BEHAVIOURAL RESPONSES OF NEWFOUNDLAND WOODLAND CARIBOU TO PREDATOR CUES

by

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ABSTRACT

Insular Newfoundland woodland caribou (*Rangifer tarandus*) have experienced tremendous population declines since the early 2000s, attributable to density-dependent processes mediated largely by predation. Given the diversity of island predators (black bears, coyotes, lynx and bald eagles), caribou are thought to perceive and react to the different predators in a manner that accordingly minimizes the probability of death and maximizes benefits of fitness-enhancing activities. The presence of predators requires prey species to divert energy resources from foraging and feeding behaviours to vigilance and predator avoidance behaviours. This study was designed to identify and describe caribou behavioural responses to predator encounters. Experimental approach trials (n=137) were employed in the calving region of the Middle Ridge caribou herd (central Newfoundland) in order to simulate different predator visual cues and to elicit corresponding caribou flight responses. Approach trials encompassed the time period when calf mortality by predation is highest. The flight initiation distance of caribou (the distance between approacher and caribou at the moment of initial flight) was found to differ in accordance with the colour of clothing (tan or black) but not the movement mode (walk or crawl) employed by human experimenters. Flight initiation distance was greater in response to black approaches and was greatest during the two week calving period from late May to mid June. There was little evidence that vegetation resources influenced the decision to remain or flee; however this finding may reflect the calving range fidelity of caribou to areas of consistent forage quality. This study yields important findings concerning variation in predator avoidance behaviour of caribou in response to historical (i.e., black bear, *Ursus americanus*) and novel (i.e., coyote, *Canis latrans*) predators. Differential behavioural responses to predators are particularly important to understand as rapidly growing anthropogenic landscape development and use is leading to increased predator encounters.

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1 General introduction

1.1 Background of caribou antipredator behaviour in Newfoundland

In Canada, most caribou (*Rangifer tarundus*) populations are in decline and many are at record low numbers (EC 2011, Festa-Bianchet et al. 2011). The need to understand the mechanisms contributing to wide-spread changes in caribou persistence becomes particularly poignant considering that the majority of caribou and reindeer (*Rangifer tarandus*) populations studied globally are reported to be in decline (Vors and Boyce 2009). Although many caribou populations fluctuate on multi-decadal timescales, reflecting changing vegetation availability and predation pressure, recent abundance changes are further attributed to a combination of pressures from increased human activities and climate change (Festa-Bianchet et al. 2011). These additional pressures raise concerns over whether caribou populations will be able to recover from current declines.

The lethal effects of predation are well-recognized factors in caribou population changes (Bergerud and Elliot 1986, Seip 1991, Hayes et al. 2003, Wittmer et al. 2005). However, predators also alter the fitness of prey through non-lethal effects by displacement of prey from their preferred habitats, and activities. To maximize reproductive fitness, prey must make trade-off decisions between energy allocation towards predation evasion and acquiring adequate resources. Antipredator behaviours enhance fitness of prey when they allow prey to avoid death and do not greatly interfere with other energetically favourable activities (Lima and Steury 2005). Likewise, foraging and rest activities enhance fitness when predation does not result. The optimal point at which to shift from foraging and rest behaviours to antipredator behaviours (Cooper and Frederick 2007) depends on a suite of biological factors, including breeding status, habitat and predator lethality (i.e., the probability of being killed on contact). Predator-prey interactions are dynamic and predators can stimulate phenotypic changes in prey life history traits, altering prey development, morphology, physiology and behaviour (Preisser et al. 2005, Blumstein 2006). These trait changes can have stronger effects on population fitness than direct mortality effects (Preisser et al. 2005) and may also have ‘spillover’ effects on other members of the ecological community (Peacor and Werner 1997, Preisser et al. 2005, Sih et al. 2010). The far-reaching consequences of non-lethal predator-prey interactions clearly merit consideration in ecosystem conservation research and management efforts.

On insular Newfoundland, caribou have declined island-wide by 66% since the early 2000s, mediated largely by unprecedented calf mortality rates (Weir et al. 2014). Predation is the primary proximate cause of calf mortality in Newfoundland where caribou face a diverse spectrum of predators including black bears (*Ursus americanus*), bald eagles (*Haliaeetus leucocephalus*), lynx (*Lynx canadensis*) and most recently, coyote (*Canis latrans*). In the last 30 years, Newfoundland caribou have also exhibited decreases in body size, antler size and birth weight suggesting limited access to food resources mediated by density-dependent and climate change effects (Mahoney et al. 2011, Trinidade et al. 2011, Weir et al. 2014). These physical changes may also be augmented by predator-induced costs of heightened vigilance and flight, diverting time from foraging and imposing high energetic costs on these caribou herds.

Predators induce energetically significant behavioural changes in prey; energy needs are compounded for individuals that are energetically invested in breeding, gestation, lactation, or other demanding conditions. Calving season marks a period of high energetic stress for caribou cows as parturient cows need to find sufficient forage to recover depleted body mass following the winter season, to sustain lactation, and to maintain antipredator behaviours necessary to protect vulnerable offspring (Taillon et al. 2012). Caribou calves are most susceptible to predation mortality during the first 6 weeks after birth (Bergerud 1971, Lewis et al. 2014, Weir et al. 2014). Trade-offs between antipredator behaviour and resource acquisition may be markedly apparent during this critical period, particularly in parturient females.

1.2 Scale of behaviour

Individuals alter their behaviour to dampen the effects of fitness-diminishing pressures such as predation, for example, by spatially and temporally segregating themselves from ranges occupied by predators. In caribou, large scale spatial segregation from predators occurs when some herds migrate annually over hundreds of kilometers, or on a medium scale (1 to 100km) when caribou choose habitats different than predators or alternate prey species, thereby reducing their chance of encounter with predators (Bergerud and Page 1987, Seip 1991, James et al. 2004, Briand et al. 2009). On a fine scale (less than1km), prey respond to risk or disturbance in a trade-off fashion, deciding either to continue ongoing activities, or actively increase the distance between themselves and the perceived threat (Lima and Dill 1990, Frid and Dill 2002, Corcoran 2013). The way in which non-lethal predator interactions influence the energy allocation of prey, via resource use and shifts in activities, is a concept referred to as ‘the ecology of fear’ (Brown et al. 1999, Kotler and Brown 2007). Since the 1980s, with the surge of advances in technologically mediated research methods, disturbance studies have largely shifted focus from local scale aspects to regional scale aspects of behaviour (Vistnes and Nellemann 2008). In fact, comprehensive understanding of ecosystem components, such as caribou antipredator behaviour, requires observational and experimental techniques at multiple scales in order to understand the consequences of disturbance (Syms and Jones 1999). This study focuses on the fine scale behavioural responses of caribou to predation risk and considers the findings within context of broader disturbance trends.

1.3 The economic hypothesis and optimal flight theory

The economic hypothesis predicts that animals adjust their antipredator flight reactions in a manner that maximizes benefits and minimizes costs (Ydenberg and Dill 1986, Figure 1.1). The moment of flight should be optimized to economize energetic costs associated with fleeing and abandoning fitness-enhancing opportunities, but also to reduce the possibility of death or fitness-diminishing injuries (i.e., optimal flight theory, Cooper and Frederick 2007).

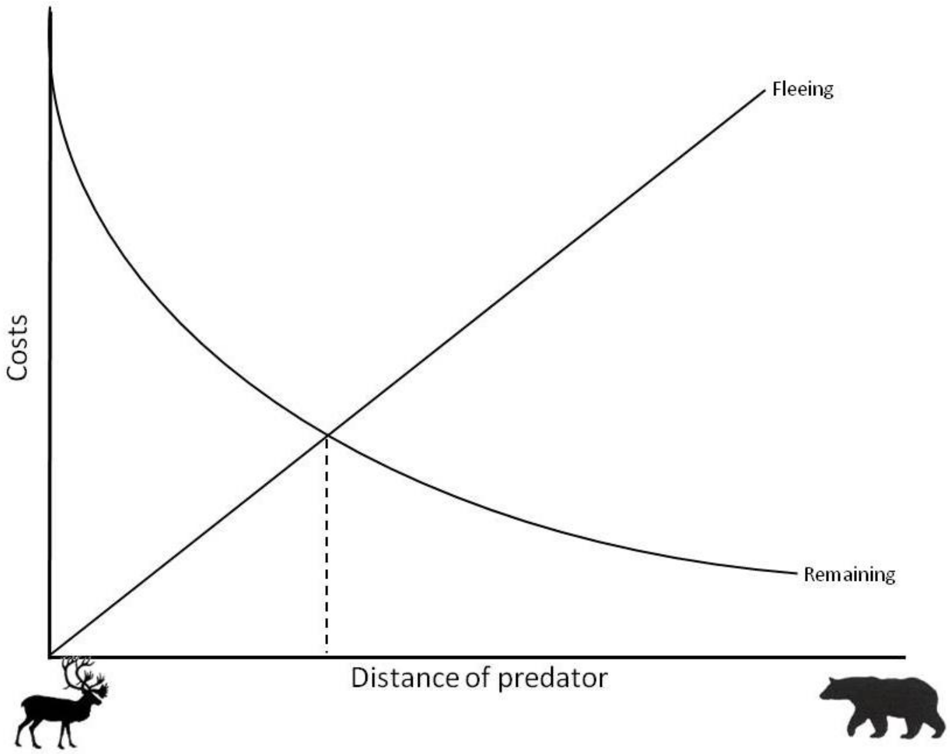

Figure 1.1 Hypothetical reaction distances of prey under the influence of a predator. The dotted line represents the optimal reaction distance where prey maximize benefits in relation to costs of both fleeing and remaining (adapted from Ydenberg and Dill 1986).

While many flight theory models consider all predator encounters to be lethal at contact (i.e., when distance = 0 between predator and prey), some predator-prey interactions, in fact, result in an escape or non-lethal injury (Cooper and Frederick 2007). The degree of threat varies with unique combinations of predator and prey species as well as predator and prey individuals (Cooper and Frederick 2010). Prey in multi-predator communities should detect and respond to distinct predators accordingly; prey with appropriate responses for one predator, but not others, may be at a selective disadvantage (Blumstein 2006). It is worth noting that actual risk may differ from a prey animal's perception of risk and may result in early or delayed flight (Sih et al. 2010). Less-than-optimal flight may occur, for example, in encounters with novel or unfamiliar predators.

A number of interacting factors contribute to the overall perceived risk of a threat and the optimal distance at which an animal will flee from a predator (Blumstein and Bouskila 1996, Frid and Dill 2002, Stankowich and Blumstein 2005). Factors may include: the structure of the environment (e.g., habitat features, distance to safety, food availabilty), social factors (e.g., group size, presence of vulnerable group members), the distribution and abundance of predators, predator features (e.g., behaviour, appearance, intent), and individual factors (e.g., experience with predators, satiation, body condition). Furthermore, these factors can vary with season, and in consequence, can underlie seasonal variation in antipredatory responses (Stankowich 2008). To provide examples, groups that are more vulnerable to predation (e.g., groups containing calves) may require more time to coordinate escape responses and, therefore, should initiate a flight response sooner (or a greater distance away) from the threat. On the other hand, groups which benefit from remaining at a site longer (e.g., due to high quality of forage or energetic stress) are expected to initiate flight at a shorter distance from the threat. These shifts in behaviour, in the face of conflicting objectives, represent trade-off decision making and serve to maximize fitness (Dill 1987). Due to numerous possible interactions between factors and the relative strengths of individual factors, prediction of optimal flight distances can be complex. There is little consensus in the literature regarding which variables are most important in predicting ungulate life histories (Weladji et al. 2002), but a few variables, such as calf presence, habitat, season, and group size, do appear recurrently in the literature as influencers of ungulate antipredator responses.

Little is known about the perceived risk of specific predators to caribou in Newfoundland as no prior studies have addressed this topic directly. The current mammalian predator guild of Newfoundland caribou lacks wolves (*Canis lupus*), the primary predator of most caribou populations elsewhere, but consists of black bears, lynx and coyotes. Black bears and lynx, like caribou, are indigenous to the island of Newfoundland, but coyotes have only expanded their range to the island within the last 30 years (Blake 2006). In the absence of wolves, it is uncertain how important bear, lynx and coyote have been in shaping the antipredator behaviours of Newfoundland caribou. Further, the manner in which caribou perceive newcomer coyotes is unknown – perhaps as high-risk canid threats, akin to their wolf predecessors, or rather as unfamiliar, baffling but benign creatures, or somewhere between these two extremes.

It is expected that caribou modify their antipredator responses as influenced by the cues of different predators. Caribou groups should react earlier to cues perceived as more threatening. Vulnerable caribou groups (e.g., those with young calves) should react most quickly to threatening cues and stronger antipredator responses should be apparent during the calving period when vulnerable calves are most abundant (Stankowich 2008). Furthermore, caribou antipredator responses may in part be mediated by environmental constraints, particularly forage and habitat quality (Tyler 1991, Lima 1998, Frid and Dill 2002 and references cited within), which affect the costs of remaining at or fleeing from a site.

1.4 Overview of study

The economic hypothesis is used in this study as a framework to formulate predictions and to streamline analyses (Ydenberg and Dill 1986, Frid and Dill 2002). The primary objectives of this study are to:

1) determine whether caribou adjust their antipredator behaviours in response to visual cues representative of different predators;

2) determine if the strength of caribou antipredator responses changes throughout the calving season; and

3) establish whether aspects of vegetation and habitat are related to caribou antipredator responses.

Wild caribou herds were approached by a human researcher to elicit antipredatory reactions. Each approach simulated different predator cues by varying the colour of the aproacher clothing (black or tan) and the movement of the approach (walking or crawling). The distance between caribou and researcher at the first sign of overt alert behaviour (alert distance), immediately before flight (flight initiation distance), the distance interval between the alert and flight distances (assessment interval distance), as well as the distance caribou moved away from their original location were measured and used to evaluate the perceived risk of threat (see Chapter 2). Differences in alert, flight, assessment and distance moved measures allow inference of a prey’s perceived risk of an encounter. These responses are relatively simple measures to obtain through systematic approaches. Flight initiation distance, in particular, is widely used to quantify perceived risk in many species and habitats (Tarlow and Blumstein 2007). Alert distance (AD), flight initiation distance (FID), distance moved (DM) and assessment interval distance (AID) were used as response variables to test the following predictions: caribou groups will have longer AD, longer FID, longer DM and shorter AID when: 1) encountering stimuli which more closely approximate local lethal predators, 2) groups are comprised of vulnerable group members such as calves and energetically stressed individuals, and 3) immediate forage quality and availability is low. It should be noted that the interpretation of overt alert behaviours in ungulates is a contentious topic in itself – it may be the distance at which caribou first become aware of an approaching threat or first signal awareness of an approaching threat. For the purposes of this study, I do not attempt to tease apart these finer points since, in either case, overt alert behaviour indicates awareness of the approacher.

While it is useful to understand behavioural responses to isolated factors of interest, realistically, ecological systems are complex, dynamic, and rarely involve a single predator. An intricate network of individual and interacting ecological factors and processes are likely responsible for caribou flight responses, with some factors being more influential than others. To account for the stochastic nature of ecosystems, this study uses information theoretic analyses to allow consideration of numerous ecological, social and geographical variables in conjunction with the experimental variables (i.e., simulated predator cues) of interest. Hence, the above predictions are assessed via traditional hypothesis testing (e.g., 2-way ANOVA) and are also considered simultaneously within predetermined, biologically-relevant, multiple regression models. The complete model sets, relevant hypotheses and model selection process are described in Chapter 2 (section 2.2.4). Models cannot fully describe all of the ecological processes influencing caribou flight responses; however, some models may highlight important influential factors of Newfoundland caribou antipredator responses to be considered in future research and management.

Field research was carried out in the interior of central Newfoundland on the Middle Ridge (MR) caribou calving grounds. The region is characterized by areas of vast, open-habitat, bog and fen complexes, interspersed with tracts of dense forest. Data collection occurred in open areas where lakes, ponds, bogs, fens and low ridges are common (Figures 1.2, 1.3). Research was conducted in the late spring and early summer of 2011 (May 19 - July 18), just prior to the initiation of calving until the caribou dispersed across their late summer range. Newfoundland caribou are seasonal migrants, moving relatively short distances between seasonal ranges. During the late spring and early summer, caribou spend significant time aggregated in open calving territory, with calving usually occurring within 10 days in late May and early June (Soulliere 2008). The majority of calf mortality (over 80%) occurs within 12 weeks of calving (Trinidade et al. 2011). Summer is a period of high predation vulnerability for calves and, due to caribou social nature and parental investment, a period during which antipredatory responses in caribou should be most evident.

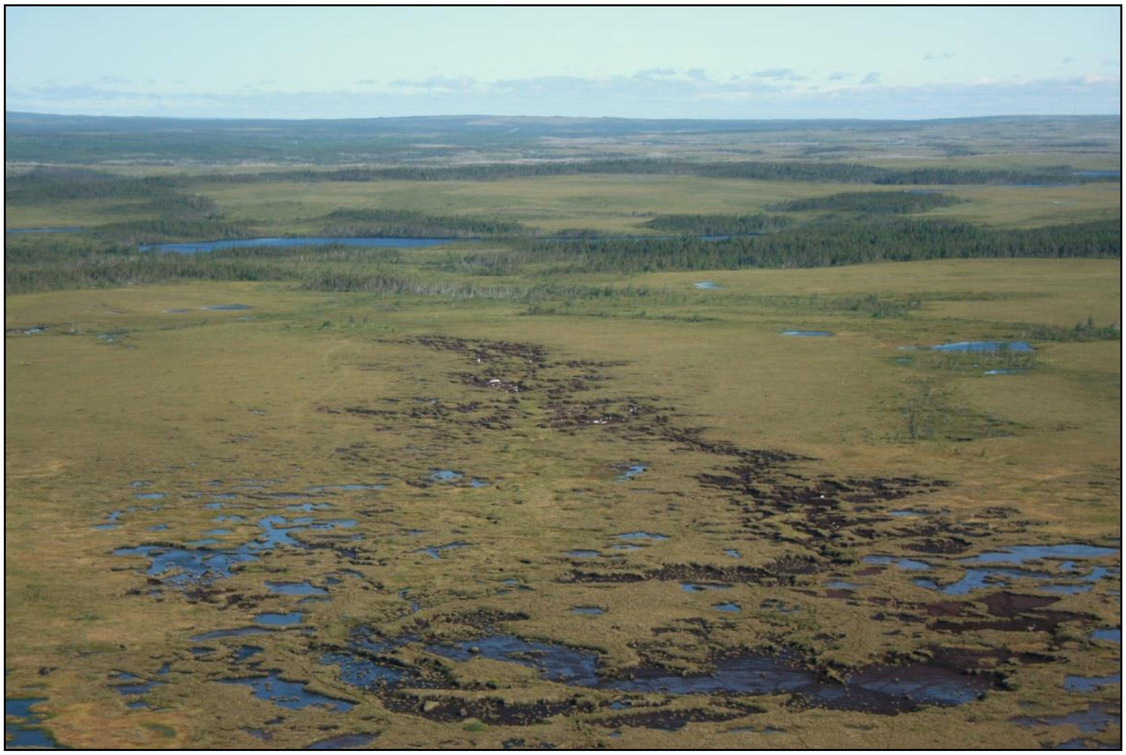

Figure 1.2 Aerial view of habitat features at the Middle Ridge study site. Note the extensive, relatively flat and open bog habitat interspersed with small ponds and forested areas.

Figure 1.3 Photograph showing habitat features of the Middle Ridge calving study site. Note the open, hummocked landscape and mixed plant composition of shrubs, graminoids, mosses and lichens.

This study examines behavioural responses of Newfoundland caribou in context of non-lethal predator-prey interactions (a component rarely addressed in comprehensive predator-prey studies) in a multi-predator ecological community. Experimental approaches are used to elicit responses to various simulated predator stimuli, and responses are measured and considered in context of relevant environmental factors. Research questions, predictions and project design were guided by various existing hypotheses and ideas pertaining to predator-prey interactions (i.e., Economic hypothesis: Ydenberg and Dill 1986, Risk-disturbance hypothesis: Frid and Dill 2002, Optimal flight theory: Cooper and Frederick 2007, and Ecology of fear: Brown et al. 1999).

1.5 Statement of Co-authorship

This thesis is the result of a research project by Kathy C. Unger, a Master of Science candidate in the Cognitive and Behavioural Ecology (CABE) Programme at Memorial University of Newfoundland. This work has been conducted as part of a broader research initiative under the Newfoundland and Labrador Sustainable Development and Strategic Science Newfoundland Caribou Strategy. Principle financial and logistical support was facilitated by the Sustainable Development and Strategic Science Division (Newfoundland and Labrador Department of Environment and Conservation), co-supervisors Dr. Carolyn J. Walsh (CJW; via NSERC Discovery Grant; Department of Psychology, Memorial University) and Dr. Rita E. Anderson (REA; Department of Psychology, Memorial University), and committee member Colleen E. Soulliere (CES; Newfoundland and Labrador Department of Environment and Conservation). Substantial logistical support for fieldwork was also provided by CES, Rob Otto, Jason McGinn, Steve Gullage, Truman Porter, Baxter Slade and field assistants: June Swift, Nathaniel Rayl, Matt Mumma, and Guillaume Bastille-Rousseau. Additional contributions to this thesis were made as follows:

i) design and identification of the research proposal: Research questions, proposal development, research design and data collection plans were done by KCU with generous guidance from CES, REA and CJW.

ii) practical aspects of the research: Collection of field data (approaches of caribou groups, measurements of behavioural responses, video recordings and vegetation surveys) was primarily conducted by KCU in central Newfoundland with the assistance of JS, NR, MM, CES and GBR. Sydney J. Worthman, derived, analysed and interpreted meaningful and valuable vigilance data from KCU's recorded field videos of experimental approaches of caribou groups as part of her honours dissertation (MUN, Department of Biology).

iii) data analyses: All statistical analyses were performed by KCU, with advice from Dave Schneider, Doug Hynes, Keith Lewis, Paul Regular, CJW and REA.

iv) manuscript preparation: As the principal author, KCU wrote all text, interpreted all results, prepared all tables and figures. Photographs presented within this thesis were taken by JS and are used with permission. All thesis chapters were greatly improved by revisions and suggestions provided by CES, REA and CJW. Chapter 2 is written in a traditional thesis format.

2 Effects of predator cues in predator avoidance behaviour

2.1 Introduction

In order to understand variation in caribou antipredator behaviours, there must be an understanding of the processes and factors influencing predator assessment and antipredator responses. In this section I discuss Newfoundland predators, predator features, and environmental variables as factors influencing caribou perception of predation risk. In addition, experimental and statistical methods are described.

2.1.1 Caribou predators in Newfoundland

Native predators of caribou in Newfoundland are black bears (*Ursus americanus*), lynx (*Lynx canadensis*) and bald eagles (*Haliaeetus leucocephalus*) (Trinidade et al. 2011). Eastern coyotes (*Canis latrans thamnos*) represent a novel predation impact since their arrival on the island in the mid-1980s and establishment in the mid-1990s, concurrent with the beginning of drastic caribou population declines (Parker 1995, Soulliere 2008, Mahoney et al. 2011). Extensive collaring and monitoring of caribou herds in Newfoundland from 1979 to 1997 and 2003 to 2012 showed that the annual survival of older age-cohorts remained relatively high and constant during this period; the annual survival of calves, however, declined remarkably (Lewis and Mahoney 2014, Weir et al. 2014). The average 6-month survival of calves between 2003 and 2012 was 35% (n=959) with the majority of calf deaths occuring within the first weeks and months after birth (Lewis and Mahoney 2014). Ninety percent of calf mortalities between 2003 and 2012 were attributed to predation and examination of calf remains determined that 35% of predator related deaths were due to coyotes, 34% to bears, 20.9% to ‘unknown’ predators, 5.5% to lynx and 4.6% to eagles (Lewis and Mahoney 2014, Weir et al. 2014). Each of the predators identified in the calf mortality study have unique features, such as colour and hunting mode, which may identify them to caribou. Bald eagles are aerial predators, lynx are ambush predators, and bears and coyotes can be ambush, coursing or stalking predators (Pierce et al. 2000, Soulliere 2008).

