants (- 6.7 ± 5.7% ; $t_{1,42} = 1.61$, $P = 0.12$). In addition to habituating more rapidly to benign approaches, less lateralized elk also exhibited greater increases in flight response distances when exposed to aversive approaches by humans, during predator-resembling chases ($R^2 = 0.427$, $F_{1,16} = 11.19$, $P < 0.01$). The mean change in flight distance was 62% greater in residents (+ 94.6 ± 11.3%) than migrants (+ 58.5 ± 14.6 % ; $t_{17} = 1.40$, $P = 0.090$). In models weighing the contributions for each of laterality scores, personality scores, and their combination, the habituation response was best explained by laterality alone (Table 4-1), whereas the response to aversive conditioning was best predicted by personality (Table 4-1).

Laterality and Personality as Two Axes of Individual Variation

We used the gradient of personality types derived previously for the BNP 2010 and 2011 populations and JNP 2012 populations (Chapter 2) to derive a similar personality gradient for the BNP 2012 population. This method uses non-metric dimensional scaling (NMDS) to reduce the multiple personality traits comprising elk behavioural syndromes to two dimensions (BNP 2012; n = 53, loss criterion = 0.007), compared to the previously derived personality gradients in BNP 2010 (n = 35, loss criterion = 0.011), BNP 2011 (n = 50, loss criterion = 0.008) and JNP 2012 (n = 22, loss criterion = 0.007). In each case, we used the first dimension to represent a gradient of personality types we labelled "shy" to "bold", where bold personality types were socially and physically dominant, had shorter flight response distances, showed greater exploration of novel objects, adopted more peripheral positions within the herd, and exhibited slightly less vigilance behaviour.

The association between laterality and personality differed for the two populations. In BNP, there was no association between laterality and our composite measure of personality ($R^2 = 0.020$, $F_{49} = 3.92$, $P = 0.054$; Figure 4-4), but in JNP, almost 60% of the variation in lateralization was explained by personality ($R^2 = 0.58$, $F_{20} = 26.43$, $P < 0.001$; Figure 4-4). AIC ranking of logistic models showed that measures of laterality and personality together provided the strongest prediction of migratory strategies for elk in each of the three year-location populations (Table 4-2). As single models, the laterality model outranked the personality model alone in Banff (both 2011 and 2012), but the personality model outranked the laterality model in JNP (Table 4-2). For individual personality trait comparisons to each of laterality and personality see Appendix (Table A-2).

We used the global medians for both laterality (BNP = 0.12, JNP = 0.17) and personality (BNP = 2.0, JNP = 0.17) to summarize variation among individuals in our populations in four quadrants describing weak or strong laterality and shy or bold personality (Figure 4-5). We then calculated the proportion of migratory elk found in each quadrant compared to the proportion of migratory elk in the entire marked population for each of BNP and JNP. Migrants were found in the "weak & shy" quadrant more often that would be predicted by the independent assortment of these two variables in both BNP (93% higher than expected; $\chi^2_3 = 11.41$, $P = 0.010$) and JNP (186% more than expected; $\chi^2_3 = 8.43$, $P = 0.038$). The apparent complementarity of increasing laterality with decreasing shyness resulted in occupancy of the complementary categories "strong & shy" or "weak & bold" for 68% of all elk in BNP and 90% in JNP (Figure 4-5).

DISCUSSION

The migratory behaviour of ungulates around the world is gradually being replaced with year-round residency, often near human habitation. Our study explored the possibility that this change in behaviour is mediated by consistent individual variation in behaviour, as measured by gradients of personality, as well as by the degree of behavioural plasticity. We used elk front-limb biases as proxies for individual variation in this plasticity. Our results showed that absolute values of lateralization were higher for migratory elk than resident elk, in two different elk populations. We used measures of habituation to benign approaches by humans, and sensitization to aversive chases by humans, to reveal a predicted and negative correlation between behavioural plasticity and lateralization. In effect, the less lateralized individuals appeared to use the degree of threat evident in their earlier exposure to each kind of stimulus to moderate their subsequent response to that stimulus; demonstrating both increased learning ability, but also increased behavioural flexibility. We found the strength of correlations between gradients of personality type and laterality were weak in Banff, but moderate in Jasper, but that both metrics contributed to the strongest predictive model of migratory strategy.

Our results provide a mechanistic explanation for the hypothesis that loss of migration is an adaptation by ungulates to human-disturbed areas (Berger 2004; Bolger et al., 2008). In both populations, elk with weaker laterality appeared to be better able to exploit these evolutionarily novel environments (Lowry et al., 2013) because they possess higher levels of behavioural plasticity, which may also represent higher learning ability (Fawcett et al., 2013). As a learning process, the capacity to habituate to benign stimuli is clearly adaptive (Bejder et al., 2009). Wariness responses are energetically costly (Gates & Hudson, 1978), and so strategic and context-dependant vacillation of wariness can improve individual fitness (Rodriguez-Prieto et al., 2010). In anthropogenic habitats where disturbance may be less predictable, but more likely benign (Conover, 2002), flexibility in wariness responses can result in energetic savings. In areas where disturbance is more likely to be dangerous, such as outside refugia and along migratory routes (Hebblewhite & Merrill, 2009), the cost of an under-response can be death, and strong laterality can allow inflexible but stronger wariness responses that reduce this risk. Strong laterality may thus only be maladaptive in human-disturbed contexts, but remain adaptive for migratory animals that use human disturbed habitat less frequently (*sensu* Brown et al., 2007).

There is reason to suspect that migrants would benefit from lateralization because of the way it affects the speed of cerebral processing. In vertebrates, the left cerebral hemisphere is specialized for processing routine foraging and social tasks while the right is optimized for novel stimuli, such as predation risk (Ehrlichman, 1986). Strong laterality may thus allow parallel processing that allows migratory elk to forage efficiently while simultaneously monitoring for predators (*sensu* Tommasi, 2008). Cerebral specialization also appears to make animals able to respond more rapidly to lesser stimuli; increasing their sensitivity to stimuli overall (Sirot, 2010). Such traits have been correlated with high laterality in both dogs (Siniscalchi et al., 2014) and humans (Arrington & Rhodes, 2010). Conversely, animals that habituate, which requires desensitization, may have innately low sensitivity to stimuli (Domjan, 2010).

Laterality appears to delineate a gradient of individual variation in plasticity, but one that is not entirely separate from personality. Both gradients were correlated with responses to each of benign and aversive stimuli, but habituation responses were best modeled by laterality, whereas aversive stimuli were best modeled by personality. This difference may have occurred because the two plasticity measures are responses on different temporal scales. In general, longer-term and more durable learning is associated with the development of personality (Caspi, 2005), and previous aversive encounters may cause long-lasting behavioural change (e.g. Wiedenmayer, 2004). Our aversive conditioning trials were conducted over a longer period than our measurements of habituation responses, and so our methods may have unintentionally measured behavioural plasticity on two different time scales that are each best modeled with a different dimension of consistent individual variation.

The migratory strategy of elk in both study areas and years was best predicted by the combination of laterality and personality, a result that bears on several related findings by others. Koolhaas (2007) suggested that coping styles, which are typically characterized along a gradient of reactive – proactive behaviour, define a unique, but overlapping, axis with metrics of temperament. A distinction between these two axes has been supported by several others (reviewed by Coppen et al., 2010), but laterality and personality appear to have co-evolved in other species such as zebrafish (*Danio rerio*; Dadda et al., 2010) and rainbowfish (*Melanotaenia negrans*; Brown & Bibost, 2014). Such co-evolution resembles the complementarity of multiple behavioural tendencies as defined by behavioural syndromes (Sih et al., 2004). In our study system, the increased behavioural plasticity of weakly lateralized elk would be expected to complement, or even cause, the greater neophilia we previously detected in bolder elk (Chapter 2). Such complementarity is presumably the reason such high proportions of animals were either strongly lateralized and shy, or weakly lateralized and bold, in each of BNP (68%) and JNP (90%). The 32% increase in this tendency in JNP, compared to BNP, might be related to a higher density of predators, more frequent interactions with humans, or other factors that bear on the relative advantages of co-evolved behavioural tendencies. For example, higher predation risk selected for strongly lateralized poeciliad fishes (*Brachyrhaphis episcopi*; Brown et al., 2007), and predation risk has also been correlated with boldness in a cyprinid fish (*Rutilus rutilus;* Chapman et al., 2011).

Together, our results demonstrate high potential relevance of measuring both lateralization and personality in the context of wildlife management, especially for habituated animals that invoke human-wildlife conflict. We have shown that laterality can be measured with simple and non-invasive methods, even in large, wild animals. We suggest that this approach could make it possible to identify the animals that are most prone to habituate while they are young enough to alter their behavioural trajectories and before conflict intensifies. This approach could increase the efficacy of aversive conditioning as a management technique, which has already been shown to reduce habituation behaviour in elk (Kloppers et al., 2005), brown bears (Rauer et al., 2003), and wolves (Hawley et al., 2009). More management tools are needed to meet the challenges of ever-expanding human populations that are increasingly intolerant of traditional methods, such as lethal management (Walter et al., 2010). For example, the current management of elk in Banff culls up to 20 habituated animals each year to promote human safety and ecological integrity, but this practice is unpopular with many members of the public and the practice is reviewed annually to justify its continuation.

Application of behavioural metrics to problems in wildlife management has the potential to advance a more basic understanding of variation in individual behaviour and to address many pressing problems in conservation biology. There is a strong heritable component to each of personality (Cattel et al., 1955) and laterality (Vallortigara & Rogers, 2005) and their coevolution has been correlated with strategic life choices (Dochtermann & Dingemanse, 2013). It follows that the rapidity with which human-dominated landscapes are changing (Lowry et al., 2013) exerts strong selective gradients on both the heritable and plastic components of these traits. It should be possible to predict the direction of the resulting selective gradients and the relative advantages of individuals with different sets of traits. For example, similar acknowledgements have already been applied to promoting greater success for captive breeding and reintroduction programs (Seddon et al., 2007), which supported the selection of bolder personalities for reintroduced black rhinos (*Diceros bicornis*; Watters and Meehan, 2007), and pre-release training about predators for bilbies (*Macrotis lagotis*; Moseby et al., 2012). Similarly, both personality and lateralization could be relevant to anticipating which individuals will overcome the effects of climate change on forage availability (e.g. Pettorelli et al., 2005) and predator-prey dynamics (e.g. Barton, 2014), or prevail in urban environments (following Atwell et al., 2012). Most kinds of conservation threats favour bolder, more flexible individuals (St. Clair et al. in press), which is likely to result in wildlife populations that are increasingly susceptible to habituation. Predicting those changes may make it possible to identify and promote optimal levels of boldness and lateralization in contexts ranging from conservation to conflict.

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Table 4-1. Generalized linear models for elk wariness changes in response to different modes of human-induced stimuli. Response variables are individual mean changes in flight response distance as a result of either "benign" (i.e. habituation responses to consecutive human approaches) or "aversive" (sensitization in response to predator-resembling chases). Parameter *P*-values compare relative ability of laterality to predict behavioural changes compared to personality, best ranked models are italicized.