Newfoundland caribou populations offer a unique opportunity to quantify caribou-predator risk assessment in herds that, since the extirpation of wolves (*Canis lupus*) in the 1920s (Maunder 1982), have not experienced canid-type predators until the relatively recent arrival of the coyote. Throughout most of North American and Eurasian caribou range, the primary documented predator is the wolf (Seip 1991, Ripple and Beschta 2012a). With a long shared evolutionary history, wolves have had a major role in shaping the antipredator strategies of caribou (Seip 1991). In some regions of Canada, wolf predation is implicated as the limiting factor to woodland caribou survival (McLoughlin et al. 2003). However in other regions, predators other than wolves have important impacts, such as black bears (Newfoundland: Trinidade et al. 2011), grizzly bears (central Canadian Arctic: Gau et al. 2002), lynx (Alaska: Stephenson et al. 1991), coyotes (Gaspésie: Crete and Desrosiers 1995, Boisjoly et al. 2010) and wolverine (Alaska: Dalerun et al. 2009). The additive effects of multiple predator species may severely limit caribou populations, and evolutionary relationships with multiple predators may regionally shape caribou behaviours.

Both bears and coyotes occupy habitat niches, often early successional habitat in areas disturbed by anthropogenic activities (e.g. forest cuts, roads, cultivated lands), which do not coincide or minimally coincide with caribou habitat niches (Boisjoly et al.

2010, Bastille-Rousseau et al. 2011). However, spillover predation into adjacent caribou territory or individual specialist predators may contribute to substantial predation or interactions with caribou.

Black bears are large omnivores, most typically characterized by uniform black fur and a brown muzzle (Powell et al. 1997). In Newfoundland, black bears are significantly larger than those on the mainland, averaging 222 and 395lbs (101 and 179kg) for females and males, respectively (Mahoney et al. 2001). Black bears are considered solitary animals throughout the year, except during the breeding season in summer months (Powell et al. 1997) although new technologies are revealing bears, including Newfoundland black bears, to be more social than previously thought (Rayl 2015 personal communication). Black bears give birth in January with cubs leaving the den in mid-spring (Powell et al. 1997). The diet of bears is highly variable and shifts seasonally with availability of vegetation, ants, fish and mammals (Powell et al. 1997). One study shows that black bears preferentially choose areas of high vegetation abundance over areas of high caribou neonate encounter probability, likely taking advantage of neonates opportunistically during movements between vegetation patches (Bastille-Rousseau et al. 2011). Recent studies of black bear movements in Newfoundland, however, show that some individuals migrate to caribou calving areas prior to caribou parturition suggesting deliberate selection for regions of high calf densities and implicating some bears as potential caribou calf specialists (Rayl 2012). Black bears may be more deliberate neonate predators than other active predators since their annual interval for prey acquisition is limited by hibernation (Garneau et al. 2008). Scat analyses of bears in Newfoundland in the summer of 2009 have shown grass, ants, wood and moose to be the most frequently encountered food items, while the occurrence of caribou in scat was relatively low in relation to other food items (Zieminski unpublished data).

Eastern coyotes are medium-sized omnivores, tawny-grey in colour, with white or light-grey throat and belly, black-tipped hairs covering the back and bushy tail, and reddish-yellow long legs, paws and muzzle (Parker 1995). Eastern coyotes, larger than their counterparts in southern and western ranges of the continent, typically range in weight from 25-40lbs (11-18kg) (Parker 1995). Evidence suggests that eastern coyotes are the result of coyote-wolf breeding events during the twentieth century as coyotes expanded their range northeastwards (Mastro 2011, Benson et al. 2012). Eastern coyotes may be part of social packs ranging from 2-8 coyotes, but are more characteristically known to be solitary or paired opportunistic scavengers (Parker 1995). Breeding coyote pairs may be monogamous for many years and establish natal dens late in the winter season. In the spring, litters of 4-6 pups are common (Parker 1995, Mastro 2011). The food habits of coyotes typically consist of foods which are most readily available in a given environment, such as small mammals, ungulates, fruit and other vegetation (Parker 1995). When actively hunting ungulates, coyotes are typically coursing hunters (Pierce et al. 2000).

Since their arrival in western Newfoundland during the mid-1980s, the eastern coyote has successfully expanded its range across the entire insular portion of the province, likely due to lack of predators, large litter size, and its adaptive nature. The first reported sighting of the coyote was during the spring of 1985 when “wolf-like” dogs were seen on the ice near the Port au Port Peninsula (Blake 2006). Their presence was confirmed in 1987 when a road-kill pup near Deer Lake was determined to be that of a coyote (Blake 2006), although evidence found at caribou calf kill sites may indicate coyote presence as early as the late 1970s (Mahoney 2012 personal communication). Scat analyses in Newfoundland have shown snowshoe hare, moose and caribou to be the most frequently encountered food items in coyote scats, and the relative prominence of each fluctuates with season, with caribou occurring in scat most frequently in winter (Zieminski unpublished data 2013, McGrath et al. 2009).

2.1.2 Predator recognition

2.1.2.1 Predator cues

In order to reduce the occurrence of predation, prey animals must be able to distinguish predators as a source of threat and be able to adapt predator avoidance strategies to corresponding levels of threat. Caribou may have specific responses to particular predators (e.g., bear, coyote) or to particular aspects of predators (e.g., hunting approach, colour) (Walther 1969, Bergerud 1971, Soulliere 2008). Predator avoidance or escape mechanisms effective against accustomed predators may be maladaptive against unfamiliar predators (Bergerud 1971). Prey use predator cues to recognize threats and these cues may be general or specific to each predator (Sih et al. 2010). General cues are cues which may pertain to numerous predators, such as a size threshold or a novel presence, while specific cues are unique to one predator, such as a chemical odor or unique patterning (Sih et al. 2010).

Prey respond most effectively to the cues of their predators where there exists an established co-evolutionary relationship (Blumstein et al. 2009, Sih et al. 2010), even where predators have been absent for many generations (e.g., elk respond to reintroduced wolves in Yellowstone National Park; Ripple and Beschta 2012b). Prey that lack an evolutionary link with their predators may exhibit weak or inappropriate antipredator strategies. Non-native predators tend to be more successful where prey rely on predator-specific cues and lack recognition of general cues that designate the newcomer predator as a threat (Sih et al. 2010). General predator cues allow prey to respond to a wider range of predators, but may have severe energetic consequences if potential threats are numerous and require frequent response.

2.1.2.2 Prey detection of predators

Animals acquire information about predation risk through one or multiple sensory modes (Lima and Steury 2005). The choice of which stimulus type to test in an experimental antipredator study is not straightforward since careful consideration must be given to the physiological ability of an animal to detect the cue and to the information derived from the cue (Blumstein and Bousklia 1996). Lizards, for example, may rely heavily on chemoreception for detecting predators (Labra and Niemeyer 2004), while some avian species differentiate their predators by listening to vocalizations (Adams et al. 2006). Some aquatic animals can use chemical cues to determine not only predator presence, but also the type, size and diet of the predator (Lima and Steury 2005). The challenge of understanding predator detection and assessment becomes more complex when the same cues elicit different responses (Blumstein and Bouskila 1996). For example, Ramp et al. (2005) found predator scent to incite one macropodid species to engage in predator investigation behaviour, while the same scent elicited aversive responses in a sympatric macropodid species.

It is unlikely that caribou rely exclusively on one sensory mode to detect predators, but some cues may be more provocative than others, especially in varied contexts. Reindeer herd management, for example, is based largely on the antipredatory responses of ungulates -- auditory signals, visual signals, and less often scent markers, are used by managers to control herds (Baskin 1974). Variations of whistles and shouts are used to calm or move animals, while visual techniques of shape and motion are used to achieve threatening stimuli to direct herds (Baskin 1974). Bergerud (1974) documented that alert and flight responses of female caribou in Newfoundland were motivated by a combination of sight, scent and sound stimuli, but that females were particularly sensitive to stimuli during calving season and were observed to consistently flee at long distances based only on sight stimuli.

Auditory cues may provide information about predator presence, distance, direction, identity, number and intent (e.g., kudu, *Tragelaphus strepsiceros,* modify vigilance levels in response to the hunting sounds of African wild dogs; van der Meer et al. 2012). The hearing capacity of reindeer is similar to other ungulates and ranges from 70 Hz to 38 kHz at a sound pressure of 60 Pa, making the frequency range ideal for detecting the vocalizations of conspecifics at long distances (Flydal et al. 2001), enabling *Rangifer* to acquire information about predators.

Olfactory cues may provide information about past predator presence and perhaps information about age, condition, and diet, but not precise information about the current location of a predator (Blumstein and Bouskila 1996). Scent markers, as indicators of predation risk, may also be difficult to interpret in a context where scent could deter other predators from the area, reducing overall risk to prey. Most accumulated knowledge of *Rangifer* olfactory capacity is limited to anecdotal observations by hunters, herders, hikers and researchers and it is believed that scent alone can trigger flight responses (Reimers and Colman 2006). Although it is assumed that scent detection can be minimized by approaching caribou groups using a head or cross wind, reindeer in Norway showed no differences in responses whether approached upwind or downwind (Reimers et al. 2006).

Visual cues provide the most reliable information of predator presence, including information about predator distance, direction, condition, number and behaviour (e.g., intent, speed of approach or retreat, activity). Because visual cues provide rich information about the probability of predation, visual recognition of predators relative to olfactory and auditory recognition is more likely to be experience-independent and therefore evolutionarily retained in the absence of predators (Blumstein et al. 2002). Vision is the sensory mechanism that usually provides the greatest awareness of stimuli far from the viewer's location, and is thus, often the most effective means of detection of predators by prey (Cronin 2005). Ungulates rely on visual acuity to detect predators, particularly in open habitats (Mitchell and Skinner 2003), where visual detection of predators may be more reliable than olfactory or auditory cues (Sarno et al. 2008). In open habitats, caribou likely gain in their ability to detect threats since sight is not obstructed by dense vegetation and terrain features (Reimers et al. 2006). Prey visual systems tend to sample broad spatial fields allowing detection of predators from many directions (Cronin 2005). In caribou, laterally placed eyes increase omnidirectionality of detection, even while the head is down during grazing (Reimers and Colman 2006). In many open terrain ungulates, visual acuity is best in line with the horizon, areas where predators are likely to appear (Cronin 2005). Colour vision is not thought to play a large role in detection of predators, since spectral properties of scenes, not objects, are important in the evolution of general visual abilities (Cronin 2005). However, reindeer are known to see near ultraviolet light range and this may influence the manner in which they perceive predators by allowing caribou to see enhanced contrasts of certain colours in their environment (Hogg et al. 2011). Urine, food and predator fur may all appear more highly contrasted against certain environmental surroundings.

2.1.3 Humans as simulated predator models

Similar to prior risk-assessment type studies (Aastrup 2000, Matson et al. 2005), human approaches are used in this study to assess reaction behaviours of ungulates. Ungulates pay attention to human approach behaviours (Stankowich 2008) and are expected to perceive human disturbances as predation threats (Webster 1997, Frid and Dill 2002). Risk-assessment type responses have been observed in a number of species when exposed to non-lethal disturbance stimuli (Frid and Dill 2002). The economic hypothesis may therefore explain avoidance of non-lethal human activity, suggesting that when disturbed, an animal should follow the same economic principles used by prey encountering predators (Frid and Dill 2002). The distances at which white-tailed deer and mule deer demonstrate predator alertness are similar whether approached by humans or coyotes (Lingle and Wilson 2001). Ungulates demonstrate perception of variable risk to different approaches by adjusting their flight initiation distance (Stankowich 2008). Humans on foot, specifically, are far more provocative to ungulates than other types of anthropogenic disturbances (i.e., vehicles, aircraft and noises; Stankowich 2008). Although human approaches limit the extent to which study results can be generalized to other predators, human approaches are a practical and controllable means to elicit antipredatory responses in the absence of reliable predation events (Soulliere 2008).

2.1.4 Selection of experimental cues

For this study, visual cues were used to simulate predator presence since the modality of vision is a highly evolved and specialized sensory mode for detecting multiple predators (Cronin 2005), and visual cues also provide awareness of predator presence and predation risk with the most certainty. The active presence of a persistent and dynamic visual cue may also heighten risk responses of prey, making them more easily identifiable and measurable for observers.

Black clothing was used in this study to mimic the appearance of a black bear, while tan clothing was chosen to approximate coyote appearance, the two top predators of caribou in the region. It is important to note that although the term colour is used throughout this paper for ease of discussion, black is not a true colour since black objects absorb all the colours of the visible spectrum and reflect none of them to the eyes (Adams 2014 personal communication). Caribou, therefore, do not distinguish colour differences between black and tan objects, but rather differences in luminance, contrast and/or spectral properties.

Crawling approaches are more similar to a coyote stalking approach and a bear ambush attack, since the approacher is more often visually obscured by vegetation and terrain features. Walking approaches may simulate the occasional upright posture of black bears, but more relevantly, are likely more detectable due to the approacher appearing taller and larger. Bergerud (1971) found that he could elicit aggressive behaviour from female caribou with calves in Newfoundland when he approached them by crawling as opposed to walking, suggesting that Newfoundland caribou can distinguish between different approach types and assign different levels of risk.

Colour-movement combinations which resemble highly threatening predators should elicit stronger antipredator responses. The walking-tan combination should be perceived as a novel stimulus to prey animals of the region, since insular Newfoundland lacks naturally-occurring, upright and tan-coloured predators. Caribou have no evolutionary history or extensive experience with an upright, tan predator (with the exception of encounters with humans in other seasons) and, therefore, were expected to demonstrate delayed recognition, delayed assessment, delayed flight or even investigatory behaviour in response to the novel stimulus. An alternate prediction was for caribou to respond solely to the cue most important to caribou for predator recognition - either colour or movement mode.

Caribou were approached directly because a more direct approach is thought to elicit a greater flight response since it may convey intent to capture the focal animal (Frid and Dill 2002, Frid 2003). Anecdotal observations suggest caribou respond less reactively when approached at an angle of less than 95 degrees, and in the direction of the group’s movement (Mahoney 2011 personal communication), presumably because prey perception of risk decreases when a predator appears to be on a trajectory that bypasses the target prey (Stankowich and Blumstein 2005).

2.1.5 Environmental effects on antipredator responses

In addition to the features of predators and prey themselves, environmental variables influence the responsiveness of prey to predator encounters. For example, consider topography and forage. Variation in topography can create micro-niches of varied snow-melt and consequently varied vegetation phenology, or can serve as 'escape terrain', terrain on which predators may have difficulty following (e.g., deep snow, thick vegetation or rugged and rocky ground; Gustine et al. 2006). Access to high quality forage is important to ungulates for tissue growth and replenishment of body reserves following winter (Finstad 2008). A high quality diet is particularly important to parturient and lactating females (Cebrian et al. 2008). At northern latitudes, spring and summer conditions permit short and intense pulses of plant growth which represent a period of nutritionally valuable resources for caribou. This attractive and time-limited resource availability may shift caribou behaviour more strongly towards time investment in resource acquisition with a higher tolerance for predation risk. Flight initiation distance (FID) and fleeing probability increase when prey are at a site that is relatively poor in resources (e.g., little food), because the benefits of clinging to a poor resource patch are less likely to outweigh the risk of remaining there (see data on waterstriders, *Gerris remiges*, in Ydenberg and Dill 1986).

With an assortment of native and novel predators, each with a suite of distinguishing features, Newfoundland caribou likely perceive threat variably in each unique predator encounter and by using a variety of sensory modalities. This study uses experimental human approaches to assess caribou risk assessment of black bear-like and coyote-like visual cues. Caribou responses are considered in context of biologically relevant environmental variables.

2.2 Methods

2.2.1 Study area and subjects

Field studies were conducted in the northern portion of the Middle Ridge (MR) calving grounds (located approximately 48°12’N, 55°22’W), where terrain is categorized as a Central Newfoundland Forest Ecoregion (Damman 1983). The entire MR study area occupies 13,369 km^2 and includes the provincial Bay du Nord Wilderness Area and the provincial Middle Ridge Wildlife Reserve, which cover 22% and 4.5% of the total study area, respectively. Data collection occurred in open areas where lakes, ponds, bogs, fens and low ridges are common. Forested regions consist largely of balsam fir (*Abies balsamea*) with dense moss understory (*Hylocomium splendens* and/or *Pleurozium schreberi*), or in drier areas dwarf shrub heath, black spruce (*Picea mariana*), some white birch (*Betula papyrifera*) and pure trembling aspen (*Populus tremuloides*). Some areas are composed of raised bogs where unique compositions of *Sphagnum flavicomans*, *S. imbricatum*, *Carex exilis*, *Aster nemoralis* and *Myrica gale* occur (Damman 1983). Plant communities of these regions consist largely of ericaceous dwarf shrubs, mainly sheep laurel (*Kalmia angustifolia*), Labrador tea (*Rhododendron groenlandicum*), blueberry (*Vaccinium angustifolium/boreale/myrtilloides*), leather leaf (*Chamaedaphne calyculata*) and crowberry (*Empetrum nigrum*), with patches of stunted larch (*Larix sp.)*, black spruce and balsam fir. *Cladonia spp.* lichens and *Sphagnum spp.* mosses are common (Trinidade et al. 2011). Some regions of the study area have moderate tracts of old burned forest. The mean elevation for the MR region is 200 m.a.s.l., with late spring and early summer (May-July) mean temperatures of 11.6ºC, and mean precipitation of 81.2 mm (based on climate data obtained from Environment Canada for all years on record for Gander International meteorological station from 1937-2011). The 2011 season of study, was slightly cooler and markedly wetter than overall means for the region at temperatures of 10.8 ºC and mean precipitation of 143.3mm; 87.7% of experimental trials occurred during overcast or fog conditions.

During the course of the field season, numerous bald eagles were sighted in early June, and eight bears were observed on seven occasions throughout the field season. No lynx or coyotes were observed directly, although coyotes were heard in one instance and scat and tracks of both coyotes and lynx were encountered. In addition to natural predators, the Middle Ridge herd is subject to hunting pressure outside of the study field season. Human presence was typically absent in the study area during the calving season but caribou may have experience with humans (e.g., hunters, hikers, photographers, vehicle traffic) and domestic animals (including dogs) during other seasons. In some parts of the calving range there is all-terrain vehicle (ATV) access, although no ATVs were observed or heard over the course of the study. Occasional low-flying planes and helicopters were heard and seen. One highway with moderate traffic on the western edge of the study area was a source of noise in some parts of the calving range. Concurrent with this study, experimental trials were being carried out in the southern portion of the MR study area with the purpose of diverting caribou predators to artificial food sources in order to reduce neonate predation (Lewis et al. 2014). The two study regions are separated by approximately 50 km, and therefore, are not thought to bear significant influence on each other. There is no indication from telemetry data of bear movement between MR North and MR South areas (Soulliere 2014 personal communication).

Field sites were accessed by helicopter or by vehicle and then on foot from ATV trails. Three remote campsites were used during the course of the field study. Locations for remote camps were chosen based on their proximity to high densities of caribou (as assessed aerially on the day of helicopter drop-off). A cabin was used when caribou were aggregated within driving and/or walking access.

Calves were first observed by researchers on May 27th of the study year. Calves were identified by their small size and females were distinguished from immature males by dark vulva patches, presence of udder, or association with a calf. The population size of this herd is estimated at close to 10,500 animals (Lewis et al. 2014). Since caribou spend significant time in groups during late spring and early summer and any individual caribou within a group may detect and respond to predation threat, alerting other members of the group, the sampling units of interest were social groups (one or more adult caribou obviously in a social aggregation, within at least 75m of each other; Soulliere 2008) of the Middle Ridge herd.

2.2.2 Experimental trials

Caribou groups were found on foot each day by walking from a base camp or from a helicopter drop-off point. A typical approach event began by locating a group ideally a distance of 200-500m away, but never closer than 125m in order to ensure that the duration of approach was adequate to allow for perception of and response to the stimulus. Other flight response studies suggest that *Rangifer* do not behaviourly respond to human approachers farther than 450m away (Nieminen 2013). Once located, groups had to meet the following requirements in order to be considered appropriate for an approach trial: 1) First, caribou must have had an unrestricted view of the approacher, and *vice versa*, for a minimum of half the duration of the approach. In trials where vegetation and terrain properties obstructed visual contact for more than an estimated 50% of the approach duration, or if the approacher was not able to detect alert and flight responses, the trial was abandoned. Some tolerance for interrupted visual contact was allowed since there was always a second observer to verify caribou responses and because actual predators, especially stalking predators, are likely to remain out of visual detection range of caribou for even greater durations. 2) Groups could not have been demonstrating alert responses (e.g., erect posture oriented toward approacher, tail signaling; see Figure 2.2) at any time previous to the beginning of approach. If there was a choice of groups to approach, researchers chose groups which were an ideal distance away, downwind, and from which researchers were offered some visual cover at their trial start position.

Upon selection of a suitable group, video recordings were made for 5 minutes prior to the start of the approach from the start position to document pre-disturbance behaviour. During this time, groups were scanned by two observers using binoculars and the following parameters were recorded: date, group size, group composition (sex and age class of individuals), number of vigilant caribou in group (number of caribou in group with head erect above shoulder level, Soulliere 2008), habitat type (sparse forest, dense forest, forest regrowth, barren, bog/fen), topography (description of terrain between approacher and caribou group: flat, moderate, steep), gain (difference in height between approacher and caribou during approach: positive, no change, negative, or combination), ambient temperature (°C), cloud cover (mostly clear, partly overcast, mostly overcast and fog), wind direction (N, NE, E, SE, etc.), wind speed (rating of 0 to 10 on the Beaufort scale), estimated average distance between adult caribou within group (m), estimated average distance between cow and calf pairs (m), group activity (at rest, active, rest and active, travel), estimated distance to dense vegetative cover (more than 1.5 m in height), and insect harassment (number of Culcidae, Simuliidae and Tabanidae flies instantaneously counted on the observer's forearms or apparatus, recorded to a maximum of 10). The maximum insect harassment score was also assigned when Oestridae fly (i.e., ectoparasitic warble and bot flies) presence was obvious by caribou behaviour (e.g., head drooping and head shaking; Morschel and Klein 1997). Variables are described in more detail in sections 2.2.4 and 2.2.5.

The approach used in a given trial was one of four pre-assigned approach types chosen by block randomization. The approach types were either walking or crawling, further characterized by black or tan clothing (Figure 2.1). Clothing worn during approaches were a black or tan coloured cotton or fleece sweatshirt with the hood covering the head, black or tan rain pants, black or tan gardening or winter gloves, and a bug net covering the face of the approacher. The face was covered with bug netting to avoid potentially influencing caribou perception of risk due to eye contact or other facial features (Burger and Gochfeld 1993).

Figure 2.1 Four experimental approach types: walk-black (B), crawl-black (C), walk-tan (E) and crawl-tan (F), used to approach and provoke predation-risk responses in caribou groups. A and D show black bear and coyote, top predators of the Middle Ridge study region, for visual comparison.