					LATERALITY[a]		**PERSONALITY**[b]	
TREATMENT	**MODEL**	**AIC**	**LL**	**n**	**z**	**p**	**z**	**p**
benign[c]	***laterality***	-0.347	6.87	28	2.19	0.029	~	~
	personality	-0.210	4.94	28	~	~	-0.90	0.366
(Banff)	both	-0.288	7.03	28	2.09	0.045	-0.54	0.590
benign	***laterality***	-0.790	9.90	20	2.62	0.009	~	~
	personality	-0.727	9.27	20	~	~	-2.31	0.021
(Jasper)	both	-0.712	10.12	20	1.23	0.220	-0.62	0.538
aversive[d]	laterality	0.579	-2.92	17	-3.35	0.001	~	~
	personality	0.180	0.468	17	~	~	4.90	<0.001
(Jasper)	both	0.263	0.766	17	-0.71	0.480	2.76	0.006

[a] Absolute front limb biases for digging behaviour. [b] Gradient of "boldness" of personality type. [c] Consecutive passive human approaches separated by 7-10 minutes. [d] 10 minute long predator-resembling chases. These responses were considered "habituation responses".

Table 4-2. Logistic regression models predicting migratory choices by elk in Banff and Jasper national parks, AB. Personality values are based on the delineation of behavioural syndromes into a single dimension. Laterality is the absolute value of the strength of front limb biases during winter digging behaviour.

Model	**Study Area**	**AIC**	χ^2	**L-L**	**R**$^{2\ b}$	**p**	**res:mig**^{c}
personality[a]	Banff 2010	41.08	7.17	-18.54	0.162	< 0.01	14:21
personality	Banff 2011	66.21	6.78	-31.11	0.098	< 0.01	21:29
laterality	Banff 2011	63.07	9.93	-29.53	0.144	< 0.005	21:29
combined	Banff 2011	***61.61***	13.38	-27.81	0.194	< 0.005	21:29
personality	Banff 2012	50.77	3.25	-23.39	0.065	0.072	14:24
laterality	Banff 2012	50.65	3.36	-23.33	0.067	0.067	14:24
combined	Banff 2012	***49.11***	6.91	-21.55	0.138	0.032	14:24
personality	Jasper 2012	19.60	11.13	-7.80	0.417	< 0.001	14:7
laterality	Jasper 2012	19.69	11.04	-7.84	0.413	< 0.001	14:7
combined	Jasper 2012	***19.10***	13.63	-6.55	0.510	< 0.005	14:7

[a] Laterality not recorded in 2010. [b] Nagelkerke's pseudo R^2. [c] Number of individuals that were either resident or migrant.

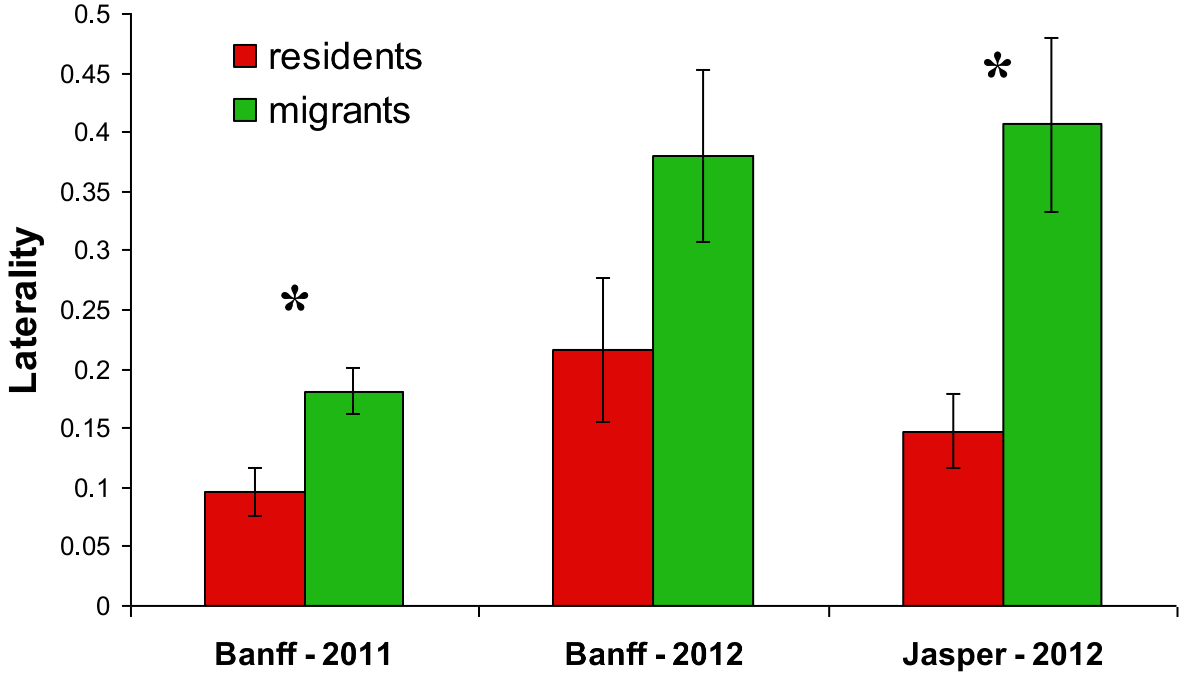

Figure 4-1. Comparison of behavioural lateralization in migratory (n = 29, 24, 7) and non-migratory (n = 21, 18, 13) elk in Banff (2011 & 2012) and Jasper (2012) National Parks, AB. Absolute strength of lateralized biases (Y-axis) calculated using |(L-R)/(L+R)|, from individual limb choices when elk dig through snow. Error bars represent SE.

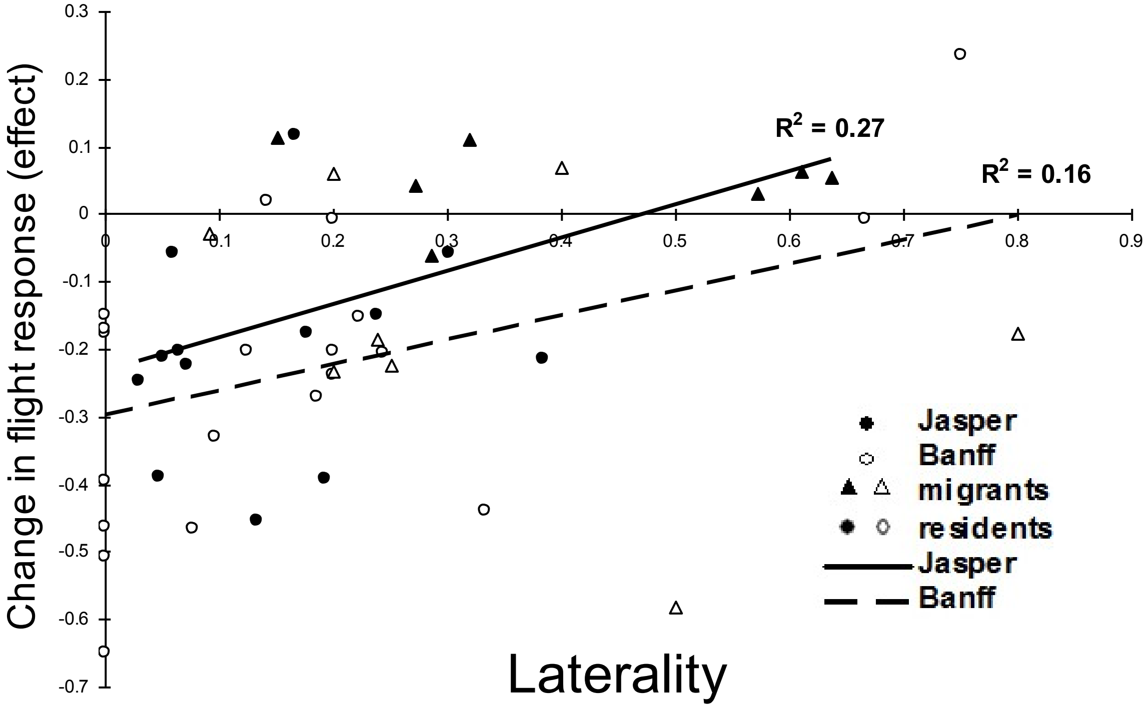

Figure 4-2. Correlation between laterality and mean individual flight response changes between two consecutive benign human approaches. Each elk was subjected to multiple trials during which its flight response distance was tested twice consecutively, within a 7-10 minute period, and these changes were averaged for each individual. Negative values on the Y-axis thus indicate the mean change by that individual was a habituation response. Laterality was based on individual mean front limb biases, using |(L-R)/(L+R)|. Trials were conducted on migratory/resident elk in Jasper (n = 7/13) and Banff (n = 14/15) National Parks, AB, in the winters of 2012-13.

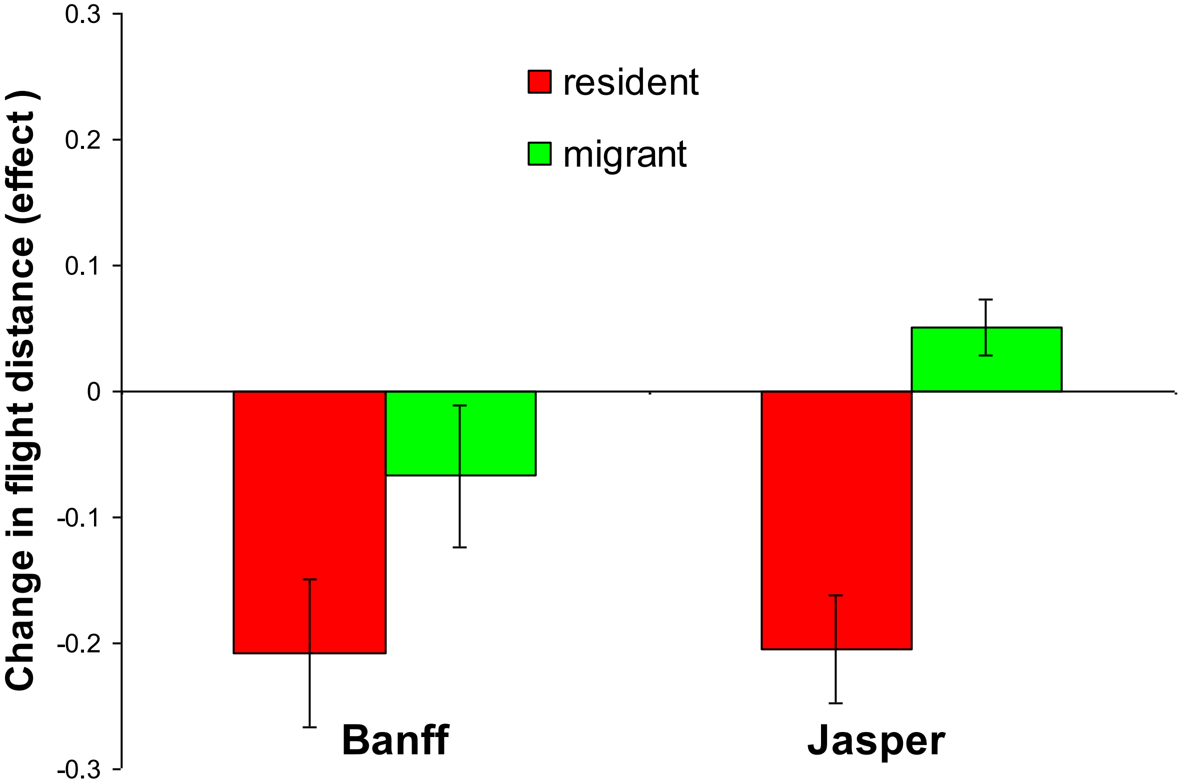

Figure 4-3. Mean change in elk flight distance in response to consecutive benign approaches by a human. Effect size is for the change in flight response distance between initial approach and a second approach 7-10 minutes later. Means are based on individuals changes exhibited during multiple tests of elk that were either migratory (n = 28,7) or residents (n = 16,13). Data is from winter, 2012-2013.