Groups were approached directly, continuously and at a constant pace, with the approach aimed towards the geometric centre of the group (Soulliere 2008). Approach speeds varied somewhat between trials due to terrain ruggedness. Walking speed was typically near 0.85m/sec, while crawling speed was closer to 0.45m/sec. For the duration of the approach, the approacher continuously scanned group members to note changes in behaviour. Immediately upon detecting the first alert response (Figure 2.2) from any group member, the approacher discretely dropped a distance marker and continued to advance towards the group without pause (Figure 2.3).

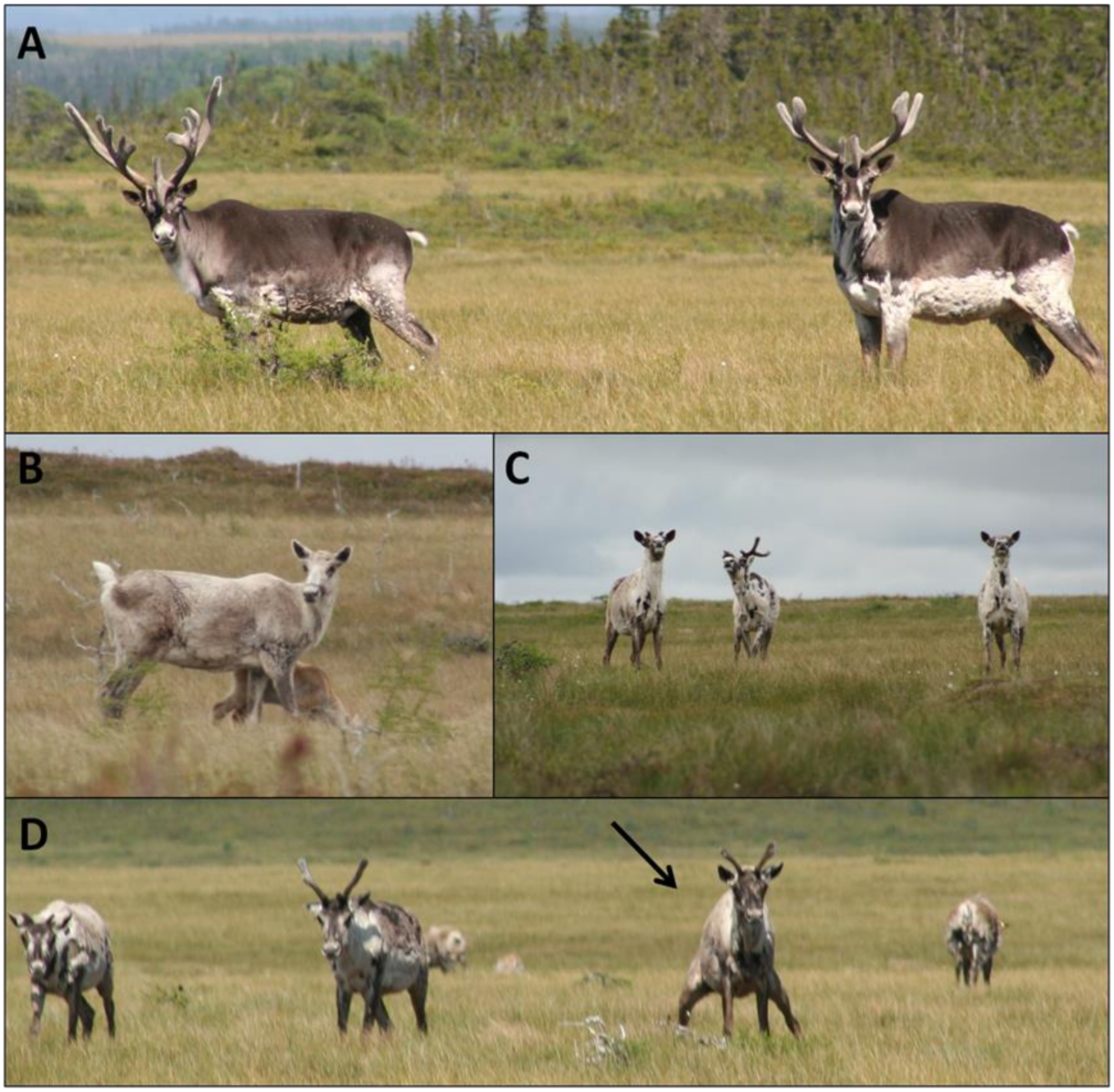

Figure 2.2 Alert behaviours of caribou observed during the 2011 season of study: (A) gaze directed towards observer, (B) erect tail, (C) sniffing, (D) alert pose (individual indicated by an arrow) characterized by a stiff posture with spread hind legs. In all photographs caribou have erect ears - also a notable alert behaviour.

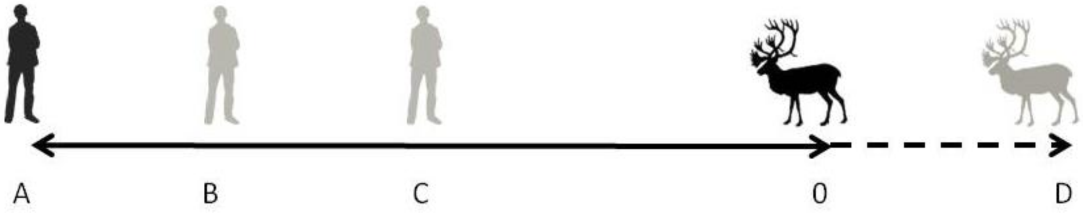

Figure 2.3 Diagram of distance measurements recorded during approach trials: A to 0 is the beginning distance, B to 0 is the alert distance, C to 0 is the flight initiation distance, 0 to D is the distance moved, and B to C is the assessment interval distance. 0 represents the geometric centre of the target caribou group prior to provocation.

Upon detection of the first flight response (Figure 2.4), another flag was dropped and the advance continued until the approacher arrived at the centre of the original location of the caribou group (Figure 2.3). A range finder (Bushnell Elite 1500) was used to measure the distances from the original location of the group to the alert and flight distance markers, and to the beginning distance of the approach (Figure 2.3). The distance moved by caribou until stopping was visually estimated.

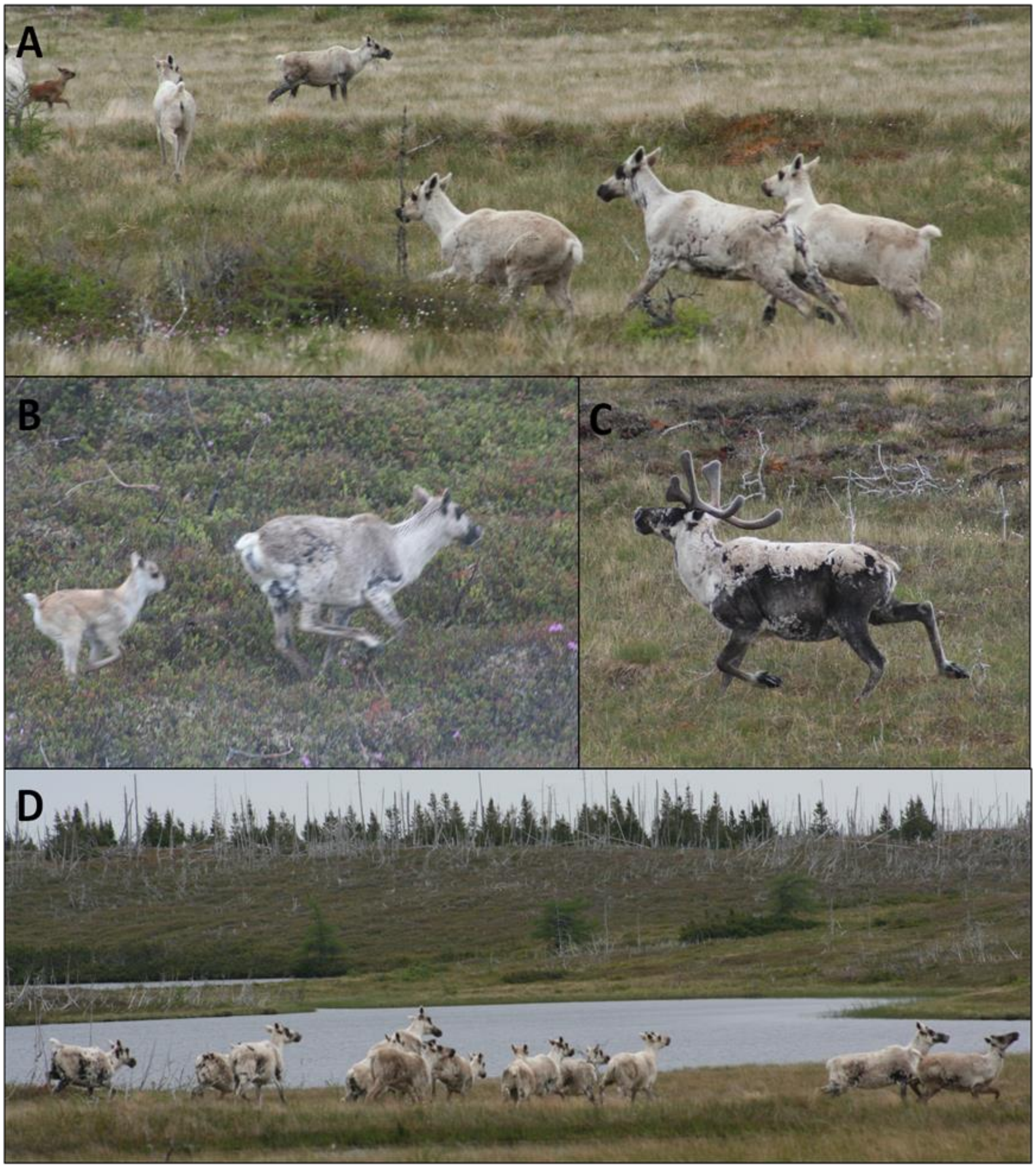

Figure 2.4 Flight behaviour of caribou following provocation by a human approacher: (A) unsynchronized group flight with individuals moving in different directions (the calf in the photograph may be searching for its mother), (B) a calf-at-heel of fleeing mother, (C) a male with head elevated during flight, possibly for enhanced sensory monitoring of approacher, (D) a group of adult females in synchronized flight, moving together in one direction. A female in the group centre is performing an excitation leap, a behaviour thought to deposit a warning scent from the interdigital glands onto the ground (Müller-Schwarze et al. 1979, Naughton 2012).

Four response distances (Table 2.1, Figure 2.3) were recorded for each approach trial. Terminology and definitions used to describe wildlife response distances vary between studies (e.g., ‘flight distance,’ ‘flight initiation distance,’ ‘approach distance,’ ‘reaction distance,’ ‘escape distance,’ and ‘flush distance’). To avoid confusion, response distance terms used in this paper follow terminology used in the ungulate flight response meta-analysis paper by Stankowich (2008), as originally defined by Taylor and Knight (2003). The only exception is the relatively recently described ‘assessment interval distance’ term, which is used as defined by Cooper and Blumstein (2014) (undefined in Reimers et al. 2006; referred to as ‘flight lag’in Soulliere 2008; and substituted by similar measures such as ‘assessment time’ in Stankowich and Coss 2006, and ‘probability of assessment’ in Reimers et al. 2009).

Table 2.1 Definitions and implications of caribou response measures.

Response	Definition	Implication
Alert distance (AD)	The distance (m) between the approacher and caribou group when the first animal shows alert behaviours in response to the approach stimulus.	The distance at which caribou either become aware of an approaching threat or signal awareness of an approaching threat.
Flight initiation distance (FID)	The distance (m) between the approacher and caribou group when the first animal flees in response to the approach stimulus.	The distance at which caribou perceive the threat of an approacher to outweigh the benefits associated with their current resource use or activity.
Assessment interval distance (AID)	The difference (m) between alert distance and flight initiation distance.	During this interval, caribou monitor approaching predators and possibly assess risk by weighing the trade-offs between fleeing and remaining as per FID economic model scenarios of (Cooper and Blumstein 2014).
Distance moved (DM)	Distance (m) fled by disturbed caribou from the initial site until coming to a stop. This measure was visually approximated.	The distance moved may correspond to the degree of perceived threat of the approacher.

Measures of distance are predominantly used, instead of measures of time, due to variability in approach velocities and to enhance the comparability of this study’s findings in the contexts of both the optimal flight theory (Cooper and Frederick 2007, Cooper 2009) and similar wildlife response studies. AID is the only dependent variable additionally analyzed in terms of time since it is the only measure of an interval of behavior. Because AID occurs relatively infrequently in the flight theory literature, describing it in terms of both distance and time may help better define its role in flight theory. Occurrences of post-flight return behaviour (known as “curiousity return behaviour" in earlier studies, e.g., Aastrup 2000) were also recorded and were considered to occur when caribou, following flight, returned some distance towards the approacher while remaining alert to the approacher's presence, in some cases circling the approacher and sniffing the air (Aastrup 2000).Video recordings were made for the duration of the approach, and when possible, for any post-disturbance behaviour and post-flight return behaviour. Videos were used to measure the duration of approaches, verify observations and for additional behavioural analyses of vigilance (Worthman 2014).

After any successful or unsuccessful approach of a caribou group, a new course was set away from the group, opposite the group's direction of travel in order to avoid repeat encounters with the same caribou later in the day. Due to the highly mobile nature of caribou, the large population in the study region, and flux nature of social aggregations, the risks of pseudo-replication and habituation were considered to be low.

Observations and approach trials were conducted over 60 days (May 20 – July 18, 2011) with up to 6 successful attempts in a day. Trials occurred as early as 0910h and as late as 1836h (median 1300h).

2.2.3 Vegetation surveys

In order to assess the quality and abundance of forage, vegetation plots were surveyed in areas where caribou were observed prior to approach trials. Four 1m² plots were laid out 15m from the estimated centre of the geometric distribution of the target caribou group prior to disturbance, in each of the cardinal directions (Figure 2.5). This resulted in a square site measuring 21.2m^2. The percent foliage cover of major plant groups were visually estimated within each 1m² plot. Foliage cover was defined as the percentage of the sample plot occupied by the vertical projection of foliage and branches (Walker and Hopkins 1990). For example, shrubby or herbaceous cover would include the area of the shadow cast by plant leaves and stems if the sun were directly overhead. Moss and lichen cover estimates were essentially percent ground cover estimates since these groups lack vertical growth. This means that total cover of a plot could surpass 100 percent since there was overlap of plant groups at various heights. Estimations were fit into cover classes with assigned ranges (e.g., A<2%, B=2-5%, C=6-10%, etc.). Cover and height estimations were recorded following consensus by two observers. The species present at each site were also recorded, as well as the number and height of trees. Plants were deemed caribou foods if they had previously been found in caribou scat or rumen samples in Newfoundland using available data from between 1987 and 1997 (Newfoundland and Labrador Department of Environment and Conservation unpublished data, Appendix I). All of the major plant groups recorded included species known to be consumed by caribou. Average cover of plant groups at each site were later calculated using the formula:

$$Average\ \%\ cover\ group\ A = \left[\frac{total\ \%\ cover\ of\ group\ A\ in\ all\ plots}{number\ of\ plots\ estimated}\right]$$

Figure 2.5 Photograph of a 1m² sampling quadrant at a vegetation site.

2.2.4 Statistical analysis

Descriptive statistics were used to summarize the group characteristics of approached caribou groups. Analysis of variance between-subjects, was used to determine whether the experimental treatments of approacher colour (black, tan) and movement (walk, crawl) significantly influenced AD, FID, and AID, and also to assess differences in the response variables as a function of season. ANOVAs were followed by Tukey Honest Significance Difference tests where applicable. The occurrence of post-flight returns in relation to colour and approach movement was tested using χ^2 analyses. Generalized linear model (GLM) analyses were used to further examine the effects of the experimental treatments on caribou antipredator responses in context of relevant environmental variables. DM was not analyzed beyond descriptive statistics because it was a visually estimated measure and deemed lower in quality relative to other response data. GLM model selection was accomplished with the Akaike Information Criterion, adjusted for small sample sizes (AICc) described below. Throughout the GLM analyses, I distinguish between *a prioiri* and *post hoc* hypotheses. I do this to emphasize hypotheses developed prior to data collection, guided by the economic hypothesis (i.e., *a prioiri* hypotheses), but to still allow for consideration of other potentially important factors (i.e., *post hoc* hypotheses).

2.2.4.1 Data screening

Seven approach trials were removed from the data set because they violated the minimum cut-off of 125 m for the beginning distance of approach, reducing the overall sample size to N=130. Reported sample sizes vary between analyses according to the maximum available data for the given analysis (i.e., some variables were missing or uninterpretable for certain trials). Remaining outlying data points were retained in the analysis since they may represent extreme, but true, ranges of measured variables. A negative binomial error structure was designated for assessment interval data, while a Gaussian (normal) distribution was retained for all other data (O’Hara and Kotze 2010).

Many measured vegetation characteristics (e.g., height, cover, number of caribou foods present, number of species present) were highly interrelated according to principal components analyses (PCA). Vegetation variables were reduced to five characteristics (average ericaceous shrub cover, graminoid cover, lichen cover, moss cover, and number of caribou food species) with the largest loadings in PCA and accounting for a wide range of variability.

2.2.4.2 Modeling of antipredator responses

Generalized linear models using R (version 2.12.2 (2011-02-25)) were used to evaluate variables as predictors of AD, FID, and AID. This procedure identifies factors that contribute to variation in dependent variables by providing parameter estimates, t-values and significance levels. In addition to experimental variables, group, habitat, ecological and geographical variables were used in the modeling of antipredator responses and are summarized in Table 2.2.

Table 2.2 Explanatory variables used in predator encounter response analyses. Variables indicated by a star (*) are literature-supported factors in *Rangifer tarandus* flight initiation distance.

Category	**Variable (type)**	**Abbr.**	**Description or definition**
Experimental (predator cue simulation)	Approach movement (nominal)	approach	Crawling or walking
	Colour (nominal)	colour	Black or tan
Group	*Group size (continuous)	grp.size	Number of caribou in social aggregation of more than one caribou (including calves).
	*Calf presence (binomial)	calf.p.a	Presence or absence of calf caribou
	Number vigilant (continuous)	num.vig	Number of caribou in a group displaying vigilant behaviour prior to the approach event (including calves).
Habitat	*Habitat type (nominal)	habitat	Sparse forest, barren or bog/fen.
	Plant group	gram.cov	Visually estimated horizontal ground cover

	cover (continuous)	lich.cov ericS.cov moss.cov	for each of graminoid, lichen, ericaceous shrub and moss plant groups (%).
	Number of foods (continuous)	foods	Number of caribou food species surveyed at a site.
Ecological	Insect harassment (nominal)	insect.h	Number of biting insects counted instantaneously to a maximum of 10. Maximum score assigned when oestrid flies present.
	Date (continuous)	JD	Julian date
	*Season (nominal)	n/a	pre-calving: week 0 (May 20 – May 26) calving: weeks 1- 2 (May 27-June 9) post-calving I: weeks 3-4 (June 10-June 23) post-calving II: weeks 5-6 (June 24-July 7) post-calving III: weeks 7-8 (July 8- July 18)
	Wind speed (nominal)	wind.spd	Classification of 1-12 based on the Beaufort scale.
Geographical	Topography (nominal)	topog	General description of landscape between the approacher and target caribou group: Flat, moderate, or steep.
	Gain (nominal)	gain	Difference in height between approacher and caribou during approach (+, 0, -, combination).

2.2.4.3 Model set construction

Burnham and Anderson (2002) strongly advocate for a well-developed set of *a priori* candidate models based on substantial, prior information about the system being studied in order to reduce model selection uncertainty. Variable selection and model construction were done with flight initiation distance as the response variable in mind since the primary objectives of this study were derived from optimal flight theory and because there is much more literature pertaining to flight. These same models were applied to AD and AID due to their relationship with FID and because each dependent variable evaluates different aspects of caribou response to an approacher (Table 2.1).

Two candidate model sets, resulting in 22 GLM models, were constructed; 13 models addressed *a priori* hypotheses (i.e., hypotheses developed prior to data collection, guided by the economic hypothesis) and 9 models explored *post hoc* objectives (i.e., additional hypotheses arising during data collection and analysis). *A priori* models test hypotheses pertaining to predator effects and vegetation effects; *post hoc* models test the influence of various abiotic factors, social group characteristics and relevant interactions (Table 2.3). As a first step in creating the *a priori* candidate model set, the 'base model' was built using four empirically-established influencers of caribou antipredator behaviour: season, calf presence, habitat and group size (see Table 2.3, Model 1). Subsequent models built upon the base model variables with different combinations of the experimental variables and vegetation variables. Models were compared to the base model and against each other to determine improvement. The global model (Table 2.3, Model 13) combines all variables and was used to assess error distributions.

Table 2.3 Summary of hypotheses tested by each model of the *a priori* and *post hoc* GLM candidate sets. Model sets were used with each of the following three antipredator response variables: AD, FID, and AID.

Model	*A priori* hypothesis
1	Season, habitat, calf presence and group size influence antipredator responses of caribou. *This is the base model.*
2	Colour and approach movement influence antipredator responses of caribou above the base model. *This is the predator effects model.*
3	Lichen cover influences antipredator responses of caribou above the base model.
4	Moss cover influences antipredator responses of caribou above the base model.
5	Ericaceous shrub cover influences antipredator responses of caribou above the base model.
6	Graminoid cover influences antipredator responses of caribou above the base model.
7	The number of caribou foods present influences antipredator responses of caribou above the predator effects model.
8	Lichen cover influences antipredator responses of caribou above the predator effects model.
9	Moss cover influences antipredator responses of caribou above the predator effects model.
10	Ericaceous shrub cover influences antipredator responses of caribou above the predator effects model.
11	Graminoid cover influences antipredator responses of caribou above the predator effects model.
12	The interaction of approach movement and colour influences antipredator responses of caribou above the base model.
13	All vegetation and predator effects variables account for antipredator responses of caribou.
Model	***Post hoc* hypothesis**
14	The number of caribou vigilant in a group influences antipredator responses of caribou above the predator effects model.
15	The interaction between the number of caribou vigilant and group size influences antipredator responses of caribou above the predator effects model.

16	The interaction between the number of caribou vigilant and season influences antipredator responses of caribou above the predator effects model.
17	The interaction between the number of caribou vigilant and habitat influences antipredator responses of caribou above the predator effects model.
18	The interaction between the number of caribou vigilant and calf presence influences antipredator responses of caribou above the predator effects model.
19	Insect activity influences antipredator responses of caribou above the predator effects model.
20	Topography influences antipredator responses of caribou above the predator effects model.
21	Gain influences antipredator responses of caribou above the predator effects model.
22	Wind speed influences antipredator responses of caribou above the predator effects model.

2.2.4.4 Model selection

Multiple antipredator response models were evaluated using the Akaike Information Criterion (AIC) adjusted for small sample sizes (AICc) and AIC weights (ω_{i}; Burnham and Anderson 2002). The AIC, as part of the information-theoretic approach, differs from traditional model selection based on significance tests. The AIC approach is similar to an optimization scheme that evaluates model terms to minimize model bias while maximizing model precision (Gunn et al. 2004). Within each candidate set, the models with the lowest AICc values were selected as the most parsimonious and models within 2 units of the minimum AICc were interpreted as having strong support (Burnham and Anderson 2002). Akaike weights were calculated to gauge the relative contributions of models in predicting caribou antipredator responses. Note that the degree of significance of model parameters and the AIC criteria do not directly evaluate how well models predict caribou antipredator response, rather they assess models relative to one another within a candidate set.