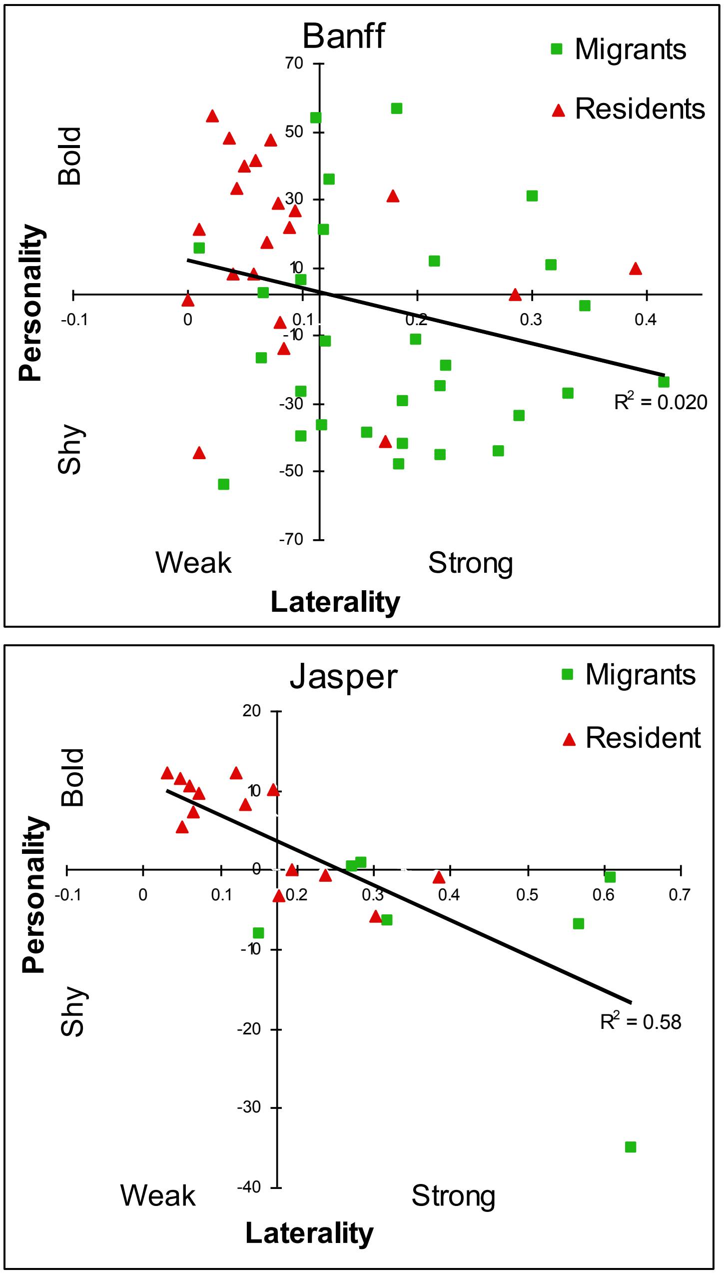

Figure 4-4. Correlations between gradients of laterality in wild elk in Banff **(top)** and Jasper **(bottom)** National Parks, AB. Banff data is from a single elk herd composed of a mix of both migratory and resident individuals. Jasper data is from three discrete herds within which two are migratory, and one largely non-migratory. X and Y axes are at global medians for each of laterality and personality, and define quadrants of Weak vs. Strong laterality and shy vs. bold personality type.

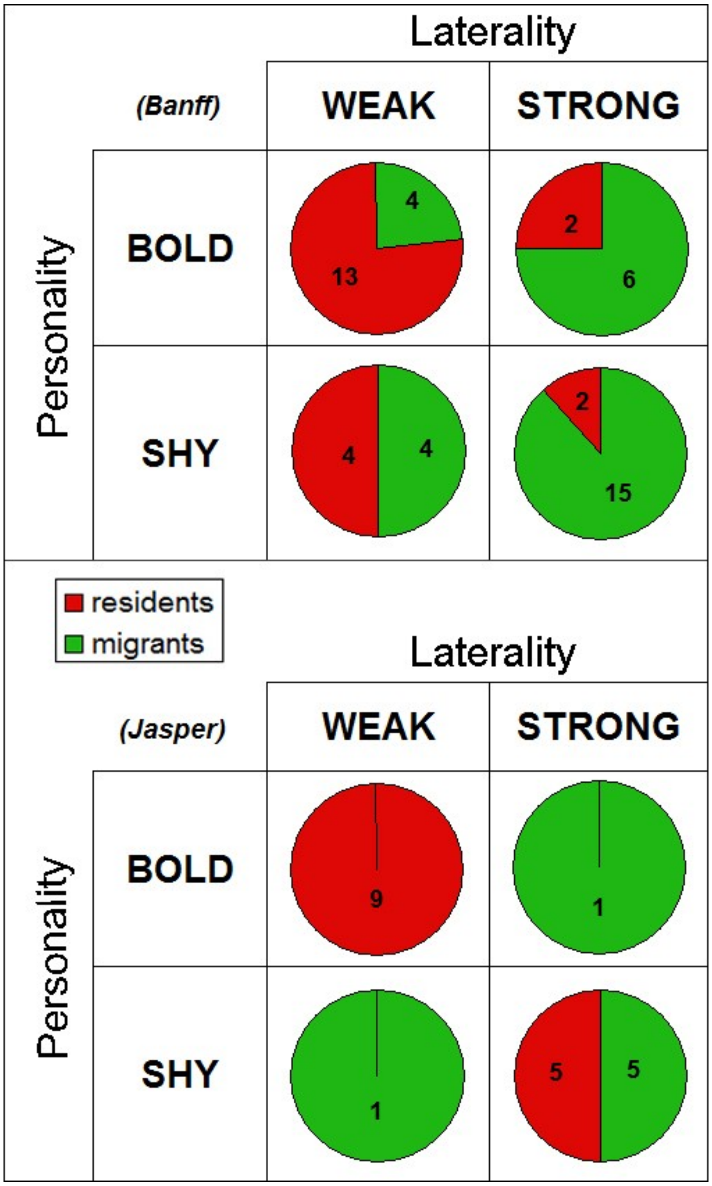

Figure 4-5. Proportions of migrant and resident elk classified by absolute magnitude of "laterality", using front-limb biases, and a "personality" gradient derived from a behavioural syndrome with 5 separate personality traits. Numbers on graphs are actual numbers of resident and migrant individuals. Data is from populations in Banff (top) and Jasper (bottom) National Parks, AB.

Chapter 6

General Discussion

Summary of Results

The purpose of this thesis was to quantify behavioural variation among and within individuals and to identify its potential application to wildlife management, particularly in the context of habituation and migration by ungulates. I addressed this purpose by studying wild populations of elk (*Cervus canadensis*) in Banff and Jasper National Parks, which are comprised of both migratory and non-migratory individuals, and a captive population near Edmonton, Alberta, Canada. In wild population, declining migratory behaviour and increasing habituation can cause excess herbivory, trophic disruptions to both predator and vegetation communities, and direct threats to public safety. I hoped to provide new information and innovative tools for wildlife managers to address these problems by identifying the behavioural characteristics of elk that were associated with each of them. I explored these behavioural characteristics in each of the data chapters of this thesis with successive foci on behavioural types along a continuum of shy-bold personality types, responses to aversive conditioning, and plasticity correlates with expressions of lateralization. I related each of these attributes to the migratory strategies of individuals.

In Chapter 2, I demonstrated that both wild and captive elk exhibit behavioural syndromes and show that wild individuals of different migratory strategies (resident vs. migrant) have different mean values in a composite metric of personality based on up to 7 different traits. The expression of these behavioural traits was consistent within individuals and among years, and was not influenced by age. Using multivariate techniques, I was able to delineate these behavioural syndromes along a gradient I interpreted approximately as shy to bold. Bolder elk were characterized by lower flight distances, reduced responsiveness to sounds, occupancy of more peripheral positions within groups, greater exploration of novel objects, increased vigilance, social dominance over shyer conspecifics, and a greater frequency of leading other elk to new habitats.

Together, these results support other studies that demonstrate a correlation between aggression and risk-taking behaviour during foraging (e.g., Bell, 2007). Elk with bolder personalities were more likely to adopt non-migratory, resident strategies, while elk with shyer personalities were more likely to migrate. This pattern was evident in both Banff, where migrants and residents formed a single overwintering group, and Jasper, where elk formed three discrete herds, within which most individuals shared the same migratory strategy. Although few studies have addressed these correlates in wild populations, similar results have been reported in fish. Bolder salmonids (*Salmonidae spp*.) were favoured in habitats with higher levels of human disturbance (Huntingford & Adams, 2005) and a boldness trait in roaches (*Rutilus rutilus*) was positively correlated with the choice to migrate (Chapman et al., 2011). In the roach system, bolder individuals used migration as a way to access an area without predators, similar to the way bolder elk in my own study were more likely to live as residents in a predator refuge. The presence of a similar gradient of shy through bold individuals in the captive elk population I studied demonstrated that variation in personality can be maintained even in the absence of predation or habitat heterogeneity.

In Chapter 3, I related differences in elk personality to responses to aversive conditioning (AC) for wild elk in Jasper, with the goal of providing new insights for the management of habituated wildlife. Implementation of AC successfully increased the wariness of these elk, supporting prior demonstrations of the efficacy of this tool for increasing wariness in black bears (*Ursus americanus*; Rauer et al., 2003), elk (Kloppers et al. (2005) and wolves (*Canis lupus*; Hawley et al., 2009). I went beyond these other studies by showing that elk with bolder personality types exhibited greater responsiveness, which I measured as larger gains in wariness during conditioning, but also greater subsequent losses in wariness (or recidivism) following the conditioning period. If this result can be generalized to other species, it may explain other findings, such as why more habituated black bears responded more strongly to AC chases (Mazur, 2010) although, contrastingly, it was the less habituated bears in that study that exhibited greater recidivism.

In Chapter 3, I also implemented two different approaches to AC; one that allowed targeted elk to remain in groups, and another that focused on isolating target individuals. My use of Isolation AC provided a novel application of modern horse-training techniques (reviewed by McGreevy, 2007) with a goal of using isolation to impart higher levels of stress to increase the aversion caused by the stimulus. Although Isolation AC was no more effective at increasing wariness, it produced lower recidivistic losses. Nonetheless, the net effect of AC remained similar for the two treatments. This finding reinforces a view that learned wariness by habituated animals will gradually disappear when the aversive stimulus is removed (Lattal & Lattal, 2012).

Proceeding from Chapter 2, I found that resident elk had greater increases in wariness during conditioning than migrant elk did, but residents also had subsequently greater recidivistic reductions in wariness once conditioning had ceased. One year after AC treatment, migrants had retained about half of their conditioned increases in wariness, whereas residents had lost all conditioned gains. The net effect of AC on residents vs. migrants reinforced my conclusion from the rest of this chapter that personality had little influence on the net effectiveness of temporary regimens of aversive conditioning.

In Chapter 4, I examined the metric of cerebral lateralization as a potential mechanism for the apparent plasticity in wariness responses by the bolder elk found more often in human-disturbed areas. I calculated the lateralization of individuals by recording which front hoof was used to crater in snow, which is comparable to metrics used for domestic animals, and also humans. Although the direction of biases for using the left vs. right front limb differed between populations in Banff and Jasper, the absolute magnitude of individual laterality was higher in the animals with lesser responsiveness to both benign and aversive stimuli.