2.2.5 Overview of variables predicting flight initiation distance

The selection of which environmental variables to measure and to what detail is difficult since there is little consensus in the literature regarding which variables are most influential in predicting ungulate life histories (Weladji et al. 2002). While many variables potentially predict caribou behaviours, few variables are well-established in the literature as prominent factors in antipredator responses specifically in context of human approachers on foot. Among the few empirically-supported factors (i.e., calf presence, habitat, season, group size), even fewer are consistent in the direction of their reported effect (Table 2.4). Variables measured in this study were carefully considered for their biological relevance in the context of behavioural response to threat and more specifically, within the framework of the economic hypothesis (Ydenberg and Dill 1986).

Table 2.4 Supporting literature for the effect of group size, calf presence, season and habitat on flight initiation responses of *Rangifer* when approached by a human on foot. (*) indicates studies analyzed in the meta-analysis of ungulate flight responses to human disturbance by Stankowich 2008.

Variable	**FID (m)**	**Study**
Group size	Small >large	Reimers et al. (2006)* Soulliere (2008)
	Large >small	Aastrup (2000)*
	No difference	Colman et al. (2001)*
Calf presence	Female groups w/calves > w/o calves	Nieminen (2013)
	Groups w/calves <w/o calves	Baskin and Scogland (2000) Soulliere (2008)
Season	Peri-calving>early summer	Soulliere (2008)
	Early summer > late summer	Aastrup (2000)*
	Summer>all other seasons	Reimers et al. (2006)* Nieminen (2013)
Habitat	No effect	Reimers et al. (2006)*

2.2.5.1 Experimental variables: Colour and movement mode

Colour and movement mode are the experimental variables in this study, representing predator cues of interest. Since beginning this study in 2011, to my knowledge one study has been published demonstrating predator appearance to influence FID of ungulates (cf. Reimers and Efstetol 2012). Stankowich and Coss (2007) found black-tailed deer showed variability in alarm responses (e.g., foot-stomping and snorting) to a range of predator and conspecific models, suggesting that ungulate flight responses may be influenced by predator appearance.

There is no direct support for predator movements (e.g., crawling, stalking, ambling etc.) affecting FID of ungulates; however, there is evidence to suggest that ungulate responses differ in relation to different anthropogenic approach stimuli. Stankowich (2008) concluded that humans on foot were more provocative to ungulates than most vehicles and anthropogenic noises, and Reimers et al. (2003) found that wild reindeer showed stronger responses towards skiers compared to snowmobiles. Approach velocity was found to be positively correlated with response distances; i.e., higher speeds invoked greater flight responses (Reimers et al. 2003, Stankowich 2008). It is reasonable to conjecture that the diverse movement styles of predators, encompassing differences in predator shape, visibility and approach velocity, may trigger variation in ungulate flight responses.

2.2.5.2 Base effects variables: Group size, calf presence, season and habitat

In a comprehensive review of flight responses in ungulates, Stankowich (2008) found group size, calf presence, season and habitat, among other factors, to affect FID of ungulates. These four variables were considered most often in ungulate flight response studies and were therefore included in all models as ‘base effects’ to reduce overall model variability.

Group size. Stankowich (2008) found a weak but overall tendancy for larger, rather than smaller, ungulate groups to show longer flight responses to human approachers. Consistent with this finding, Aastrup (2000) found caribou in groups to have longer FID or flight thresholds than individuals. In other words, caribou in groups were shown to take flight earlier, when approachers were still relatively far away. In contrast, Reimers et al. (2006) and Soulliere (2008) found reindeer in southern Norway and caribou in Newfoundland, respectively, to have longer FID in smaller groups than in larger groups. Colman et al. (2001) found no differences in flight responses of different sized groups of Svalbard reindeer. The overall effect of group size on flight responses in

Rangifer remains inconclusive, but there is sufficient support to merit further consideration of the variable.

Calf presence. The presence of calves is considered to be the most important factor influencing group vulnerability during the summer and is therefore considered in all models. Stankowich (2008) showed that in four of five studies involving caribou or reindeer, groups with calves reacted to various types of anthropogenic disturbance by increasing their FID (aircraft: Klein 1974, Calef et al. 1976, Miller and Gunn 1979; human: Bergerud 1974; as cited by Stankowich 2008). Nieminen (2013) also reported that groups with calves significantly increased their FID during the summer when approached by humans on foot. On the other hand, Soulliere (2008) and Baskin and Skogland (2000) showed caribou groups with calves reduced FID in response to human approaches. Similarly, Mahoney et al. (2001) (also analyzed by Stankowich 2008) showed that snowmobile approaches in Newfoundland produced similar findings. There is obvious variability in the direction of flight response in the presence of calves, but none-the-less, there is a clear influence.

Season. Caribou and reindeer are reported to increase FID responses to disturbance in early summer, midsummer, calving and winter seasons in the ungulate flight response meta-analyses by Stankowich (2008). In response to human approachers, Reimers et al. (2006) showed Norway reindeer flight distances were greatest in July, and Aastrup (2000) specified that Greenland reindeer were most sensitive during the calving period. There are difficulties in ascertaining seasonal trends between studies due to differences in seasonal conditions between geographic and temporal localities, and thus differences in season definitions (e.g., calving or rutting season may vary in onset and length between *Rangifer* populations). During the spring and summer months, group composition, group size, calf presence and calf vulnerability change markedly, and these changes are largely shaped by the event of calving. In this study, Julian date was used in GLM analyses to capture broad seasonal trends in context of other predictor variables and for ease of comparison to other studies. After ascertaining the influence of Julian date on antipredator responses, season was redefined and analyzed as five categorical periods in order to more precisely interpret differences in FID in reflection of changes in caribou group dynamics over the course of the Newfoundland spring-summer calving season (see variable 'season' in Table 2.2) and in relation to date of the first observed calves of the study year (May 27th).

Habitat. Stankowich (2008) found weak and heterogenous effects of habitat on the flight responses of ungulates; flight responses were greater in open habitats than in closed, wooded habitats. However, no effect was found for the influence of habitat on flight responses of *Rangifer* in the only study to consider approach by humans (Reimers et al. 2006). The four other approach studies involving *Rangifer* in the Stankowich (2008) meta-analysis involved vehicle or aircraft disturbance and reported an array of response outcomes in variably defined habitats (grass > grass with scrub, aircraft: Calef et al. 1976; closed > open terrain, aircraft: Miller and Gunn 1979; open > closed terrain, vehicle: Horejsi 1981, Tyler 1991; no effect, vehicle: Mahoney et al. 2001; as cited by Stankowich 2008). There is lack of strong evidence for habitat effects on caribou flight response likely due to differing definitions of habitat between studies. Despite this discordance, I feel habitat is crucial to consider since caribou use habitat at many scales across many seasons. Therefore, even a broadly defined habitat classification tailored to the region of study, may encompass important resource or topographical components which may otherwise be unaccounted for.

2.2.5.3 Other variables in *a priori* analyses: Vegetation characteristics

Vegetation plays a role in habitat structure, but also as an energy resource, influencing the flight probability of herbivores. Ydenberg and Dill (1986) demonstrated that prey weigh the benefits of clinging to a resource patch against the risk of remaining. Tyler (1991) found that feeding Svalbard reindeer were less likely to flee from a snowmobile approach than reindeer that were lying down and not feeding (lying reindeer may also feel more vulnerable). Aastrup (2000), Reimers et al. (2006) and Stankowich (2008) found no direct effect of vegetation on FID of *Rangifer*, but Stankowich (2008) did find evidence for an effect of habitat structure. Based on the theoretical assertion of Ydenberg and Dill (1986) for the influence of resource patches on flight behaviour, local vegetation characteristics were investigated in more detail.

2.2.5.4 Variables in *post-hoc* analyses: Vigilance, wind speed, topography and insect harassment

A number of variables are known to play a strong role in caribou antipredator behaviour (e.g., vigilance, insect harassment), but have no demonstrated effects on FID. Conversely, other variables (e.g., wind speed, topography) have been shown to influence FID but their mechanism for influencing antipredator behaviour is less clear. These two sorts of variables were explored in *post-hoc* analyses.

Vigilance. Vigilance is operationally defined and measured as time spent with the head raised about shoulder level (Childress and Lung 2003), in the act of being alert or aware of ones' surroundings (Roberts 1996, Treves 2000), and plays a major role in the detection of predators (Hopewell et al. 2005). Vigilance increases fitness by decreasing the risk of mortality (Lima 1998, Watson et al. 2007). When the head of an animal is raised, the visual, olfactory and auditory organs are raised concurrently, increasing the range of the environment that can be observed (Lima and Bednekoff 1999a, Cresswell et al. 2003). Although head-up posture may serve additional functions, such as scanning for conspecifics (Lung and Childress 2007) and handling food items (Illius and Fitzgibbon 1994), there is evidence that more vigilant individuals detect predators more quickly (Lima and Bednekoff 1999a). Head-up posture may comprise only a portion of an individual's vigilance, but is useful in that it is easily identifiable by observers and because overt vigilance might be partly motivated by the need to verify a stimulus detected while the head was down. Aastrup (2000) interpreted longer flight distance responses of Greenland caribou groups as an indication of higher vigilance levels, but made no direct measurement of vigilance prior to caribou-observer encounters. Reimers et al. (2009) found variation in vigilance levels and flight responses between reindeer groups in Norway, but found no evidence to support a relationship between vigilance and flight responses. Soulliere (2008), likewise, found no direct relationship between vigilance and FID but showed that maternal caribou in Newfoundland showed lower levels of vigilance and were the first to run and ran farthest when disturbed. Since none of these papers confirm a link between vigilance and flight responses, vigilance was left out of primary analyses. However, because vigilance plays a clear role in antipredator behaviour, vigilance was considered in post-hoc analyses.

Wind Speed. Reimers et al. (2006) found reindeer to have reduced FID when wind speed was greater. Wind speed was therefore considered in *post hoc* analyses.

Topography. Topographical variability may affect the ability of caribou to visually detect an approaching threat, and may influence the level of vigilance and antipredatory responses. Aastrup (2000) found no effect of topography on the flight responses of Greenland caribou. Reimers et al. (2009), on the other hand, found reindeer FID was greater in rugged than in level terrain. Reimers et al. (2011) similarily found that reindeer were alerted to approachers at a farther distance on rugged terrain than on level terrain and conjectured that reindeer may perceive level terrain as more secure. Topography and gain were thus considered in post-hoc analyses.

Insect harassment. Insect harassment is widely documented as influencing caribou behaviours and contributing to energetic and physiological costs (Toupin et al. 1996, Hagemoen and Reimers 2002, Colman et al., 2003, Bergerud et al. 2008, Hughes et al. 2009, Witter et al. 2012, Cuyler et al. 2012). During the summer season, insect activity can contribute to reduced *Rangifer* body condition through direct costs of blood loss and immune response, but also through indirect costs of altered activity budgets (Morschel and Klein 1997, Hagemoen and Reimers 2002, Colman et al. 2003, Hughes et al. 2009, Witter et al. 2012). On the island of Newfoundland, a number of ecto-parasites, namely oestrid flies (warble flies '*Hypoderma tarandi*' and nose bot flies '*Cephenemyia trompe*'), are recognized as factors in the summer movement behaviour and energy use of caribou (Colman et al. 2003, Hagemoen and Reimers 2002, Witter et al. 2012). The presence of only a few adult oestrid flies can provoke intense avoidance behaviours in *Rangifer*, including bursts of running and increased vigilance, disrupting foraging opportunities and increasing energy output (Hagemoen and Reimers 2002, Colman et al., 2003, Bergerud et al. 2008, Hughes et al. 2009, Witter et al. 2012, Cuyler et al. 2012). In high numbers, black flies (*Sulidae*), deer flies (*Tabinidae*) and mosquitoes (*Culicidae*) can also motivate insect avoidance behaviour in caribou (Morschel and Klein 1997, Hagemoen and Reimers 2002, Witter et al. 2012). Insect harassment and forage quality are reported to be important drivers of *Rangifer* summer-range ecology (Skarin et al. 2008) often forcing caribou to choose between areas of low quality forage and areas of intense insect activity (Witter et al. 2012). To my knowledge, there is no literature demonstrating an effect of insect harassment directly on FID during encounters with predators, but it is not unreasonable to conjecture that if insect harassment can influence behaviours of caribou such as habitat choice (Toupin et al. 1996, Skarin et al. 2008, Skarin et al. 2010), and tolerance to disturbance (Pollard et al. 1996, Skarin et al. 2004), then insect harassment may affect antipredator behaviour of caribou. Insect harassment is also an additive energetic stress and, therefore, may influence the economic decisions of caribou. Throughout the course of the field study, summer temperatures in Newfoundland were uncharacteristically cool resulting in low levels of insect activity (Thomas and Kiliaan 1990, Weladji et al. 2003, Witter et al. 2012) and infrequent incidences of observed insect harassment -- oestrids were observed in less than 5% of trials (6/130). Therefore, any influence of oestrids or other insects on caribou behaviour is likely statistically undetectable in this study period and hence was not considered in primary analyses. However, because a vast volume of literature indicates insect harassment as a significant factor in caribou health and summer ecology, the influence of insects was explored in *post-hoc* analyses.

2.2.5.5 Variables not used in caribou antipredator behaviour models

Distance to refugia. In studies on perceived risk in animals, the distance of prey from their refugia has a large and significant effect on flight initiation distance; animals farther from their refugia tend to flee at greater distances (Stankowich and Blumstein 2005). Refugium in this sense is a place of increased protection or safety specifically from predation. Increased cover and crypsis of prey animals increases the perception of not being seen by predators (Stankowich and Blumstein 2005). Columbian black-tailed deer (*Odocoileus hemionus columbianus*), for example, tend to flee uphill and into taller vegetation, using these landscape features as refuge from danger (Stankowich and Coss 2006).

Woodland caribou tend to select large areas of open bog/fen type habitat and it is thought they do so to spatially segregate themselves from alternative prey species such as moose (*Alces alces*; James et al. 2004). Wolves and coyotes tend to occupy habitats concurrent with moose habitat (James et al. 2004, Boisjoly et al. 2010). Briand et al. (2009) found that caribou do not select for dense shrub cover during calving season, and in fact, avoid regenerated shrub areas throughout the year, suggesting that caribou distance themselves from alternate prey habitat, and in consequence, predator habitat. Within an open habitat, caribou may be better able to scan for approaching predators. Futhermore, James et al. (2004) observed that caribou groups with calves during late winter calf surveys were on average approximately half a kilometre further from moose and wolf-preferred habitats than were groups without calves, although this difference was not significant. This observation may illustrate a tendancy for caribou groups comprised of more vulnerable group members to distance themselves from areas of perceived danger. Therefore, it makes sense to consider open tracts of bog/fen habitat as refugia for caribou groups from predator occupied habitats.

As a precaution, the relationship of caribou groups to nearest cover (any group of trees and shrubs at least 1.5m tall) was considered in this study, but no correlation was found between nearest cover and FID (r=-0.038, df = 120, p = 0.681). Caribou fled into cover following only 6% of approaches (n=113) and in several instances fled partway towards the observer before fleeing away, even with available nearby cover. Presumably caribou rely on their speed and agility to move quickly away from perceived danger and may prefer to remain in open areas where quicker and unobstructed retreat is possible. There is no literature-supported evidence that FID of caribou is influenced by distance to cover and therefore this factor was not analyzed.

Alert distance and beginning distance. It is widely acknowledged that FID increases with increasing AD and BD (Blumstein 2003, Reimers et al. 2006, Soulliere 2008, Nieminen 2013, Cooper and Blumstein 2014). A number of disturbance studies have used BD, AD, or similar measures (e.g., encounter distance, sight distance) as covariates in predicting FID (Stankowich and Coss 2006, Reimers et al. 2006, Nieminen 2013). The relationship between AD, BD and FID is variable and unclear, particularly across taxonomic groups, and may in some cases be an artifact (Blumstein 2010, Dumont et al. 2012, Cooper and Blumstein 2014). The relationship between AD, BD and FID is acknowledged in this study; BD is moderately correlated with AD (r=0.42 df=123, $p<0.001$), FID (r=0.22, df=125, p=0.01) and AID (r=0.34, df=122, $p<0.001$), while AD is correlated with FID (r=0.81, df=122, $p<0.001$) and AID (r=0.46, df=122, $p<0.001$). However, because the primary objective of my study is to identify factors which caribou associate with predation risk, I chose not to use AD and BD as predictors of FID. Rather, I chose to assess AD, FID and AID as response variables since each variable reflects a different aspect of caribou antipredator behaviour.

Temperature. Temperature was not included in the analyses since it is known to correlate with season and insect activity and could behave as a confounding variable (Skarin et al. 2010).

Weather. Few scans were collected in unusual weather conditions or those that hindered my ability to maintain visual contact (e.g., severe rain, dense fog, high winds) with target caribou groups. The data collected do not yield enough variation in weather conditions to maintain sufficient statistical power, so weather variables were not considered.

Wind direction. Similarly, in an attempt to remain undetected by caribou until the beginning of an approach, caribou were predominantly approached from downwind or crosswind directions, resulting in low variation in wind direction data. Neither Reimers et al. (2006), nor Aastrup (2000) found an effect of the position of the observer with respect to wind direction (i.e., upwind, downwind or crosswind) on FID of reindeer and caribou.

Distance between neighbours, distance between calf and cow, and activity. The average distance between calf and cow, and the average distance between individual caribou and their nearest neighbour and group activity were recorded as possible novel indicators of group vulnerability. Computer simulations have shown nearest neighbour distance and group density to be good predictors of predation risk at relatively short attack distances (Hirsch and Morrell 2011). However, in this study data for these variables were unfortunately too sparsely recorded to make analysis meaningful. Both variables likely change during the course of the calving season, both with group size and group type and are, therefore, likely represented by other variables in the analyses.

2.3 Results

2.3.1 Summary of group characteristics

Throughout the late spring and early summer of 2011 (May 19 - July 18), 130 caribou groups were approached in the Middle Ridge caribou calving region. Group sizes of approached caribou ranged from 1 to 195 with a median of 9 animals (25% and 75% quartiles = 3 and 19 animals, respectively). Group sizes increased with later seasons ($F_{(4,125)}$= 3.46, p=0.01); the largest groups were encountered during post-calving periods II and III (late June through July). Females were present in 96% of observed groups, and in 67% of all groups they were accompanied by calves. Calves were first observed on May 27th of the study year. Males occurred in 31% of groups and were seen mostly in late June and early July in small numbers. On average, group compositions were largely female (72%), while calves, adults of unknown sex, males and yearlings made up the remaining group proportions (15%, 6%, 6%, and 1%, respectively).

2.3.2 Behavioural responses to predator effects

2.3.2.1 Summary of experimental approaches

Caribou groups, on average, became alert of approachers at a mean distance of 135.5 m (n=125, SD= 66.3 m), assessed approachers over a mean distance of 32.3 m (n=125, SD= 39.2 m), initiated flight on average at 103.1 m (n=127, SD= 60.7 m), and moved away from their original location a mean distance of 16.4 m (n=118, SD= 25.7 m; Figure 2.6, Table 2.5). The mean duration of approaches until alert was 222 seconds (n=89, SD= 163.5 seconds, Figure 2.6) and until flight was 279 seconds (n=92, SD=180.7 seconds, Figure 2.6). The beginning distances (BD) of approaches did not vary with season, group size, approach colour or approach movement (Table 2.5), indicating that BD was appropriately controlled and did not influence caribou responses. A significantly higher proportion of caribou were observed in a head-down, feeding position before the start of an approach trial relative to immediately before flight (Worthman 2014), suggesting that a significant proportion of caribou in a group may have switched from feeding to predator monitoring as they were approached. During flight, most caribou groups (81% of 110 groups) moved away from the approacher together in one direction. The frequency of group splitting or scattering was similar in response to all treatments: 21% of black approaches, 18% of tan approaches, 19% of walking approaches and 20% of crawling approaches. Flight was followed by post-flight returns in 31% of trials which is comparable to results of Aastrup (2000), who saw curiousity behaviour in nearly 34% of encounters during calving, and Soulliere (2008), who observed returns in 26% of trials. Most post-flight returns (55%) occurred from late June through July (during the season designated as post-calving II) between 5 and 6 weeks after the onset of calving (χ^2= 10.2, df = 4, p = 0.04). Post-flight returns did not vary with approach movement or colour.

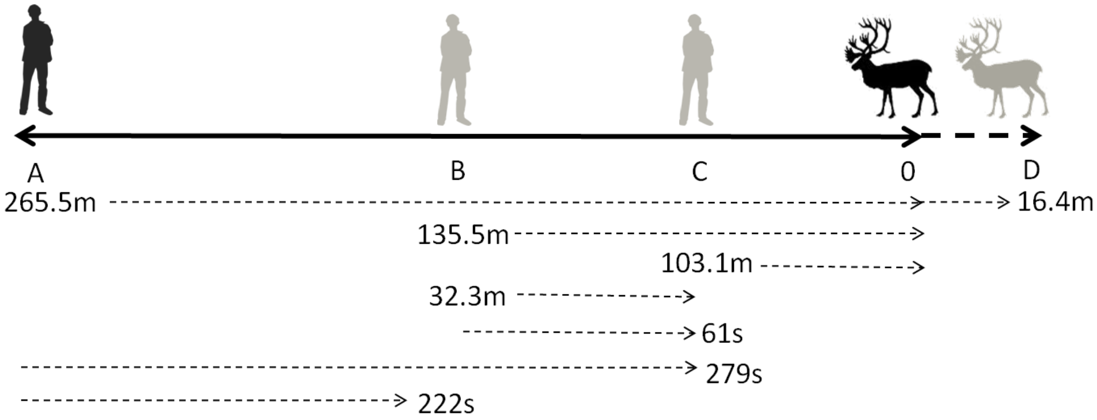

Figure 2.6 Summary of variable means during approaches of caribou groups by a human: beginning distance (A to 0), alert distance (B to 0), flight initiation distance (C to 0), assessment interval distance (B to C), assessment interval duration (B to C), duration of approach until alert (A to B), duration of approach until flight (A to C) and run distance (0 to D).

2.3.2.3 Approach colour and movement

Black approaches elicited significantly longer AD ($F_{(1,123)}$ =6.8, p=0.01) responses than tan approaches (Figure 2.7, Table 2.5). In other words, caribou showed earlier alert behaviour in response to black approaches than tan approaches. There was no significant main effect of approach movement on AD and no significant interaction of colour and movement for AD.

FID was affected by the experimental variables in the same way as AD. Black approaches elicited significantly longer mean FID ($F_{(1,125)}$ =23.7, p<0.001) responses than tan approaches (Figure 2.7, Table 2.5) and there was no significant effect of approach movement or of an interaction between colour and movement.

AID was significantly longer for tan approaches ($F_{(1,123)} = 4.4$, $p=0.04$, Figure 2.7, Table 2.5) than black approaches. Caribou groups overall spent 1.6 times longer, in terms of distance, assessing tan approaches before flight. AID was significantly longer for walk approaches in terms of distance ($F_{(1,123)} =6.39$, $p=0.01$, Figure 2.7, Table 2.5) and significantly shorter in terms of assessment interval time ($F_{(1,90)} =4.9$, $p=0.03$, Table 2.6) than crawl approaches. Due to differences in velocity of approach, caribou predictably spent longer distances assessing walk approaches; approaches by walking cover greater distances in relatively shorter time than crawling, allowing caribou to assess a walk approach over a longer distance but for shorter time duration. It is inconclusive whether the speed or the shape of the approach was more dominant in effect on assessment interval. There was no significant interaction of colour and movement for AID.

The mean distance moved away by caribou was not different between black or tan approaches. However, caribou moved out of my sight following 5.4% of black approaches but not following tan approaches.

Although not statistically significant, there was a higher tendency for post-flight returns to occur following walk-tan approaches than other approach types. Perhaps not coincidentally, walk-tan approaches yielded the longest mean AID (50.4 m, Table 2.5) and the shortest mean FID (69.1 m, Table 2.5). Together, these findings may suggest a weak effect of a walk tan approach on caribou antipredator responses.

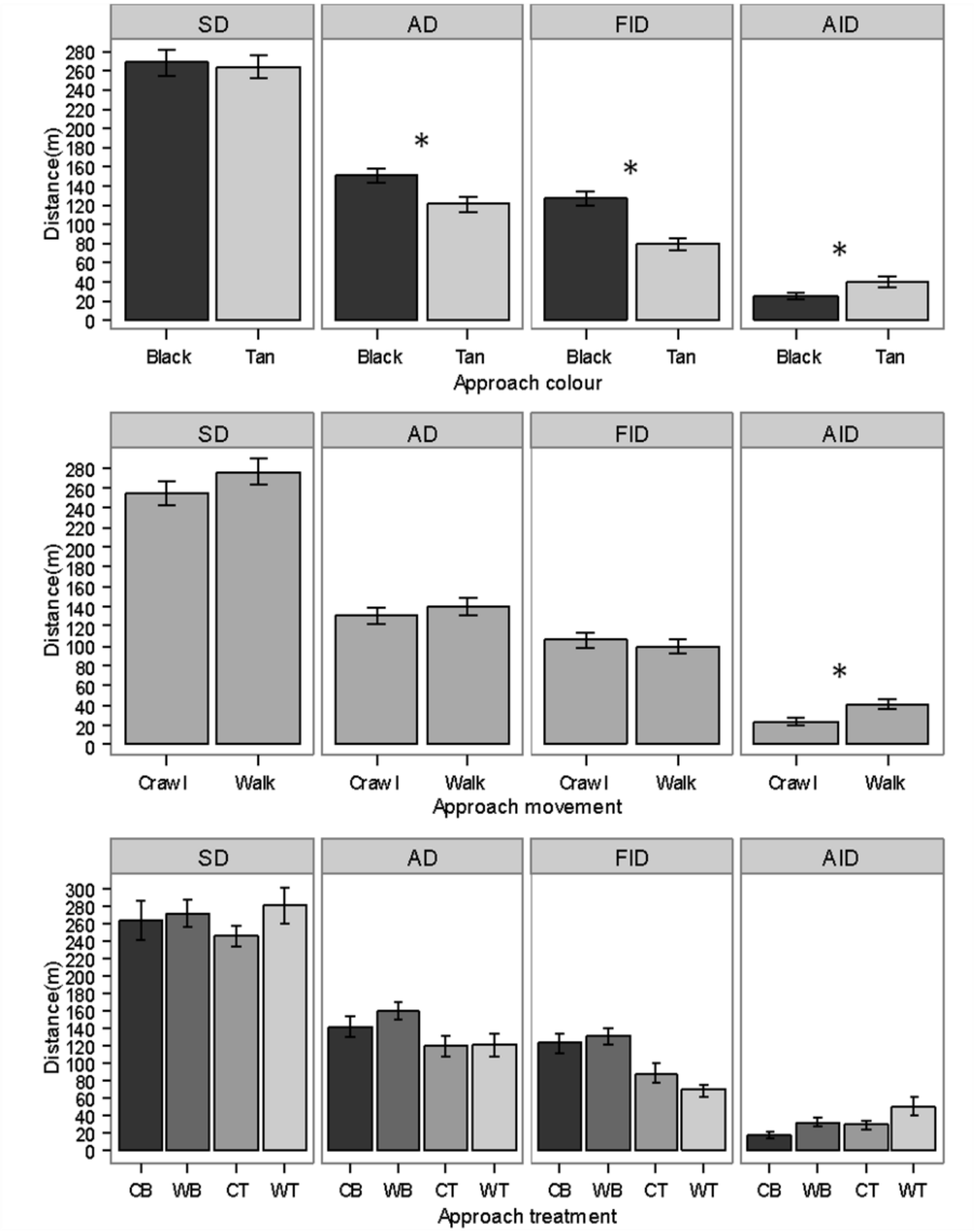

Figure 2.7 Mean beginning distance (BD), alert distance (AD), flight initiation distance (FID) and assessment interval distance (AID) in response to human approachers dressed in black or tan clothing (top panel), crawling or walking (center panel) and colour-movement combinations (bottom panel). (*) indicates a significant difference (p>0.05). Standard error bars (1 x SE) are shown.

Table 2.5 Mean beginning distances, alert distances, flight initiation distances and assessment interval distances (in meters) of Newfoundland caribou when approached by a human in the summer of 2011.

Measure	**Condition**	**Treatment**	**n**	**mean**	**SE**	**Range**
Beginning distance	All	All	129	265.5	9.1	127-800
	Colour	Tan	65	263.2	12.2	127-550
		Black	64	267.8	13.8	130-800
	Movement	Walk	63	276.6	13.4	128-550
		Crawl	66	255.0	12.6	127-800
	Colour x movement	Walk-tan	32	281.3	21.1	128-550
		Crawl-tan	33	245.7	12.3	127-451
		Walk-black	31	271.7	16.5	130-458
		Crawl-black	33	264.2	22.1	151-800
Alert distance	All	All	125	135.5	5.9	20-416
	Colour	Tan	63	120.5	8.8	20-416
		Black	62	150.8	7.5	51-297
	Movement	Walk	60	126.3	7.8	20-297
		Crawl	65	144.0	8.7	40-416
	Colour x movement	Walk-tan	30	121.1	13.7	20-416
		Crawl-tan	32	121.8	11.8	36-305
		Walk-black	30	160.1	9.7	77-285
		Crawl-black	32	142.1	11.2	51-297
Flight initiation distance	All	All	127	103.1	5.4	20-305
	Colour	Tan	63	78.8	6.6	20-305
		Black	64	127.1	7.4	44-297
	Movement	Walk	62	100.2	7.1	20-237
		Crawl	65	105.9	8.1	25-305
	Colour x movement	Walk-tan	31	69.1	7.1	20-177
		Crawl-tan	32	88.2	11.0	25-305
		Walk-black	31	131.4	9.4	44-237
		Crawl-black	33	123.1	11.4	45-297
Assessment interval distance	All	All	125	32.3	3.5	0-290
	Colour	Tan	63	39.5	6.0	0-290
		Black	62	25.0	3.3	0-127
	Movement	Walk	60	41.3	6.1	0-290
		Crawl	65	24.0	3.4	0-103
	Colour x movement	Walk-tan	30	50.4	11.1	0-290
		Crawl-tan	33	29.5	5.2	0-93
		Walk-black	30	32.3	5.0	2-127
		Crawl-black	32	18.3	4.2	0-103

Table 2.6 Mean assessment interval times (in seconds) of Newfoundland caribou groups when approached by a human wearing black or tan clothing and either walking or crawling in the summer of 2011.

Measure	Condition	Treatment	n	mean	SE	Range	Sum
Assessment Interval Time	All	All	89	60.9	9.2	0-626	5421
	Colour	Tan	41	76.0	17.1	0-626	3114
		Black	48	48.1	8.7	5-345	2307
	Movement	Walk	44	43.0	4.9	0-131	1890
		Crawl	45	78.5	17.3	4-622	3531

2.3.3 Behavioural responses in context of environmental variables

2.3.3.1 Antipredator model trends

General and generalized linear models with the lowest AICc values, and within 2 units of the lowest AICc values, were selected as the best predictive models of AD, FID and AID (Tables 2.7, 2.9 and 2.11, respectively). Overall, models which include the predator effect variables (i.e., approach colour and approach movement) have lower AICc values and explain variability of AD, FID and AID better than those models which do not include the predator effect variables. None of the best ranked models include an interaction between approach and colour.

2.3.3.2 Alert distance models

AD responses are best explained by a model containing the base variables (i.e., habitat, group size, calf presence, Julian date), graminoid cover, colour and approach movement (Tables 2.7 and 2.8). AD was significantly reduced in bog/fen habitats, in response to tan approaches, and with increasing Julian date. Greater graminoid cover and the presence of calves significantly increased AD. Contrary to expectation, group size was not a significant factor in predicting AD.

Table 2.7 AICc alert distance (AD) model selection results (n=122). The base model (1) contains only empirically-supported predictor variables. Predator effect models (11, 2, 10, 12, 8, 7, 9, 13) contain the experimental variables - colour and approach. Vegetation effect models (11, 10, 8, 7, 9, 6, 5, 3, 4, 13) contain plant group cover or food number variables. The global model (13) contains all predictor variables. Models with lowest AICc rankings are in bold.

No.	**Model variables**	**K**	**Loglik**	**AIC$_c$**	**Δ_i**	**ω_i**
11	**habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ gram.cov**	**10**	**-668.35**	**1358.68**	**0**	**0.41**
2	habitat+grp.size+calf.p.a+JD+approach+colour	9	-670.57	1360.75	2.08	0.15
10	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ ericS.cov	10	-669.71	1361.41	2.73	0.11
12	habitat+grp.size+calf.p.a+JD+approach:colour	10	-670.05	1362.09	3.41	0.08
8	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ lich.cov	10	-670.26	1362.49	3.82	0.06
7	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ foods	10	-670.4	1362.77	4.1	0.05
9	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ moss.cov	10	-670.57	1363.12	4.44	0.04
6	habitat+ grp.size+ calf.p.a+ JD+ gram.cov	8	-673.02	1363.31	4.64	0.04
1	habitat+ grp.size+ calf.p.a+ JD	7	-674.71	1364.4	5.72	0.02
5	habitat+ grp.size+ calf.p.a+ JD+ ericS.cov	8	-674.17	1365.61	6.93	0.01
3	habitat+ grp.size+ calf.p.a+ JD+ lich.cov	8	-674.38	1366.04	7.37	0.01
4	habitat+ grp.size+ calf.p.a+ JD+ moss.cov	8	-674.7	1366.68	8.01	0.01
13	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ approach:colour + gram.cov+ ericS.cov+ lich.cov+ moss.cov+ foods	14	-668.1	1368.12	9.44	0.00

Table 2.8 Summary of the general linear model (model 11, R^2=0.24) for predicting alert distances (AD) of caribou groups disturbed by an approaching person in Middle Ridge, Newfoundland in May-July of 2011. The reference mean estimate (405.92) is the mean of the observations barren habitat, colour black, calves absent, approach crawl, and subsequent estimates are differences from this reference mean. (*) indicates p-values of 0.05 or less.

Response	Parameter	Estimate	SE	*t*	P
AD	Intercept	405.92	72.37	5.61	1.46e-07 *
	bog/fen	-41.59	18.86	-2.21	0.029 *
	sparse forest	29.57	31.25	0.95	0.346
	grp.size	0.1	0.19	0.53	0.594
	calf.p.a1	32.74	13.04	2.51	0.013 *
	JD	-1.58	0.45	-3.49	0.001 *
	approachW	15.84	10.99	1.44	0.152
	colourT	-29.43	11.22	-2.62	0.01 *
	gram.cov	1.17	0.57	2.05	0.043 *

2.3.3.3 Flight initiation distance models

FID responses are best explained by a model containing the base variables (i.e., habitat, group size, calf presence, Julian date), graminoid cover, colour and approach movement (Tables 2.9 and 2.10). FID was significantly reduced in bog/fen habitats, in response to tan approaches, and with increasing Julian date. Greater graminoid cover and the presence of calves significantly increased FID. Contrary to expectation, group size was not a significant factor in predicting FID.

Table 2.9 AICc flight initiation distance (FID) model selection results (n=124). The base model (1) contains only empirically-supported predictor variables. Predator effect models (11, 2, 12, 10, 7, 8, 9, 13) contain the experimental variables - colour and approach. Vegetation effect models (11, 10, 7, 8,9,13, 6, 5, 3, 4) contain plant group cover or food number variables. The global model (13) contains all predictor variables. Models with lowest AICc rankings are in bold.

No.	**Model variables**	**K**	**Loglik**	**AIC_c**	**Δ_i**	**ω_i**
11	**habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ gram.cov**	**10**	**-656.11**	**1334.17**	**0**	**0.61**
2	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour	9	-658.95	1337.48	3.31	0.12
12	habitat+ grp.size+ calf.p.a+ JD+ approach:colour	10	-657.91	1337.77	3.6	0.1
10	habitat+ grp.size + calf.p.a+ JD+ approach+ colour + ericS.cov	10	-658.58	1339.11	4.94	0.05
7	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ foods	10	-658.75	1339.44	5.27	0.04
8	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ lich.cov	10	-658.88	1339.71	5.54	0.04
9	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ moss.cov	10	-658.95	1339.84	5.67	0.04
13	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ approach:colour + gram.cov+ ericS.cov+ lich.cov+ moss.cov+ foods	14	-655.79	1343.43	9.26	0.01
6	habitat+ grp.size+ calf.p.a+ JD+ gram.cov	8	-668	1352.36	18.19	0.00
1	habitat+ grp.size+ calf.p.a+ JD	7	-669.7	1354.36	20.19	0.00
5	habitat+ grp.size+ calf.p.a+ JD+ ericS.cov	8	-669.55	1356.36	22.19	0.00
3	habitat+ grp.size+ calf.p.a+ JD+ lich.cov	8	-669.6	1356.46	22.29	0.00
4	habitat+ grp.size+ calf.p.a+ JD+ moss.cov	8	-669.69	1356.63	22.46	0.00

Table 2.10 Summary of the general linear model (model 11, R^2=0.38) for predicting flight initiation distances (FID) of caribou groups disturbed by an approaching person in Middle Ridge, Newfoundland in May- July of 2011. The reference mean estimate (333.94) is the mean of the observations barren habitat, colour black, calves absent, approach crawl, and subsequent estimates are differences from this reference mean. (*) indicates p-values of 0.05 or less.

Response	Parameter	Estimate	SE	*t*	P
FID	Intercept	333.94	58.45	5.71	8.85e-08 *
	bog/fen	-50.28	15.26	-3.3	0.001 *
	sparse forest	31.64	25.69	1.23	0.221
	grp.size	-0.17	0.16	-1.08	0.282
	calf.p.a1	27.87	10.71	2.6	0.011 *
	JD	-1.17	0.37	-3.18	0.002 *
	approachW	0.62	9.04	0.07	0.946
	colourT	-44.4	9.2	-4.83	4.31e-06 *
	gram.cov	1.09	0.47	2.32	0.022 *

2.3.3.4 Assessment interval distance models

Variability in AID was most influenced by a model containing the base variables (habitat, group size, calf presence, Julian date), number of foods, colour, and approach movement (Table 2.11 and 2.12). Increased group size, walk approach, and tan colour significantly increased AID. An increased number of food species significantly decreased AID.

Table 2.11 AICc assessment interval distance (AID) generalized linear model selection results (n=122). The base model (1) contains only empirically-supported predictor variables. Predator effect models (7, 10, 2, 12, 8, 9, 11,13) contain the experimental variables - colour and approach. Vegetation effect models (7, 10, 8, 9, 11, 13, 5, 3, 6, 4) contain plant group cover or food number variables. The global model (13) contains all predictor variables. Models with lowest AICc rankings are in bold.

No.	Model variables	K	Loglik	AIC_c	Δ_i	ω_i
7	**habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ foods**	**9**	**-534.54**	**1088.68**	**0**	**0.63**
10	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ ericS.cov	9	-536.02	1091.65	2.97	0.14
2	habitat+grp.size+calf.p.a+JD+approach+colour	8	-537.69	1092.66	3.98	0.09
12	habitat+grp.size+calf.p.a+JD+approach:colour	9	-537.21	1094.03	5.35	0.04
8	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ lich.cov	9	-537.6	1094.8	6.12	0.03
9	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ moss.cov	9	-537.61	1094.83	6.15	0.03
11	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ gram.cov	9	-537.61	1094.83	6.15	0.03
13	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ approach:colour + gram.cov+ ericS.cov+ lich.cov+ moss.cov+ foods	14	-533.24	1098.41	9.73	0.00
1	habitat+ grp.size+ calf.p.a+ JD	6	-545.81	1104.35	15.67	0.00
5	habitat+ grp.size+ calf.p.a+ JD+ ericS.cov	7	-545.15	1105.28	16.6	0.00
3	habitat+ grp.size+ calf.p.a+ JD+ lich.cov	7	-545.71	1106.41	17.73	0.00
6	habitat+ grp.size+ calf.p.a+ JD+ gram.cov	7	-545.8	1106.59	17.91	0.00
4	habitat+ grp.size+ calf.p.a+ JD+ moss.cov	7	-545.81	1106.6	17.92	0.00

Table 2.12 Summary of the generalized linear model (model 7, R^2=0.17) for predicting assessment interval distance (AID) of caribou groups disturbed by an approaching person in Middle Ridge, Newfoundland in May- July of 2011. The reference mean estimate (4.38) is the mean of the observations barren habitat, colour black, calves absent, approach crawl, and subsequent estimates are differences from the reference mean (intercept). (*) indicates p-values of 0.05 or less.

Response	Parameter	Estimate	SE	*t*	P
AID	Intercept	4.38	1.27	3.45	0.001 *
	bog/fen	0.15	0.3	0.5	0.615
	sparse forest	-0.32	0.55	-0.59	0.559
	grp.size	0.01	0.00	2.8	0.006 *
	calf.p.a1	0.11	0.23	0.47	0.638
	JD	-0.01	0.01	-0.95	0.342
	approachW	0.67	0.19	3.52	0.001 *
	colourT	0.54	0.2	2.74	0.007 *
	foods	-0.08	0.04	-2.34	0.021 *

2.3.3.5 Season

Since GLM analyses showed Julian date to significantly influence AD and FID (Tables 2.8 and 2.10, respectively), the data sampling period was divided into five seasons to reflect changes in caribou group dynamics in relation to calving (Table 2.2). Season was a significant predictor of FID (F(4,122)=4.88, p=0.001) and AD (F(4,120)=3.53, p=0.009), but not AID. The longest FIDs occured during the calving and post-calving I seasons (Figure 2.8). Mean FID and AD were significantly longer during the calving season in comparison to post-calving seasons II and III (Figure 2.9).

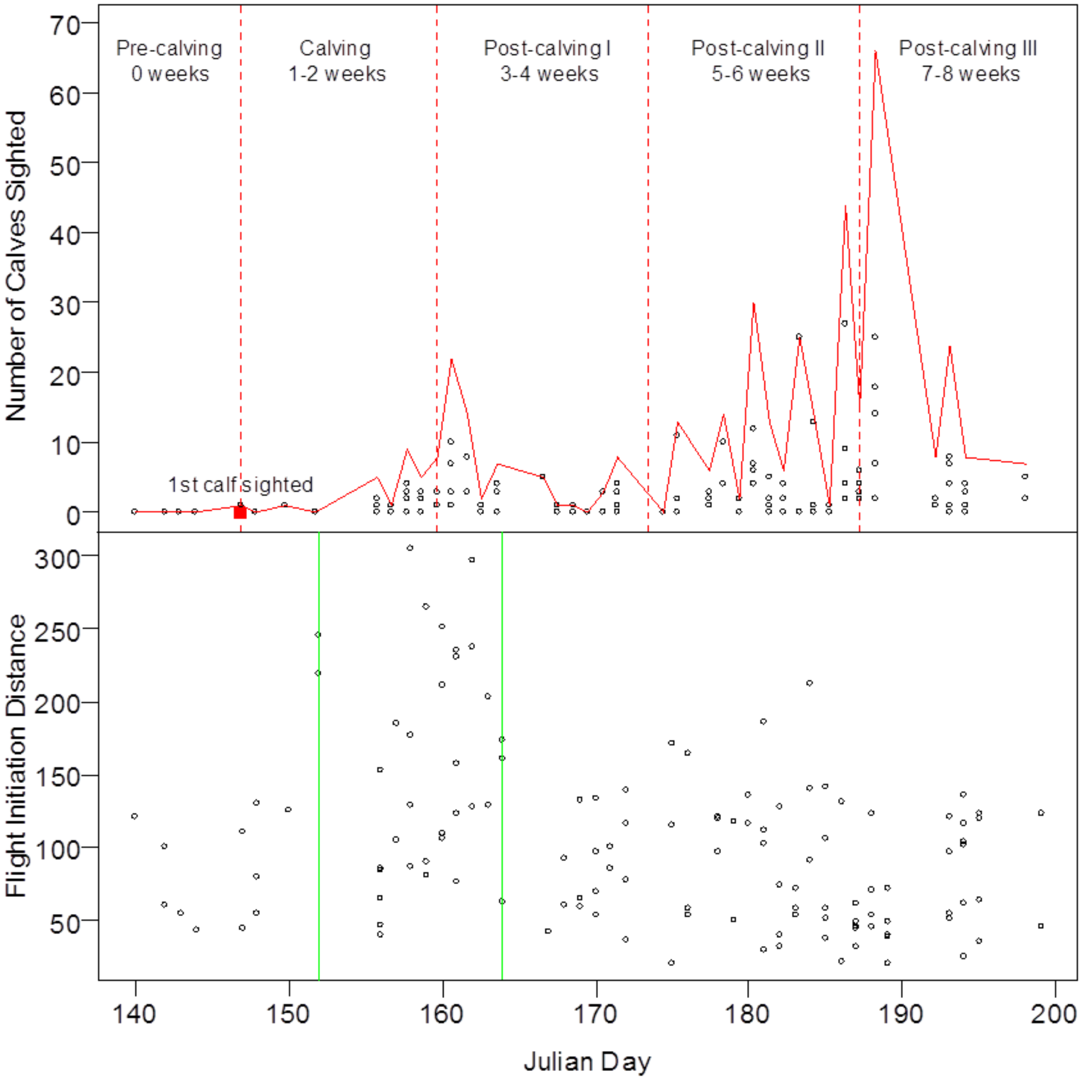

Figure 2.8 Number of calves sighted and flight initiation distances for each group approached on each day of the sampling period. The peaks of the solid line in the upper panel represent the cumulative number of calves observed for each day. Dashed lines separate the seasons designated for this study. Solid lines in the lower panel enclose the greatest FID values and are extended to include 20% of the overall sampling period days.