This result was consistent with the greater responsiveness of more habituated animals of other species (Bejder et al., 2009), which may help to interpret the variation in habituation responses that has been reported in house sparrows (*Passer domesticus;* Ensminger & Westneat, 2012) and yellow baboons (*Papio cynocephalus*; Strum, 2010). In the elk I studied, habituation responses were more strongly correlated with laterality than with personality, indicating the potential importance of this additional axis of behavioural variation (Vallortiagra & Rogers, 2005). Ungulates are known to exhibit high individual variation in wariness responses (e.g. Recarte et al., 1998) and increase plasticity of response may pre-adapt some individuals to thrive in urban areas, as appears to occur in juncos (*Junco hyemalis*; Atwell et al., 2012). In elk, laterality alone could predict migratory strategies, but the combination of laterality and personality provided a more robust explanation. Similar complementarity in these axes was context dependent in convict cichlids (*Archocentrus nigrofasciatus*; Reddon & Hurd, 2009), but it appeared to distinguish populations in my studies of elk in Jasper and Banff.

Applications and Implications

Despite the ongoing increase in personality research on non-primate species, there are still very few studies of behavioural syndromes with application to wildlife management (Dingemanse et al., 2012). Such studies are urgently needed for ungulates, whose large size and gregarious nature can cause rapid changes to habitat (e.g. Geist, 1982; Putman, 1996). The effective management of these species is sure to be limited if their populations are assumed to exhibit homogenous responses to human disturbance and the presence of behavioural syndromes is ignored (*sensu* Sih et al., 2012).

My finding that migratory elk were typically strongly lateralized and with shyer personality types, whereas resident elk were typically weakly lateralized with bolder personality types, may offer some general insights for the loss of migratory behaviour in ungulates around the world (reviewed by reviewed by Berger, 2004). Because personality and laterality appear to be quantify different dimensions of consistent individual behaviour (Coppens et al., 2010), their expression likely predisposes individuals to particular life history strategies (*sensu* Biro & Stamps, 2008; Dochtermann & Dingemanse, 2013). Bolder animals that are less lateralized are more likely to discover the novel food resources of human-dominated areas and might learn more quickly that predators avoid these areas. The same characteristics make these animals more likely to habituate to people, further amplifying their benefits and reducing their costs of co-occurrence. In effect, expanding human populations are likely selecting for animals that are increasingly bold and flexible, and a similar process may apply to other species that exploit human-disturbed areas (Walter et al., 2010).

By seeking to identify the behavioural types comprised by suites of related behavioural responses (as defined by Wilson et al., 1994), managers could predict the potential for particular behaviours (such as conflict with people) without needing to observe them directly or wait until conflict develops. For example, the raiding of crops by specific baboons (Strum, 2010) or consumption of garbage by particular bears (Linnel et al. 1999) might be predicted by previous expressions of bold behaviours or high flexibility in behavioural responses. For elk, I used the provision of novel objects and recording of responses via remote cameras to identify bolder individuals, which were also less wary of people and less sensitive to novel sound stimuli. Similar applications to other management contexts have revealed that neophobic (shy) cattle exhibit more desirable patterns of habitat use (Wesley et al., 2012), and bold feral cats are most vulnerable to communicable feline diseases (Natoli et al., 2005).

In my own focal context of aversive conditioning and habituated wildlife, knowledge of animal personality is likely to support management that is more ethical, as well as effective. Aversive conditioning is already considered to be a more ethical alternative for managing habituated, hyper-abundant populations than translocation (e.g. Whitwell et al., 2012) or lethal management (e.g. Koval & Mertig, 2004), but knowledge of personality could make a further ethical contribution by limiting the unnecessary conditioning of non-target animals. Peripheral exposure to aversive stimuli can actually elicit desensitization responses that are counter to the goal of sensitization (Domjan, 2010), and mitigating this effect was one of the motivations for my exploration of the Isolation-based method of AC I devised for Chapter 3. Further research will be needed to determine the generality of the tendency I reported for bolder elk to exhibit less recidivism when treated with Isolation AC.

More generally, an understanding of individual variation and associated plasticity in responses may enhance wildlife management and conservation in diverse contexts (Reale et al., 2007). For example, it may help managers to predict the effects of other phenomena, such as the introduction of predators (e.g. Niemala et al., 2012) or the loss of habitat (e.g., Sol et al., 2013). Quantifying metrics of personality and lateralization might find application in specific forms of mitigation, such as the creation of new, artificial waterholes for elephants (*Loxodonta spp*.; Smit et al., 2007) or the provision of supplemental feed sources for moose (*Alces alces*; Gundersen et al., 2004). In general, applications that promote coexistence between people and wildlife should likely target bolder, more flexible individuals for retention or reintroduction (e.g., Ngokaka et al., 2010).

My study illustrates one example of the variation in individual behaviour that is expected to arise whenever habitats provide heterogeneity in risk and reward (Wolf & Weissing, 2012). In such habitats, each individual weighs costs and benefits of particular habitat features uniquely. Increasing rates of human disturbance in landscapes around the world make these ratios of costs and benefits both individualistic and dynamic. By anticipating the sources of this complexity, humans might use the levers of fear and self-interest to manipulate individual decisions, thereby fostering greater co-existence of humans and wildlife.

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Appendix

Table A-1. Comparison of separate personality trait values for 33 Banff elk that were assayed in both 2010 (n = 35) and 2011 (n = 51; see Figure 2-2a).