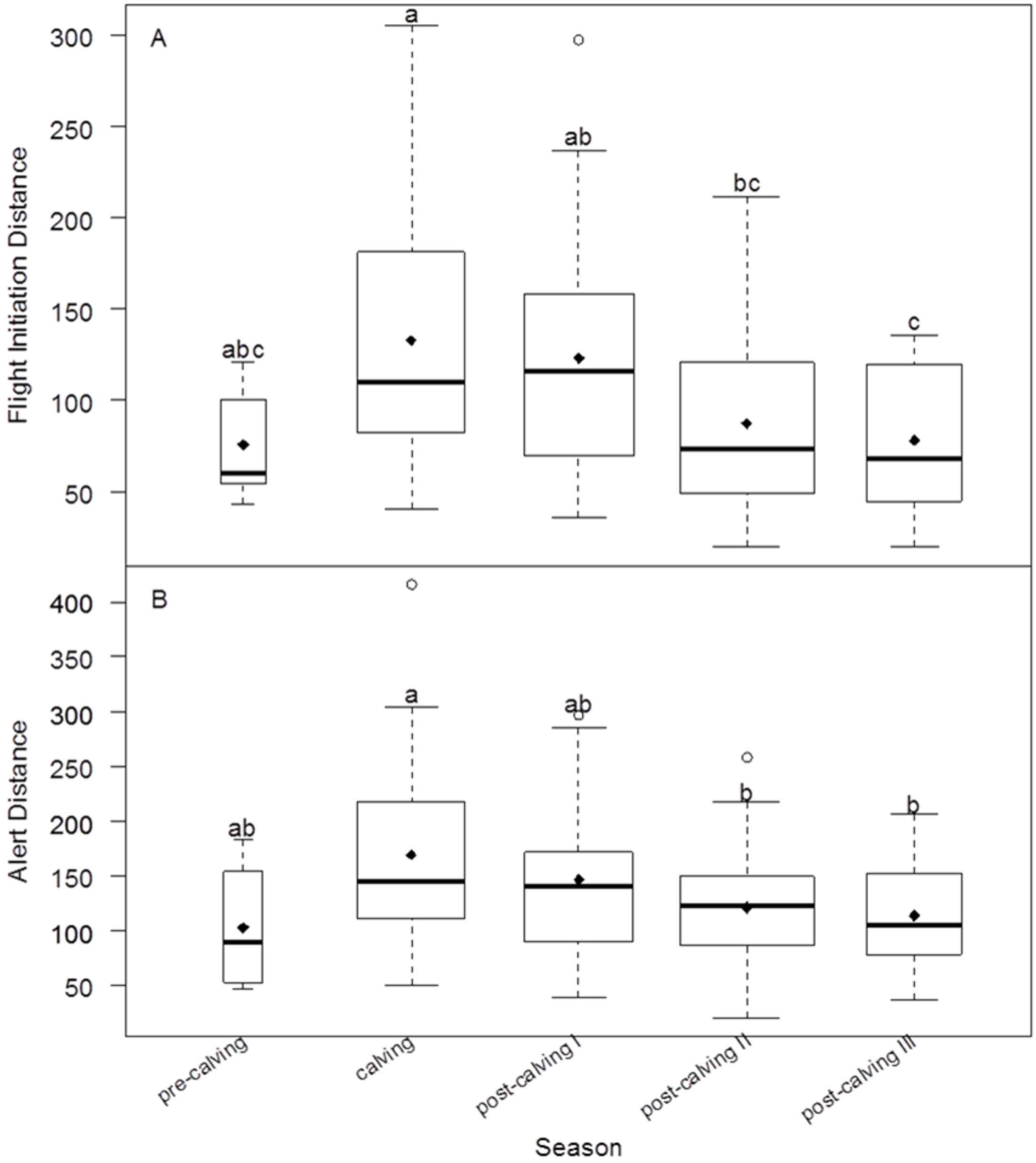

Figure 2.9 Boxplots showing FID (A) and AD (B) during pre-calving, calving, post-calving I, post-calving II and post-calving III seasons. Boxplot lengths represent interquartile ranges (IQR) and whiskers extend to the most extreme values within 1.5 times the IQR. Bold lines represent medians and bold points represent means. Dissimilar letters indicate pair-wise significant differences between means (Tukey’s HSD, all significant differences are $p<0.05$). Bar widths are proportional to the square root of sample sizes.

2.3.3.6 Vegetation

Aside from a relationship between AID and the number of food species present at a given site, GLM analyses did not indicate clear relationships between vegetation characteristics and antipredator responses. Caribou were always observed foraging prior to approach trials, suggesting that caribou foods were represented in all vegetation surveys, but also that surveys may have consistently been conducted in areas expressly selected by caribou for desirable foods. Ericaceous shrubs, mosses, lichen and graminoids were the most represented plant groups in sampled food plots. *Andromeda*, *Chamaedaphne*, *Kalmia*, *Rhododendron*, *Sphagnum* and *Cladonia* species were present in more than 60 percent of the plots. The occurrence of food species in a plot ranged from 2 to 17 species with a median of 9 (n=127). Species of the functionally classified graminoid group (grasses, rushes and sedges) occurred in over 90 percent of plots and cover increased with Julian date (F(1,126)=31.6, $p<0.0001$, Figure 2.10). Cover of other functional plant groups did not change with Julian date. Moss cover was higher than other plant group covers in 68% (n=128) of site surveys.

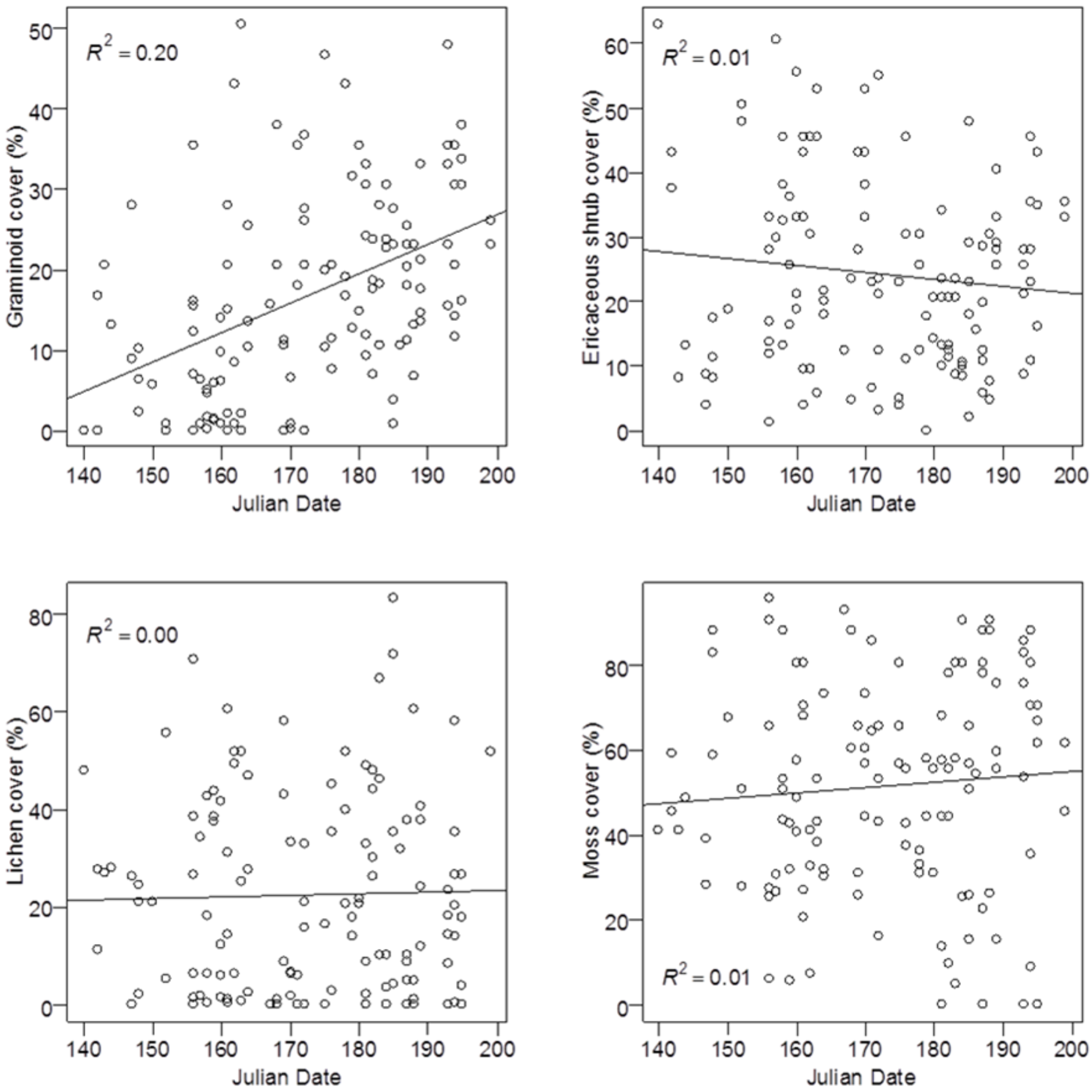

Figure 2.10 Percent cover of graminoids, ericaceous shrubs, lichen and moss by Julian date with linear regressions.

Some generalizations about the relationships between lichen, moss, ericaceous shrub and graminoid vegetation groups can be made from PCA ordination (Figure 2.11). Where lichen loading is high, the moss loading is in nearly the opposite direction. Similarly, where graminoid loading is high, ericaceous shrubs loadings are in the opposite direction. The first principal component (PC1), capturing over 53% of variation, may describe relative habitat moisture (moisture increasing to the right of the plot) while the second principal component (PC2) may be descriptive of nutrient availability (nutrient availability increasing towards the bottom of the plot), though without more detailed information about specific species distributions the preceding interpretations are only speculative.

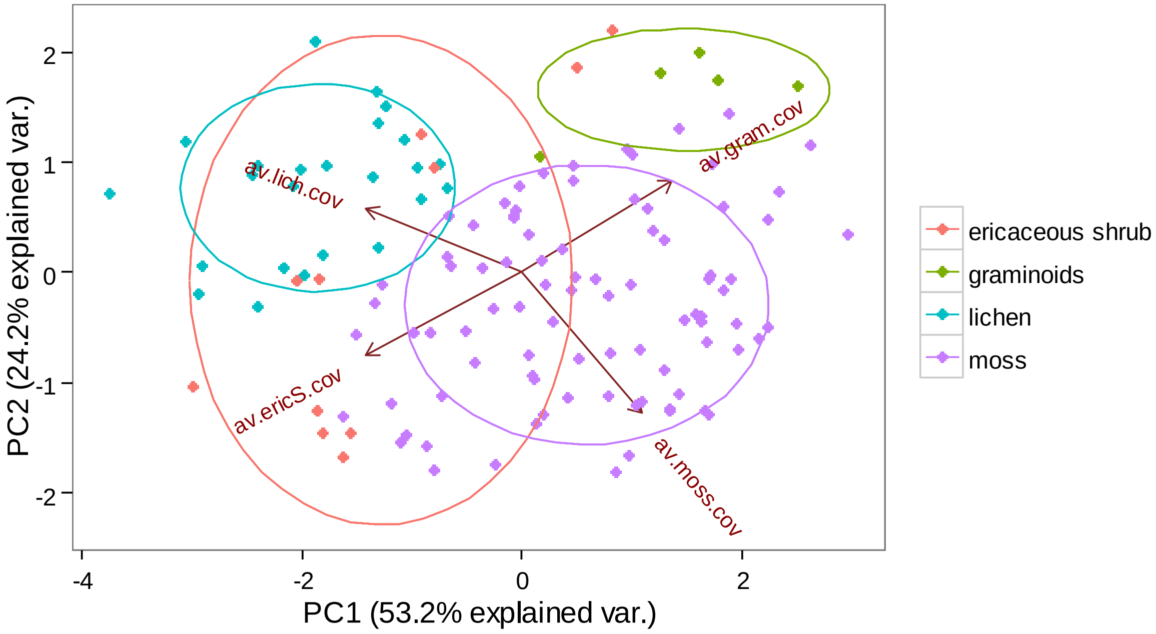

Figure 2.11 Biplot of two principal components for four vegetation characteristics: average lichen cover, average moss cover, average graminoid cover, average ericaceous shrub cover. Arrows represent loadings while points represent scores of plant groups. Colour groups represent the dominant plant group (highest percent cover) at each survey location, with 70% confidence ellipses.

2.3.4 Post-hoc hypotheses

Post hoc hypotheses differ from *a prioiri* hypotheses in that they were not guided by the economic hypothesis and that they arose as additional hypotheses during data collection and analysis. A number of novel and potentially important effects, which were not described by the top *a priori* models, were revealed in *post hoc* analyses.

2.3.4.1 Alert distance

Post-hoc hypotheses ranked by AICc showed that two models (models 22 and 11, Tables 2.13 and 2.14) best predict AD. These models include some significant variables in common with *a priori* models: calf presence, Julian date, and colour. Unique to *post hoc* analyses is the finding that AD is predicted to decrease with increasing wind speed (Table 2.14).

Table 2.13 Post-hoc AICc alert distance (AD) model selection results (n=108). Model 11_ph is the best selected model from *a priori* analyses (model 11 in Table 2.7). Group effect models (18, 16, 14, 15, 17) contain predictor variables representing group characteristics. Topographic effect models (20, 21) contain descriptor variables of topography. Model 19 tests effect of insect harassment. Models with lowest AICc rankings are in bold.

No.	**Model variables**	**K**	**Loglik**	**AIC_c**	**Δ_i**	**ω_i**
22	**habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ wind.spd**	**10**	**-592.86**	**1207.99**	**0**	**0.55**
11_ph	**habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ gram.cov**	**10**	**-593.84**	**1209.94**	**1.95**	**0.21**
18	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:calf.p.a	11	-593.98	1212.71	4.73	0.05
20	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ topog	10	-595.23	1212.72	4.74	0.05
16	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:JD	10	-595.41	1213.09	5.11	0.04
14	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig	10	-595.46	1213.18	5.19	0.04
15	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:grp.size	10	-595.47	1213.22	5.23	0.04
17	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:habitat	12	-594.78	1216.84	8.85	0.01
21	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ gain	13	-594.78	1219.43	11.44	0.00
19	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ insect.h	15	-592.31	1219.83	11.85	0.00

Table 2.14 Summary of the general linear models (Models 22, R^2= 0.26 and 11_ph, R^2=0.24) for predicting alert distances (AD) of caribou groups disturbed by an approaching person in Middle Ridge, Newfoundland in May- July of 2011. The reference mean estimates (389.23 and 405.98) are the means of the observations barren habitat, colour black, approach crawl, and subsequent estimates are differences from the reference mean. (*) indicates p-values of 0.05 or less.

Model	Parameter	Estimate	SE	*t*	P
22(wind.spd)	Intercept	389.23	75.68	5.14	1.37e-06 *
	bog/fen	-16.01	20.14	-0.8	0.429
	sparse forest	30.18	32.67	0.92	0.358
	grp.size	0.23	0.24	0.97	0.333
	calf.p.a1	29.89	14.48	2.06	0.042 *
	JD	-1.34	0.47	-2.85	0.005 *
	approachW	14.54	11.99	1.21	0.228
	colourT	-28.61	12.37	-2.31	0.023 *
	wind.spd	-6.69	3.01	-2.23	0.028 *
11_ph (gram.cov)	Intercept	405.98	78.38	5.18	1.17e-06 *
	bog/fen	-33.25	21.93	-1.52	0.133
	sparse forest	36.15	32.93	1.1	0.275
	grp.size	0.22	0.24	0.92	0.359
	calf.p.a1	32.78	14.59	2.25	0.027 *
	JD	-1.63	0.49	-3.31	0.001 *
	approachW	18.54	12.12	1.53	0.129
	colourT	-28.96	12.48	-2.32	0.022 *
	gram.cov	1.05	0.6	1.76	0.082

2.3.4.2 Flight initiation distance

Post-hoc hypotheses ranked by AICc showed that two models (models 22 and 11, Tables 2.15 and 2.16) best predicted both FID. These models include some significant variables in common with *a priori* models: habitat, Julian date, colour and graminoid cover. Unique to *post hoc* analyses is the finding that FID is predicted to decrease with increasing wind speed (Table 2.16).

Table 2.15 Post-hoc AICc flight initiation distance (FID) model selection results (n=108). Model 11_ph is the best selected model from *a priori* analyses (model 11 in Table 2.9). Group effect models (14, 16, 15, 18, 17) contain predictor variables representing group characteristics. Topographic effect models (20, 21) contain descriptor variables of topography. Model 19 tests effects of insect harassment. Models with lowest AICc rankings are in bold.

No.	**Model variables**	**K**	**Loglik**	**AIC$_c$**	**Δ_i**	**ω_i**
22	**habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ wind.spd**	**10**	**-573.24**	**1168.75**	**0**	**0.58**
11_ph	**habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ gram.cov**	**10**	**-574.05**	**1170.38**	**1.63**	**0.26**
20	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ topog	10	-575.54	1173.35	4.6	0.06
14	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig	10	-576.3	1174.86	6.11	0.03
16	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:JD	10	-576.36	1175	6.24	0.03
15	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:grp.size	10	-576.42	1175.12	6.36	0.02
21	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ gain	13	-572.65	1175.17	6.41	0.02
18	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:calf.p.a	11	-576.15	1177.04	8.29	0.01
19	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ insect.h	15	-571.91	1179.04	10.29	0.00
17	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:habitat	12	-576.02	1179.33	10.58	0.00

Table 2.16 Summary of the general linear models (Model 22, R^2= 0.36 and 11_ph, R^2= 0.35) for predicting flight initiation distances (FID) and of caribou groups disturbed by an approaching person in Middle Ridge, Newfoundland in May- July of 2011. The reference mean estimates (302.87 and 321.22) are the means of the observations barren habitat, colour black, approach crawl, and subsequent estimates are differences from the reference mean. (*) indicates p-values of 0.05 or less.

Model	Parameter	Estimate	SE	*t*	P
22(wind.spd)	Intercept	302.87	63.11	4.8	5.64e-06 *
	bog/fen	-19.58	16.79	-1.17	0.247
	sparse forest	36.08	27.24	1.32	0.189
	grp.size	-0.15	0.2	-0.77	0.444
	calf.p.a1	20.47	12.07	1.7	0.093
	JD	-0.84	0.39	-2.15	0.034 *
	approach	-6.89	10	-0.69	0.493
	colourT	-46.86	10.31	-4.54	1.57e-05 *
	wind.spd	-6.2	2.51	-2.47	0.015 *
11_ph (gram.cov)	Intercept	321.22	65.26	4.92	3.42e-06 *
	bog/fen	-36.77	18.26	-2.01	0.047 *
	sparse forest	41.75	27.42	1.52	0.131
	grp.size	-0.16	0.2	-0.81	0.42
	calf.p.a1	23.24	12.15	1.91	0.059
	JD	-1.13	0.41	-2.76	0.00683 *
	approach	-3.01	10.09	-0.3	0.766
	colourT	-47.16	10.39	-4.54	1.59e-05 *
	gram.cov	1.06	0.5	2.13	0.035 *

2.3.4.3 Assessment interval distance

The best AICc ranked model to predict AID includes topography as a factor (model 20, Tables 2.17 and 2.18). This model includes some significant variables in common with *a priori* models: group size, approach movement, and colour. Unique to *post hoc* analyses is the finding that AID is predicted to be longer when topography is moderate (Table 2.18)

Table 2.17 Post-hoc AIC assessment interval distance (AID) model selection results (n=108). Model 7_ph is the best selected model from *a priori* analyses (model 7 in Table 2.10). Group effect models (18, 16, 14, 15, 17) contain predictor variables representing group characteristics. Topographic effect models (20, 21) contain descriptor variables of topography. Model 19 tests effects of insect harassment. Models with lowest AICc rankings are in bold.

No.	**Model variables**	**K**	**Loglik**	**AIC_c**	**Δ_i**	**ω_i**
20	**habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ topog**	**10**	**-536.73**	**1095.72**	**0**	**0.73**
21	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ gain	13	-534.26	1098.39	2.67	0.19
18	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:calf.p.a	11	-538.66	1102.08	6.36	0.03
7_ph	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ foods	10	-540.76	1103.79	8.07	0.01
16	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:JD	10	-540.79	1103.85	8.13	0.01
14	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig	10	-540.86	1103.98	8.26	0.01
15	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:grp.size	10	-541.39	1105.05	9.33	0.01
22	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ wind.spd	10	-541.68	1105.63	9.91	0.01
17	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ num.vig:habitat	12	-540.12	1107.53	11.8	0.00
19	habitat+ grp.size+ calf.p.a+ JD+ approach+ colour+ insect.h	15	-540.42	1116.06	20.34	0.00

Table 2.18 Summary of the general linear model (model 20, R^2= 0.26) for assessment interval distance (AID) and of caribou groups disturbed by an approaching person in Middle Ridge, Newfoundland in May- July of 2011. The reference mean estimate (26.55) is the combined means of the observations barren habitat, colour black, approach crawl, and subsequent estimates are differences from the reference mean. (*) indicates p-values of 0.05 or less.

Model	Parameter	Estimate	SE	*t*	P
20 (topog)	Intercept	26.55	48.59	0.55	0.586
	bog/fen	21.03	13.24	1.59	0.116
	sparse forest	-24.22	20.31	-1.19	0.236
	grp.size	0.4	0.14	2.83	0.006 *
	calf.p.a	8.33	8.6	0.97	0.335
	JD	-0.29	0.29	-1.01	0.313
	approachW	23.04	7.13	3.23	0.002 *
	colourT	21.91	7.45	2.94	0.004 *
	topog	44.2	14.28	3.1	0.003*

2.4 Discussion

2.4.1 Antipredator responses to simulated predator approaches

From an evolutionary view point, adaptive predator recognition and corresponding antipredator response is beneficial to reduce energetic costs related to flight, and the risk of predation. In this study, I showed that caribou discriminated between and responded differently to distinct simulated predator approaches. Caribou responded strongly (i.e., increased alert distance, increased flight initiation distance and decreased assessment interval distance) to black approaches (bear model) compared to tan approaches (coyote model). The posture of the approacher (crawling or walking) did not influence caribou flight or alert responses, but walk approaches lengthened AID. Predator traits associated with greater risk appear to amplify the perception of risk, expressed as stronger antipredator responses (Stankowich and Blumstein 2005).

2.4.1.1 Colour

Caribou became aware of and fled earlier from human approachers dressed in black compared to tan. These results are not surprising since black bears were the primary lethal predators of caribou in the Middle Ridge region at the time of field study (Weir et al. 2014). The AID is the distance interval during which caribou evaluate an approaching threat. Caribou assessed approachers dressed in black clothing over a shorter distance than approachers dressed in tan. Reimers et al. (2011) suggest that lower probability of assessment (and higher vigilance) occur in *Rangifer* herds that have more frequent interactions with lethal predators as in the case of wild reindeer in Edgeøya encountering polar bears. Work by Worthman (2014) indicates that caribou of the Middle Ridge herd were indeed more proportionally vigilant during black approaches and less vigilant during tan approaches. Prolonged assessment of tan approaches may suggest unfamiliarity with tan coloured threats, infrequent interactions with tan-coloured lethal predators or less perceptibility of tan approaches relative to the environment.

2.4.1.2 Movement

Animals pay attention to the behaviour of approachers, fleeing at greater distances when approacher behaviour is perceived as more threatening (Stankowich 2008). Crawl and walk approach movements did not influence caribou AD or FID, but caribou made longer assessments of walk approaches. It is unclear whether longer assessment was due to the shape, detectability or the velocity of the movement. Bergerud (1971) noted that on two occasions when he approached female caribou and calf pairs by crawling, he was met with aggressive behaviour from the cow, which suggests approach type-specific behavioural responses. In general, humans on foot are more provocative than vehicles, and some motor-less, outdoor, recreational activities are more disruptive than others (Colman et al. 2012). Rapidly or directly approaching humans are more provocative than slowly or indirectly approaching humans (Stankowich 2008).

It is of interest to note, although not statistically significant, that tan-walk approaches elicited the longest AIDs, the shortest FIDs, and the most number of post-flight returns. Together these outcomes suggest that caribou spent more time overall considering walk-tan approaches than other approaches. The walk-tan approach has the least semblance to any true caribou predators in the region so caribou may find an upright, tan creature unfamiliar and baffling, thus requiring prolonged assessment. Another possibility is that caribou perceive walk-tan encounters as unthreatening. A walking human approacher wearing tan-coloured clothing is approximately the correct height and colour of a caribou and could conceivably be mistaken at first glance for one of the hundreds of caribou of the region which form the fluid social aggregations common during the summer months. Baskin (1974) describes how reindeer herders attract reindeer by assuming a ‘reindeer’ configuration [a dark-coloured, horizontal shape, of reindeer size, with ‘antlers’ (raised hands) at the forward moving end] and by using a head-bobbing motion - a behaviour used among caribou to attract one another.