Elk[a]	Flight		Novel Sound		Position		Dominance[b]		Exploration		Vigilance	
	2010	*2011*	*2010*	*2011*	*2010*	*2011*	*2010*	*2011*	*2010*	*2011*	*2010*	*2011*
M	55.0	49.4	29	22	3.05	2.64	90	88.3	2.94	1.50	0.120	0.025
M	49.0	49.1	24	22	1.46	3.05	30	27.7	0.83	2.50	0.063	0.011
M	40.2	45.4	28	20	3.53	3.20	50	75.5	4.00	3.90	0.098	0.007
M	24.9	14.8	7	3	3.31	3.95	90	95.8	0.00	3.86	0.043	0.001
R	18.6	20.4	4	4	3.48	3.91	90	92.6	2.25	3.75	0.069	0.009
M	39.7	44.2	14	14	3.08	3.64	30	38.3	0.00	3.33	0.042	0.031
M	50.5	66.4	15	27	3.00	3.11	10	20.2	0.00	0.00	0.029	0.021
M	46.3	52.4	16	18	2.71	3.40	10	25.5	0.00	2.00	0.053	0.008
M	52.4	42.7	22	9	3.58	3.67	30	38.3	3.00	2.00	0.078	0.031
M	29.1	28.7	8	5	2.89	4.00	70	81.9	3.36	4.00	0.025	0.015
M	52.5	61.6	24	24	2.65	3.10	10	20.2	0.00	0.00	0.046	0.038
R	30.0	34.2	6	9	2.75	3.82	90	70.2	3.14	3.77	0.058	0.012
M	24.0	17.6	2	2	3.93	3.83	90	100	3.75	4.00	0.050	0.004
R	14.5	17.1	4	1	3.82	4.00	90	97.9	3.40	3.33	0.048	0.000
R	20.1	25.4	8	4	3.71	3.91	90	85.1	3.36	3.60	0.021	0.004
R	23.8	28.1	5	5	2.76	3.65	90	88.3	2.64	3.93	0.024	0.009
R	17.2	31.7	1	9	3.09	4.00	90	81.9	2.50	3.80	0.059	0.005
R	27.8	31.0	9	7	3.17	3.71	70	68.1	3.25	3.96	0.062	0.006
R	34.5	29.0	19	7	2.97	3.22	70	62.8	1.33	4.00	0.079	0.005
M	42.7	53.3	21	23	2.60	3.32	10	8.5	1.67	2.00	0.054	0.010
R	25.1	31.2	8	15	3.53	3.14	70	75.5	3.28	4.00	0.053	0.006
R	39.3	29.9	12	6	3.44	3.67	90	75.5	2.20	3.20	0.024	0.000
R	32.3	35.4	10	12	2.67	3.29	30	47.9	1.82	3.50	0.012	0.052
M	44.1	53.0	24	28	1.64	2.78	10	8.5	1.50	0.25	0.064	0.062
M	55.6	56.1	21	19	1.85	3.55	10	30.9	0.00	1.25	0.014	0.011
R	43.5	39.6	19	11	1.93	3.40	30	51.1	2.00	0.00	0.022	0.030
M	56.5	51.4	30	26	2.50	3.15	10	8.5	4.00	3.50	0.034	0.020
R	55.8	49.6	31	23	2.60	2.85	10	11.7	0.00	2.25	0.038	0.026
M	45.2	60.4	17	26	2.84	2.67	30	30.9	0.50	3.50	0.092	0.023
M	41.0	48.2	28	20	3.29	2.75	30	8.5	0.00	0.00	0.104	0.014
M	34.7	35.4	11	10	2.82	3.26	50	68.5	2.69	3.10	0.035	0.058
M	38.4	46.5	14	13	2.14	3.56	10	38.3	0.83	1.50	0.017	0.012
M	34.8	46.5	21	21	2.85	3.25	50	66	2.69	3.21	0.043	0.012

[a] Individual elk that was either a migrant (M) or resident (R). [b] Dominance hierarchies were scaled to account for measurement and group size differences.

Table A-2. Correlations (= r) between each separate personality trait metric and **(top)** personality (from NMDS), and **(bottom)** laterality (front limb biases) gradient values, for different populations of wild (Banff and Jasper National Parks) and captive adult female elk.

PERSONALITY

	Banff 2010	***Banff 2011***	***Banff 2012***	***Jasper 2012***	***Captive 2012-13***
flight	-0.820	-0.884	-0.990	-0.994	-0.997
vigilance	-0.041	-0.447	0.025	-0.704	no data
position	0.622	0.641	0.349	0.478	0.543
exploration	0.571	0.647	0.544	0.532	0.862
sound	-0.758	-0.447	no data	no data	no data
dominance	0.994	0.647	0.426	0.713	0.760
leading	0.545	no data	no data	no data	no data

LATERALITY

	Banff 2010	***Banff 2011***	***Banff 2012***	***Jasper 2012***	***Captive 2012-13***
flight	no data	0.290	-0.013	0.762	no data
vigilance	no data	0.160	-0.144	0.603	no data
position	no data	-0.241	-0.010	-0.268	no data
exploration	no data	-0.315	-0.158	-0.323	no data
sound	no data	0.261	no data	no data	no data
dominance	no data	-0.262	-0.102	-0.421	no data


496

Figure A-1 Examples of novel objects and scoring of elk exploratory responses. From top to bottom: 1) visit site only, 2) approach object (within one body-length), 3) investigate object (within one head-length) but no contact, and 4) physical interaction with the object.

Figure A-2. Early part of 10-minute long Isolation-based aversive conditioning trial. One human pursuer is wearing camera, second is at back left. Elk with radio-collar (left) is highly stressed and trying to return to the herd (herd is far left, out of frame), suggesting she is aware she is the target of the isolation. Elk on right is interested but not visibly stressed, suggesting she is aware she is not the target.

Figure A-3. **(top)** Throwbag in mid-air after being tossed in advance of elk attempting to run in between the two human pursuers (note 2nd pursuer on far left) during "Isolation" type aversive conditioning. Elk's trajectory is directly towards the entirety of the herd, which is off camera at a distance. **(bottom)** The aftermath, showing the elk abruptly changed direction.

Figure A-4. Young elk demonstrating left front-limb bias during "cratering" behaviour, to access snow covered forage.