2.4.1.3 Cue detectability

Since there were minimal olfactory or acoustic stimuli in this study (approaches occurred into head winds and the approacher only made walking-associated noises during approaches), threat recognition must have been associated with visual cues (i.e., movement, colour and size) of the approaching stimuli. However, it is plausible that differing responses to different colour cues could be explained by differences in cue detectability. Personal assessment of footage and photographs depicting the two coloured approaches in various habitats of the Middle Ridge study region do not suggest one colour to contrast more strongly against environmental features than the other (Figure 2.12). However, *Rangifer* have near ultraviolet vision and may uniquely perceive enhanced contrasts of certain colours in their environment (Hogg et al. 2011). Reimers et al. (2006) failed to support the prediction that flight distances would increase when human approachers dressed in dark clothing were seen against a high-contrast, snow-covered background rather than a snow-free background. Furthermore, Reimers and Eftestol (2012) demonstrated that wild reindeer of insular Edgeøya (part of the Norwegian Svalbard archipelago in the Arctic Ocean) responded more strongly to humans dressed in white clothing than dark clothing. The Edgeøya study region is strikingly similar in habitat appearance to the Middle Ridge study area (Figure 2.12) and reversed findings between the present study and the Svalbard study suggest that *Rangifer* can detect both light coloured clothing and dark coloured equally. Wild Svalbard reindeer likely associated the colour white with their top lethal predators, polar bears, while Newfoundland caribou associated the colour black with black bears.

Figure 2.12 (A) A human approacher dressed in black in the Middle Ridge region of Newfoundland (this study), (B) a human approacher dressed in tan in the Middle Ridge region of Newfoundland (this study) and (C) A human approacher dressed in white in Edgeøya, Svalbard (Reimers and Eftestol 2012).

2.4.1.4 Post-flight returns and assessment behaviours

Following flight, caribou returned towards the approacher in approximately 30% of encounters, demonstrating apparent investigatory behaviours (i.e., sniffing the air, circling the approacher, alert postures and direct gaze). Caribou in Greenland showed curiousity behaviour in approximately 70% of overall encounters, and were less likely to show curiosity during the calving season, after the hunting season, in groups with calves, and in certain localities (Aastrup 2000). Similarly, the occurrence of post-flight returns during the peak calving period was lower for Newfoundland caribou in this study. Blehr (1997) describes possible energy-saving “confirmatory behaviours” in which caribou stop to look back at the approacher during flight or on some occasions fleeing a few metres in the direction of the approacher. All of the above behaviours may indicate that caribou have difficulty or need longer to recognize and assess novel approachers as threats or non-threats.

2.4.2 Environmental factors influencing antipredator responses

The economic hypothesis by Ydenberg and Dill (1986) predicts that antipredator flight responses are optimized to maximize prey fitness benefits and minimize prey fitness costs. Lower fleeing costs might arise when a resource patch is poor (i.e., less resources are lost by leaving), rich resources are evenly distributed and easy to locate elsewhere, or ecological conditions (e.g., terrain, vegetation structure, snow) are mild at the time of disturbance, thereby not increasing locomotion costs (Frid and Dill 2002). In this study, in addition to predator traits, some group, habitat, ecological and geographical factors were found to influence caribou antipredator responses.

Overall, AD and FID shared the same significant predictors in all analyses, while AID was predicted by unique variables. This pattern suggests that the relative importance of variables influencing antipredator responses may be dynamic and changes during the progression of a predator encounter.

2.4.2.1 Group size

AIDs were longer in larger groups, while AD and FID were not influenced by group size. Owing to a dilution effect, caribou may perceive less immediate threat in larger numbers and may therefore take more time to individually weigh the threat of disturbance against the cost of fleeing. Predator assessment is not an energetically costly antipredator behaviour relative to flight because some beneficial activities, such as foraging and rest, can occur simultaneously. Reduced vigilance and increased foraging are commonly reported benefits of increased group sizes (Lima and Dill 1990). Indeed, Worthman (2014), using video recordings from this study, found that larger group size was a marginally significant predictor of lower proportional vigilance during approaches. However, as approach trials progressed closer to flight, especially immediately before flight (i.e., during the assessment interval), a significant proportion of group members switched from a head-down position to a head-up position (Worthman 2014), likely representing shifts from foraging activities to predator monitoring activities. This shift in behaviour supports the idea that caribou are indeed assessing approaching predators during AID, and that caribou in larger groups may assess approachers longer due to a diluted sense of risk.

2.4.2.2 Calf presence

Caribou alert and flight initiation responses were greater when calves were present in the group. The longest ADs and FIDs occurred during the calving period. Past studies have similarly shown that caribou groups become alert sooner and run farther in response to human approaches during the calving period (Aastrup 2000, Soulliere 2008 and references within). Summer calving season is the only factor consistent in predicting increased caribou FID throughout the literature (this study, Aastrup 2000, Reimers et al. 2006, Souillere 2008, Nieminen 2013) while the other prominent environmental factors considered (i.e., group size, habitat, calf presence) vary in the direction of their reported effects (Table 2.4).

Surprisingly, caribou groups containing calves showed lower proportional vigilance than those without (Worthman 2014), consistent with prior findings in insular Newfoundland caribou (Soulliere 2008). Similarly, groups with calves in Newfoundland have been shown to allow a closer approach than groups without calves before becoming alert (Mahoney et al. 2001, Soulliere 2008). These behaviours are unexpected since higher vigilance in groups with calves has been reported elsewhere (Alaska: Boving and Post 1997, Norway: Reimers et al. 2012) and in other ungulate species (Hunter and Skinner 1998). It is generally accepted that predation, rather than food acquisition, is the limiting factor for caribou populations during the summer - calf morality by predation is very high relative to starvation and orphaning (Wittmer et al. 2006). However, the current findings suggest that cows in Newfoundland are motivated by nutrient acquisition at the expense of adequate antipredator behaviour, perhaps investing in future reproductive effort at the expense of current reproductive success (Clutton-Brock 1991, Soulliere 2008).

It is not clear how caribou cows adjust their behaviour with respect to offspring safety or if there is any adjustment or strategy used for the protection of young. I did not witness defensive behaviour by female caribou during my field observations, but

Bergerud (1971) was twice aggressively approached by a female with calf while crawling, and he once observed a female caribou charge a black bear. The summer months following calving may be an important period during which young acquire predator avoidance behaviours from watching their mothers and group members. Head-bobbing or vocalization by a cow towards her calf may be interpreted as a communication to the calf to get up and follow (Souillere 2008). Cows which are more effective in enticing their calves to flee at the appropriate moment (i.e., the optimal flight threshold which maximizes benefits and minimizes costs) are more likely to ensure offspring survival and to transfer these successful behaviours via learning and inheritance. Caribou calves can keep up with running adults by ~3-4 days old (Antoon de Vos 1960), but likely tire more quickly than adults.

Early in the calving season, I observed that young calves often did not flee with the adults of their group, but instead dropped and hid out-of-sight in the scant shrub cover. Observations of similar calf-hiding behaviour have previously been reported for 3-4 week old woodland caribou in Newfoundland (Chubbs et al. 1993), less than 4 day old barren-ground caribou in the Northwest Territories (Antoon de vos 1960), less than 4-5 day old Rocky Mountain elk (Rearden et al. 2011), neonate black-tailed deer (Bowyer et al. 1998), and neonate Thomson's gazelles (Walther 1969). While calf-hiding behaviour is not uncommon in ungulates, it is of particular interest in Newfoundland woodland caribou since, contrary to many other ungulates, caribou cows select birth sites which do not offer dense cover from predators (Denno et al. 2005, Gustine et al. 2006). As open-terrain, and highly social ungulates, Newfoundland caribou predominantly use the follower strategy where calves keep close to their mother soon after birth (Lent 1974, Carl and Robbins 1988). Observations of calf-hiding behaviour in neonate Newfoundland caribou calves suggests that caribou may rely on strategies similar to ungulates elsewhere and raises the question of whether caribou cows select for certain micro-habitat characteristics at birth sites to help hide highly-vulnerable neonate offspring. Calf-hiding behaviour in Newfoundland caribou also suggests some plasticity in antipredator behaviour which may be beneficial in novel situations (e.g., encounters with unfamiliar predators, exploitation of new habitats).

2.4.2.3 Habitat

Habitat data demonstrate that alert and flight distances were reduced in open bog/fen habitats. Caribou may consider open habitat as relatively safe habitat where approaching predators can be easily monitored and flight can be delayed until necessary. Caribou can easily outdistance predators (Mahoney 2011 personal communication) and in ideal habitats caribou may need relatively short alert and flight distances for this tactic to be effective.

High graminoid cover was an indicator of greater ADs and FIDs. This may implicate graminoids as a less preferable food type relative to lichen, mosses and ericaceous shrubs since it was exploited for shorter durations in face of predation risk. Alternatively, graminoids may be a relatively good quality food item that may have been evenly distributed across the calving region and therefore easy to acquire in nearby patches, reducing the cost of fleeing. The young, green parts of *Carex spp.* are more easily digested relative to most mosses, lichens and shrubs (Thomas et al. 1984), perhaps making *Carex* a preferred food type for caribou, especially during specific phenological stages. In the summer of 2011 (May-July), *Carex* sedges were found in Newfoundland caribou scat more often than any other vegetation genus (Soulliere 2014 personal communication). High incidences of graminoids in scat could indicate proportionally high consumption of sedges, perhaps by virtue of selection for sedges and/or due to long periods spent in graminoid dominated habitats.

Caribou had shorter AIDs when more caribou food species were present. This is contrary to the expectation that caribou should have longer AIDs when the cost of leaving is high (i.e., incurring loss of benefits in a good resource patch). However, an abundance of food species does not necessarily translate into high food availability or quality. While a variety of food types (e.g., lichens, forbs, graminoids, willow leaves) are important spring and summer diet components of reindeer and caribou (Bergerud 1972, Lenart 2002, Finstad 2008), comparatively small differences in plant components can influence the availability of a plant species as a digestible forage option (McEwan and Whitehead 1970, White 1983, Thomas et al. 1984, Lundqvist 2003). The nutritional value, fiber content and digestibility of green vascular plants differ greatly between species and phenological stages of growth (Klein 1990, Van Soest 1994, Johnstone et al. 2002). Reindeer and caribou forage selectively across spatial and temporal scales and choose plants high in nutrients and low in secondary plant compounds (Lenart et al. 2002, Finstad 2008). It is possible that caribou select for patches of only a few specific species within their peak periods of digestibility and nutritional value. If so, at sites where a high variety of forage species occur a significant proportion of those species may be relatively undigestible at any given time during the spring or summer, crowding out more desirable food species and creating little incentive for caribou to remain at the site.

In addition, there is evidence to suggest that Newfoundland caribou may be experiencing population density-related food limitation. In the 1980s, Newfoundland caribou population densities far exceeded reported densities for *Rangifer* populations elsewhere, including other predator-free regions (Slate Islands, Norway, and South Georgia; Seip 1991). Competition for food results in reduced forage intake rates and reduced diet quality as less nutritious food items are incorporated into the diet (White 1983). Increased consumption of nutritionally-poor moss, less selectivity of ingested vegetation types, and increased tooth-wear, are indicators that Newfoundland caribou have been experiencing declines in the quality of their habitat since the 1980s (Ihl 2010, Soulliere 2014 personal communication, Weir et al. 2014). This might mean that overall preferred food availibilty is reduced across the calving range, increasing search times for adequate forage intake, thus making caribou less inclined to remain in any one resource patch. Control plots for vegetation measurements were unfortunately not done in this study due to time and resource constraints, but they would add considerable value to identifying variability in resource patch quality and heterogeneity.

2.4.2.4 Topography

Post-hoc findings show that moderate or ‘hilly’ topography was an indicator of increased assessment time. Calving woodland caribou have been shown to select for topographical features which may minimize predation risk (e.g., to increase altitudinal separation from predators or to serve as a form of escape terrain) or increase access to desired forage types due to micro-site characteristics (Gustine et al. 2006). Moderate topography may therefore allow caribou a greater perception of safety, and/or access to highly desirable resources, prolonging the assessment of the risk to energy benefit ratio.

Alternatively, hilly topography may disrupt caribou lines of sight, reducing the certainty of visual evaluations. Caribou may therefore need additional assessment duration to evaluate the approacher during opportune sightings.

2.4.2.5 Ecological factors

Post-hoc findings indicate reduced FID and AD with increased wind speed. Reimers et al. (2006) similarly observed feral reindeer to have reduced flight distances with increased wind speeds. Greater winds likely reduce caribou olfactory and auditory capacity due to the array and omni-directionality of scent and sound cues. The ensuing confusion of senses may reduce the detectability of approachers, impeding communication within the group or cause a reluctance to flee (Reimers et al. 2006).

2.4.3 Flight initiation responses in other studies

The FID of caribou in Middle Ridge, Newfoundland rank low to mid-range on the spectrum of reported flight initiation distances of *Rangifer* under comparable conditions (i.e., approached by a human on foot; Appendix IV). The overall FID of Middle Ridge caribou (103.1 m, SD=60.69) is similar to that of Gaff Topsail caribou (93 m, SD=55.26, Soulliere 2008) suggesting that the Newfoundland herds may behave similarly in encounters with predators. In general, FIDs vary between and within global regions, as well as between and within *Rangifer* subspecies (Appendix IV). Within region, longer FIDs can broadly be explained by three factors: less frequent interactions with humans (e.g., semi-domestic reindeer vs. wild forest reindeer: Neiminen 2013), provocation by threatening stimuli (e.g., polar bear-coloured stimuli in Svalbard: Reimers and Eftestol 2012; black bear-coloured stimuli in Newfoundland: this study), and increased hunting pressure (e.g., Kangerlussuaq vs. Akia population in Greenland: Aastrup 2000; wild reindeer in Norway prior to 1992 vs. after 1992: Reimers et al. 2009).

2.4.4 Assessment of predator risk

Caribou vary in their assessments and behavioural responses to predator stimuli between populations, between individuals and even within individuals. Given the array of possible influences on response it is important to understand the processes and factors influencing predator assessment in addition to the behavioural outcomes.

2.4.4.1 Dynamic influences of variables on responses

The AID occurs just prior to flight and it differs from AD and FID in that is an interval of time rather than a momentary reaction or decision. During AID, there is opportunity for information to be accumulated and evaluated. Acquired information can subsequently lead to decision making, observable as a change in behaviour (Blumstein and Bouskila 1996). Factors which lengthen AID are likely factors about which caribou need to gather more information. AID was influenced by the number of food species present, group size, colour, and approach movement. These factors are relatively dynamic (e.g., group sizes are continuously in flux and food types vary from micro-site to micro-site) or completely novel (e.g., the appearance of a moving, black stimulus). AD and FID, on the other hand, were mostly influenced by relatively constant factors: habitat, season, graminoid cover, calf presence and colour. Except for colour, caribou have information about these variables prior to a predator encounter. These constant factors may have to do with the detectability of the stimulus (e.g., the habitat is open or dense) or preconceived perceptions of vulnerabilty (e.g., females have offspring or not). The colour of the approacher is perhaps a factor which first catches the attention of caribou, eliciting alert behaviours, and perhaps because FID is highly correlated with AD, colour is a pronounced predictor of FID as well.

Furthermore, in this study, AD and FID consistently yielded the same results (i.e., both were longer in response to black approaches, calf presence and high graminoid cover) suggesting that evaluation of AD does not add practical information about caribou perceived risk above what can be determined from FID alone. However, AD may have applied value in indicating the onset of a metabolic stress response and may be useful in caribou management when delinating disturbance buffers.

Many papers surprisingly give little notice to AID relative to FID, probably because FID has been the accepted, traditionally-used, simple measure. Some studies which do consider assessment (e.g., Reimers et al. 2006, Stankowich and Coss 2006, Reimers et al. 2009) are valuable in that they show variations in assessment in relation to season, predator behaviour , sex, and alert distance, though comparisons are difficult to make due to different quantifications of assessment (i.e., assessment probability, assessment time). Though related, AID and FID convey different aspects of antipredator behaviour; AID is an information-gathering period, and in this study is shown to be influenced by dynamic variables, while FID is a momentary decision, influenced by relatively constant variables. Although the concept of assessment and resulting observable behaviours is complex (Blumstein and Bouskila 1996), AID and FID together, along with associated variables, are probably the best and most thorough indicators of perceived risk.

2.4.4.2 Multi-predator response, wolf absence and novel predators

The multi-predator hypothesis (Blumstein 2006) predicts rapid loss of antipredator behaviour and breakdown of abilities to recognize predators when there is isolation from all predators. This process, where a source of selection important in the maintenance of a particular trait is weakened, is called relaxed selection (Lahti et al. 2009). For example, reindeer and caribou from predator-free regions in Svalbard and West Greenland were about 3.5 times less vigilant to playbacks of wolf howls than those at control sites in Alaska (Berger 2007). Phenotype (i.e., behaviour) disintegration may not always occur (Coss 1999) and when prey are not isolated from all predators, antipredator traits are more likely to be retained (Blumstein 2006). Marmots in Colorado, for example, which have been free from wolf predation for more than 70 years (more than 35 generations), still respond to wolves in a non-naïve, fearful manner, possibly due to generalized responses maintained from interactions with coyotes (Blumstein et al. 2009). Under the multipredator hypothesis, antipredator behaviours are assumed to occur as suites of traits rather than independently assorting behaviours, ensuring resiliency in animal defensive systems (Blumstein et al. 2009). In other words, the extinction of a predator is not expected to create entirely predator-naïve prey populations, rather the prey population retains some defence against recolonizing predators. Moose that lost their ability to recognize wolf odour after 130 years of isolation were able to re-learn the danger of wolves, and re-establish increased levels of vigilance within one generation of exposure to wolf predation (Berger et al. 2001). Similarly, prey should not be entirely defenseless against novel predators due to retained antipredator traits. General cue similarities between native and non-native (or novel) predators may be sufficient to elicit effective antipredator responses. For example, black-tailed deer in California showed no statistical differences in antipredator responses to puma models (native) vs. tiger models (non-native) despite lack of historical experience with a vertically striped predator. This suggests that deer were able to generalize the familiar, threatening puma configuration with a uniform coat to the novel, striped coat cat (Stankowich and Coss 2007).

In light of the shared evolutionary history between caribou and wolves in Newfoundland, it is unclear how a 60-70 year absence of wolves in Newfoundland may have influenced caribou antipredator responses to canids. Across the range of caribou, wolves are historically the top predators of caribou and are thought to have a major role in shaping antipredator strategies of caribou (Seip 1991). It seems plausible that a 60 year time period, which can be conservatively estimated as 10 generations for caribou (Thomas and Gray 2002), could be sufficient ontogenic isolation from canid predators to reduce canid-specific antipredator responses in caribou. If antipredator traits are at least in part acquired by parent to offspring information transfer, then the loss of traits may be amplified with each generation. Following the extirpation of wolves in Newfoundland, caribou interactions with bears and lynx may have been sufficient to maintain aspects of predator recognition and avoidance behaviour. Bergerud (1971) considered lynx predation to be a strong factor in caribou mortality in the absence of wolves, and it is possible that selective pressure on caribou may have favoured lynx evasion behaviours, leaving caribou behaviourally vulnerable to canid predators (Soulliere 2008). However, an ambush style of attack, characteristic of lynx, reduces detection by prey until the moment of attack and death, effectively keeping prey inexperienced with lynx. Bears, on the other hand, as coursing predators, may allow caribou to have longer visual experience and more opportunities for threat recognition. While lynx may have notably contributed to the mortality of caribou, they may have had comparatively little impact on caribou antipredator strategies relative to black bears.

The responses of caribou in Newfoundland to simulated coyote cues may provide insight as to how evolutionarily established canid antipredator responses are maintained or altered in a short absence of canid-type predator cues. Longer assessment, shorter flight initiation distances and a trend towards more post-flight returns for tan approaches indicate that tan is a novel stimulus or is perceived as a less threatening cue, relative to black approaches. Perhaps coyote are indeed less successful in predation attempts than bears and therefore accurately perceived as less of a threat. Alternatively, caribou may require more time to evaluate the risk of coyote, given the relatively limited experience caribou have with the newly colonized predator. One way to interpret delayed flight in the face of coyote-like cues is that after prolonged predator assessment by individual group members, caribou ‘stick-around’ to increase group cohesion and reduce vulnerability to stalking and coursing predators. Social prey are expected to change within-group spacing and within-group spatial choice based on relative predator risk (Hirsch and Morrell 2011). Coyote attacks are most likely to escalate to kills if groups fail to stay together while fleeing (Lingle 2001). Aggregation behaviours of Newfoundland caribou are interpreted as predator avoidance behaviours (Mahoney and Schaefer 2002a) and such grouping behaviour is absent in historically predator-free regions such as Svalbard in Norway (Reimers et al. 2012). In the relatively few instances when caribou group scattering or splitting occurred during flight, it was equally likely to occur in response to a tan or black approacher suggesting that group cohesion may be a general antipredator strategy. It is uncertain whether overall responses to coyote-like cues indicate maladaptive responses to a novel threat and contribute to mortality of caribou. Perhaps caribou responses towards coyote-like cues will change as coyote presence and coyote-related mortality becomes more prevalent throughout caribou ranges and these predators become a better recognized threat. Mule deer of central Arizona, for example, have increased their use of areas with high vegetation cover in response to the introduction of coyotes to the region (O'Brien et al. 2010) and naive elk have been shown capable of increasing recruitment in part due to improved antipredatory behaviours towards black bears (Yarkovich et al. 2011).

2.4.5 Implications of non-lethal predator interactions

Predator management traditionally focuses on predators which impose high direct mortality on populations. However secondary predators and non-lethal encounters or disturbances can also contribute to population fitness costs, especially of vulnerable populations. Fitness is affected via additive mortality but also by means of frequent and provocative interactions with energetic and ecological consequences.

Disturbances during calving period have been linked to declines in calving success (Harrington and Veitch 1992). According to Bradshaw et al. (1998), a 132 kg female woodland caribou uses 3.46-5.81 megajoules (MJ) as a result of a disturbance event (i.e., loud noise associated with petroleum exploration). Energy costs were calculated as a combination of the cost of movement (i.e., a 2.11 km increase in daily distance travelled due to disturbance, ~0.74 MJ/day; Bradshaw 1994), initial flight response (i.e., 15 minutes of trotting and galloping, ~1.16 MJ; Beortje 1985), and prolonged excitement (i.e., 10-25% increase in metabolic rate, ~1.57-3.92 MJ; McEwan

1970, Fancy 1986). Caribou may lose 2.5% body mass (3.3kg for a 132kg female) if disturbed 20-34 times. Small shifts in body mass can greatly reduce parturition rates; regression-logistic curves for barren-ground caribou in northern Alaska projected a 17% decrease in parturition rates for a 6% decrease in body mass (Cameron and Ver Hoef 1994). Experimental approaches of caribou by snowmobiles in Gros Morne National Park in Newfoundland were used to assess the energetic costs of repeated disturbances; results roughly translate into mortality occurring with 48 disturbances for calves, 86 for yearlings and 108 for adults (PC 2003). It is unknown whether disturbance due to predator encounters is comparable to disturbance due to petroleum exploration or snowmobile activities. However, the above estimates of energy costs in context of anthropogenic disturbance demonstrate how repeated non-lethal predator encounters could contribute to caribou fitness.

Human activities and structures not only directly increase caribou energy expenditure, but can specifically increase predator-prey interactions by creating favorable habitats for predators such as bears and particularly coyotes (Boisjoly et al. 2010). Thus human infringement on caribou habitats not only creates human disturbance and habitat modification, but may amplify caribou exposure to predation pressure. Although bears and coyotes are not obligate carnivores or caribou specialists, habitat niche overlap of these predator-prey species may create more opportunities for lethal and non-lethal interactions with caribou. In the Gaspésie Penninsula region of Quebec, where eastern coyotes are relatively new predators and where the caribou population is endangered, caribou are thought to be spillover prey of coyotes, with primary prey being moose and snowshoe hares, found particularly in anthropogenically disturbed areas (Boisjoly et al. 2010).

Changes in prey and predator behaviours influence resource intake and life history of both prey and predators and also influence the life history of species of other trophic levels (Shmitz 2004). It is possible that newly colonized coyote are filling a role as apex predator and so it is important to consider the overall trophic and ecological implications of newcomer predators prior to making predator management decisions. In the absence of wolves, former apex predators of Newfoundland caribou and moose (Gosse et al. 2011), caribou have experienced density-dependent hardships such as low quality habitats (Weir et al. 2014). Similarly, high moose density related deforestation has been shown to be a problem for forest communities in Newfoundland (Gosse et al. 2011). A notable case study illustrating trophic cascade effects is the reintroduction of wolves into Yellowstone National Park, where reestablishment of an apex predator presence led to reduced elk browsing and increased vegetation recruitment, in turn restoring beaver and bison numbers (Ripple and Beschta 2012b). Wasser et al. (2011) endorse the application of alternative caribou conservation strategies in place of predator removal due to the high unpredictability and potential serious risks of trophic cascade effects.

2.4.6 Future work and applications

2.4.6.1 Evolutionary predator-prey relationships

A particularly intriguing aspect of this study was the opportunity to quantify the perception of risk of caribou which have had experience with coyote, a recently arrived and moderately lethal predator. Results of this study will be most relevant in comparisons with future, similar, simulated predator-*Rangifer* approach studies. Northern Labrador would be an ideal region for subsequent replication of this study where, currently, competition with wolves is thought to be limiting the range expansion of coyotes. Due to the long and continued evolutionary relationship of wolves and caribou in Northern Labrador, flight responses to wolf-like cues should be strong, while responses to non-native coyote-like cues should be weaker. Results of approach studies in Northern Labrador could provide reference for the responses observed in Newfoundland, providing additional insight into behaviour changes resulting from the recent major shifts in the predator guild. It will also be of interest to observe whether caribou responses to coyote-like cues will intensify as coyote become a better-recognized threat to caribou throughout Newfoundland and Labrador. Future studies may also consider simulating specific predator encounter scenarios of interest, for example, multiple approachers in regions where predators are known to hunt in groups (e.g., hunting coyote groups or wolf packs).

2.4.6.2 Local-scale behaviour studies in context of regional-scale disturbance

Local-scale studies of *Rangifer* disturbance avoidance behaviour (including studies of antipredator behaviour, such as this one), are necessary to complement the recent growing literature addressing regional-scale behaviour of *Rangifer*. Large-scale spatial studies of *Rangifer* populations have been successful in associating landscape disturbances of wild fire, anthropogenic activity, and infrastructure (i.e., roads, railroads, pipelines, power lines, seismic lines, utility corridors, settlements, populated industrial areas, recreational resorts, croplands, reservoirs, cutblocks, logging operation, mining activity and industrial development) with variation in caribou recruitment and shifts in range-use (Mahoney and Schaefer 2002b, Schaefer 2003, Vistnes and Nellemen 2007, EC 2011). The focus on long-term, regional-scale effects has thus helped delineate buffer or set-back zones around potential anthropogenic disturbances and identify critical habitat of vulnerable populations (Tarlow and Blumstein 2007, EC 2011). However, the fact that reindeer and caribou are reported to reduce the use of areas within 5-10 km from infrastructure and human activity by 50-95% (Vistnes and Nellemen 2007) signals that not all disturbances have the same impact, and that herds and individuals vary in their responses to disturbance. In some situations, disturbances may be a single, specific source of stress and it may be possible to link changes in animal behaviour or population viability to the isolated disturbance. However in most situations, a landscape scale disturbance is comprised of many stressors, such as human presence, loud noises, and increased predator presence, and it may be difficult to isolate which particular factor is causing the observed changes (Tarlow and Blumstein 2007). One scenario is that caribou gradually distance themselves from unfamiliar disturbances with few consequences other than a shift in habitat; a very different scenario is that caribou are eventually dissuaded from an area due to frequent, energetically costly, and potentially lethal interactions with disturbances or disturbance-associated activity. Regional studies alone may underestimate the implications of the fine-scale processes and interactions resulting in range shifts and recruitment. Use of AD, FID and AID allows us to develop a detailed awareness of how caribou perceive various types of disturbance and this level of information is necessary, as part of our overall knowledge of caribou biology, to manage disturbance impacts on caribou.

2.4.6.3 Conditioning of naïve animals

Management of at-risk caribou populations could utilize predator models to condition herds to new risks. With growing concern surrounding the declining numbers of *Rangifer* globally (Vors and Boyce 2009), diverse and radical conservation approaches are being sought. Translocation of animals to augment existing vulnerable populations has received considerable consideration in the re-establishment and preservation of caribou, such as in western Alberta, where woodland caribou populations are predicted to be extirpated within 70 years (Decesare et al. 2011, Wasser et al. 2011). Translocation is generally deemed a less controversial conservation strategy relative to predator removal or prioritization of conservation efforts for only the most viable herds (Decesare et al. 2011, Wasser et al. 2011). Previous translocation attempts of caribou have been limited in success at least in part due to predator-related mortality of translocated animals (Compton et al. 1995, Stronen et al. 2007). To improve the success of translocations, known mechanisms of antipredator response could be used to condition translocated naïve *Rangifer* to respond to predator cues when introduced to a new predator-rich area or even when faced with a novel predator in their current area (Griffin et al. 2001). Conditioning could consist of approach methods such as those used in this study, tailored to incorporate cues of specific predators. Although training effort may appear intensive or extreme, just a few conditioning trials may be sufficient in order to prevent habituation, and information transmission in social animals (such as caribou) is expected to facilitate spread of learned predator recognition (Griffin et al. 2001). This approach conditioning method may be a relatively low-cost enhancement to expensive and critical translocation projects.

2.4.6.4 Linking FID with population fitness

FID is a widely used tool for quantifying response to risk due to its very high ease of use, both as a field measure and as a concept in theoretical optimal flight ecology. While FID is a good indicator of instantaneous disturbance, it lacks a clear link with individual fitness and population viability (Tarlow and Blumstein 2007). Flight could influence a population's viability if frequent predator encounters greatly cumulate energetic and/or psychological stress causing: separation from or abandonment of calves, deterrence from preferred habitats, reduced intake of quality forage, diminished body condition and reduced breeding success. FID would perhaps be most effective in association with multiple alternative indicators of disturbance. Tarlow and Blumstein (2007) outline several tools (i.e., breeding success, mate choice, fluctuating asymmetry, immunocompetence, glucocorticoids, and cardiac response) which in concert with FID would certainly strengthen conclusions about the effects of given disturbance types. Ideally, several methods should be used in unison to achieve a complete population fitness profile; however resource and time constraints make this an unrealistic practice for most studies. Of the methods summarized by Tarlow and Blumstein (2007), indices of breeding success would be best for balancing short-term FID disturbance data with long-term population viability information. Measures of glucocorticoids, obtained from blood plasma, feces, or urine, would provide a relatively simple and non-invasive method for cross-validation of stress responses to disturbance. While other measures such as heart rate could provide more precise quantification of stress (e.g., heart rate could pinpoint the moment of alert or clarify differences in the perception of threat), logistically they may be very difficult to obtain with wild populations (however, see Espmark and Langvatn 1979 and Espmark and Langvatn 1985). The relationships between different stressor measures are not well known; further research may indicate some methods to be better than others as identifiers of stressors (Tarlow and Blumstein 2007), or may reveal strong associations between certain measures.

2.4.6.5 Variable interactions for future consideration

This study, like many others, demonstrates that FID of caribou is influenced by numerous ecological variables. Interactions between variables may mask or reduce the effect size of other factors depending on the conditions under which animals were tested (e.g., season, group size, insect harassment). Interactions between multiple factors likely explain a significant amount of observed heterogeneity across studies in the size and direction of the effects (Stankowich 2008). Stankowich (2008) proposes that specific interactions be considered in flight response studies. This study focused on the combined effects of predator colour and predator movement in context of other variables, but other interactions to examine more thoroughly in future studies include: group size x season, group size x habitat type, and presence of calves x distance to refuge (or regions of low predator occurrence or habitat type).

In this study, I have found that caribou distinguish between different predator stimuli and assign different levels of risk to different types of predatory threat; these findings are supported for *Rangifer tarandus* elsewhere (Reimers and Eftesol 2012). Inexperience with novel predator stimuli may require extra assessment effort, characterized in this study as increased assessment interval distance. Antipredator responses to simulated predator approaches are farther influenced by numerous environmental characteristics, namely season. Behavioural responses to non-lethal encounters or disturbances can contribute to an individual's energetic costs with population fitness and ecological consequences.

3 General conclusions

By examining the alert, flight and assessment responses of Newfoundland caribou groups to encounters with human approachers I have found that caribou distinguished between different predator stimuli and assigned different levels of risk to different types of predatory threat. Black bear-like approaches were most threatening and elicited 1.6 times greater flight reactions than coyote-like approaches (i.e., black>light colours). In comparison, Svalbard reindeer exhibited 2.5 times greater reactions to polar bear-like approaches (white>dark colours: Reimers and Eftesol 2012). Further, caribou assessed tan approaches and walk approaches for longer distances and these cues are interpreted to be less familiar cues relative to black and crawl. With coyote being novel predators in Newfoundland, caribou may require extra assessment effort (characterized in this study as increased assessment interval distance) to evaluate and respond appropriately to encountered coyotes. However, caribou most likely have maintained suites of antipredator traits from evolutionary relationships with wolves and other predators (as per the multi-predator hypothesis) and therefore appear to behave effectively (at least in some regards) to deter escalations during coyote encounters, by coordinating cohesive group flight.

While most flight disturbance studies place little emphasis on assessment interval in relation to flight initiation distance, in this study I show that the two measures are influenced by different factors and are thus representative of different aspects of predator recognition and response. I suggest that assessment interval be used along with flight initiation distance in flight disturbance studies to more fully describe both the process of threat assessment (assessment interval) and the decision of assessment (flight).

The responses of caribou varied not only in relation to experimental encounter types but also with different group characteristics (i.e., presence of calves, group size), ecological factors (i.e., season), habitat (i.e., habitat type) and geographical factors (i.e., topography). It is important to identify ways in which responses vary between individuals (i.e., sex, age, reproductive stage, body condition) and populations (i.e., life history, exposure to predators) to improve the relevancy and application of disturbance responses. Also, many of these factors may interact with other factors and consequently alter observed disturbance reactivity. Disturbances can be particularly detrimental during certain critical periods of an animal's life, or during seasons when animals are in poor condition or more vulnerable to injury.

Antipredator behaviour measures can help managers understand caribou-predator interactions and regulate disturbance in ways that can enhance wildlife fitness. Since NL predators are all generalist predators, meaning they rely on a wide variety of food sources, the impacts of NL predators on caribou are not likely to lessen in the future (Trinidade et al. 2011). Within context of other factors, the influence of regional scale pressures such as novel predators and anthropogenic disturbances may be additive or even multiplicative. This study further contributes to our general knowledge of how animals evaluate predator risk and, more specifically, will fill a gap in our knowledge of caribou behaviour that is vital for the future planning of any caribou management strategy.

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Appendices

Appendix I: Plant species identified as caribou food from caribou scat samples in Newfoundland between 1987 and 1997. Data from Newfoundland and Labrador Department of Environment and Conservation (Sustainable Development and Strategic Science Division).

Plant group*	**Caribou foods**	**Commonly encountered species**
Aquatics	Nuphar	*N. variegata* (Yellow pondlily), *N. odorata* (Fragrant waterlily)
	Typha	*T. latifolia* (Common cattail)
Arboreal Lichen	Alectoria	*Not identified to species*
	Bryoria	*Not identified to species*
Coniferous trees and shrubs	Abies	*A. balsamea* (Balsam fir)
	Juniperus	*J. communis* (Common juniper), *J. horizontalis* (Trailing juniper)
	Picea	*P. mariana* (Black spruce), *P.glauca* (White spruce)
	Pinus	P. strobus (White pine)
Deciduous trees and shrubs	Betula	*B. papyrifera* (White birch)
	Larix	*Larix laricina* (Larch, Tamarack)
	Nemopanthus	*N.mucronata* (Mountain holly)
	Populus	*P. tremuloides* (Pure trembling aspen)
	Potentilla	*P. fruticosa* (Shrubby cinquefoil)
	Rosa	*R. nitida* (Northeastern rose), *R. virginiana* (Virginia rose)
	Rubus	*R. idaeus* (Red raspberry), (Blackberries- *not identified to species*)
	Salix	*Not identified to species* (Willows)
	Shepherdia	*S. canadensis* (Soapberry)
	Spiraea	*S. latifolia* (Meadowsweet)
	Viburnum	*V. cassinoides* (Witherod)
Ericaceous shrubs	Andromeda	*A. glaucophylla* (Bog rosemary)
	Arctostaphyl	*A. uva-ursi* (Evergreen bearberry)
	Empetrum	*E. nigrum* (Crowberry)
	Gaultheria	*G. procumbens* (Wintergreen)
	Kalmia	*K. angustifolia* (Sheep laurel), *K. polifolia* (Bog laurel)
	Loiseleuria	*L. procumbens* (Alpine azalea)
	Myrica	*M. gale* (Sweetgale)
	Rhododendron	*R. canadense* (Rhodora), *R. groenlandicum* (Labrador tea)
	Vaccinium	*V. angustifolium* (Low sweet blueberry), *V. boreale* (Northern dwarf blueberry), *V. myrtilloides* (Velvet leaf blueberry), *V. vitis-idaea* (Partridgeberry), *V. macrocarpon* (Large cranberry), *V. oxycoccus* (Small cranberry)
Grasses	Agropyron Agrostis Bromus Calamagrosti	*Grasses, rushes and sedges were functionally grouped together and not identified to species*

	Poa	
	Danthonia	
	Festuca	
	Stipa/Oryopsis	
Rushes	Juncus Luzula	*Grasses, rushes and sedges were functionally grouped together and not identified to species*
Sedges	Eleocharis Carex Eriophorum Kobresia	*Grasses, rushes and sedges were functionally grouped together and not identified to species*
Herbs	Achillea	*A. millefolium* (Yarrow)
	Angelica	*A. atropurpurea* (Purplestem angelica)
	Artemisia	*A. vulgaris* (Mugwort)
	Astralagus	*Not identified to species* (Milk-vetch, Locoweeds)
	Trientalis	*T. borealis* (Starflower)
	Cerastium	*Not identified to species* (Mouse ear chickweeds)
	Coptis	*C. trifolia* (Goldthread)
	Cornus	*C. canadensis* (Bunchberry, Dogwood)
	Draba	*Not identified to species* (Whitlow-grasses)
	Liliaceae(Family)	*Clintonia borealis* (Blue-bead lily)
	Oenothera	*Not identified to species* (Evening primrose, Sundrops)
	Rubus	*R. chamaemorus* (Bakeapple, Cloudberry)
	Saxifraga	*Not identified to species* (Saxifrages, Stone breakers)
	Maianthemum	*M. racemosum* (Treacleberry)
	Solidago	*S. canadensis* (Canada goldenrod)
	Stellaria	*Not identified to species* (Stitchworts, chickweeds)
	Trifolium	*T. pretense* (Red clover), *T.repens* (White clover)
Mosses	Sphagnum	*Not identified to species*
Fern allies	Equisetum	*E. paulstre, E.variegatum* (Horsetails)
Ferns	Lycopodium	*L. clavatum* (Ground pine), *L. dendroideum* (Clubmoss)
Terrestrial Lichens	Cetraria	*Not identified to species*
	Cladonia	*Not identified to species*
	Parmelia	*Not identified to species*
	Peltigera	*Not identified to species*
Commonly encountered non-caribou foods	Alnus	*Not identified to species* (Alders)
	Arethusa	*A. bulbosa* (Dragon's mouth)
	Chamaedaphne	*C. calyculata* (Leather leaf)
	Drosera	*D. rotundifolia* (Sun dew)

Hieracium	*H. aurantiaca* (Orange hawkweed)
Linnaea	*L. borealis* (Twinflower)
Menyanthes	*M. trifoliata* (Buck bean, Bog bean)
Oclemena	*O. nemoralis* (Bog aster)
Sarracenia	*S. purpurea* (Pitcher plant)

*Plant groups are functionally assigned (e.g., *Cornus canadensis* is grouped with herbs, due to its vertical structure, although the Cornus genus is generally considered a deciduous shrub).

Appendix II: Data Recording Sheets

CARIBOU BEHAVIOUR DATA SHEET: SCAN

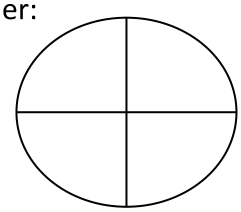
Date (d/m/y):__________ Initials:_______________ Time:________________	**UTM (at start)** E:___________ N:___________	**Event code**
Group composition # Prop. ___ UA ___ ___ FA(#wC__) ___( ) ___ MA ___ ___ Yearlings ___ ___ Calves ___ Tot. Indiv.____	**Group distribution** Dist. To cover:________ Cover:_____________ Other groups visible? Y N Av. dist. cow/calf:______ Av. dist. neighbour:____	**Group movement** Direction:________ Slope: + 0 - Activity: rest active rest + active travel # vigilant:_________ Prop. vigilant:__________
Habitat type Sparse forest__(height__m) Dense forest__(height__m) Forest regrowth__(height__m) Barren___ Bog/Fen___ Road/Trail___ Other______	**Insects** Mosq. 1 2 3 4 5+ Bl. F. 1 2 3 4 5+ Tabinids 1 2 3 4 5+ Nose B absent present Warble absent present	**Weather** Temp:_________________ Wind dir: N NE E SE S SW W NW Wind speed: 0 1 2 3 4 5 6 7 8 9 10 Cloud cover: MC PO MO Fog Precip type:________________ Precip rate: 1 2 3 4 5
Topography: flat moderate steep Exposure: N NE E SE S SW W NW Gain during approach: + 0 - +- -+	Slope: 1 2 3 4 5 Shape: plain lower mid upper ridge	

Comments:____

____

CARIBOU BEHAVIOUR: APPROACH RESPONSES

Approach type: walk crawl	Colour: black tan	
Video taken? Y N	Upwind downwind/no wind crosswind	
Distance at beginning of approach (m):______	Dir. of approach:_____________	Time:_______
Initial Alert Distance (m):_______________	FA(C_) MA UA Y C U	Time:_______
Initial Flight Distance (m):______________	FA(C_) MA UA Y C U	Time:_______
Flight lag (m):_________________________	Dir. of flight:___________	IA same as IF? Y N
Run distance (m): 1^{st} stop____2^{nd} stop____	Last flight: FA(C_) MA UA Y C U	
Curiosity return? Y N #/comp:__________________________________ Dis:__________		
Overall initial response: fright aggression curiosity vigilance other:__________		

Type of flight: Splitting (#grps/comp:____________________) Scattered Move together Other:________	Direction of flight from approacher:  Draw arrow from centre, approacher at bottom. Draw cover, ridges, wind dir. Etc.

Date (d/m/y):___________ Initials: ________________ Time:__________________	Observed browsing or signs of recent browsing? Y N	**UTM (at caribou)** E:_________________ N:_________________	**Event Code**

Plant group	**c= % Cover**							**h= Height (cm)**	**Comments (dom species etc.)**	**Picture taken of N plot? __**
	N c	**N h**	**S c**	**S h**	**E c**	**E h**	**W c**	**W h**		
Aquatics										**A > 1**
Arb Lichen										**B 2-5**
Conifer Tr										**C 6-10**
ConiferShr										**D 11-20**
Decid Tr										**E 21-30**
Decid Shr										**F 31-40**
Eric Shr										**G 41-50**
Gram										**H 51-60**
Herbs										**I 61-70**
Mosses										**J 71-80**
Fern+allies										**K 81-90**
Ter Lichen										**L 91-100**
#Trees on site: __________ Height of highest tree:_________Diameter:__________										

Nuphar (waterlily)		Ledum (Lab tea)		Brassicaceae(must., cabb.)	
Typha (cattail)		*Lonicera (honeysuckle)		Achillea (yarrow)	
Alectoria (tree lichen)		Loiseleuria (alpine azalea)		Angelica (angelica)	
Bryoria (tree lichen)		Myrica (bayberry, candleberry)		Artemisia (mugwort, sgebrsh)	
Abies (firs)		Rhododendron (azaleas)		Astralagus (milk-vetch)	
Pinus(pines)		Other Vaccinium		Borage (starflower)	
Picea (spruce)		* vitis-idaea (prtrdge brry)		Cerastium (muse ear chckwd)	
*Larix (larch, tamarack)		*macrocarpon (large		Coptis (goldthread)	

		cran)			
*Alnus		*oxycoccus (small cran)		Cornus (dogwood)	
Juniperus		*angusti./ boreale (blbrry)		Diapensia	
Betula (birch)				Draba(whitlow-grasses)	
Populus (poplar, aspen)				Other Liliaceae	
Nemopanthus (mntn hlly)		Agropyron (crested wheat grass)		Maianthemum/Smilacina	
Potentilla (cnqefil, b strwb)		Agrostis (bentgrass)		Oenothera(suncups/drops)	
Rosa (rose)		Bromus (brome grass)		Rubus	
Other Rubus (blck/rspbrr)		Calamagrosti (reedgrass)		Saxifraga (sxifrages, stonebr.)	
Rubus chamae (bake apple)		Poa (meadow grass, bluegrass)		Solidago (goldenrod)	
Salix(willow)		Danthonia (oatgrass)		Stellaria (stchwrt, chckweed)	
Shepherdia (buffalo brry)		Stipa/Oryzopsis (needle grass)		Trifolium	
Spiraea (meadowsweet)		Festuca (fescue, tufted grass)		*Sarracenia (ptchr pl)	
Viburnum		Eriophorum (cottongrass/sedge)			
Andromeda (bog rsemary)		Carex (true sedges)		Sphagnum	
Arctostaphyl (bearberry)		Eleocharis (spikesedge/thrushes)		Lycopodium	
*Chamaedapne (lthrleaf)		Kobresia (bog sedge)		Equisetum	
*Linnaea (twinflwr)		Juncus (rushes)		Cetraria	
Empetrum (crowberry)		Luzula (wood-rush)		Cladonia	
Gaultheria (wintergreen)				Parmelia	
Kalmia (bog/mntn laurels)				Peltigera	

* indicates species not identified as caribou food

Appendix III: Antipredator behaviour data

All distances are in meters. Blank values indicate no measure available. The number 999 indicates caribou moved out of sight of the observer. Letter abbreviations signify the following: CB= crawl black, CT= crawl tan, WT= walk tan, WB= walk black, F= females, M=males, C=calves and U= unknown.

Disturbance	Month	Date	Group Structure	Group Size	Beginning distance	Alert Distance	Flight Initiation Distance	Distance moved
CB	5	20	F	1	200	123	121	25
WT	5	22	F	6	315	184	60	200
CB	5	22	U	3	800		100	5
CT	5	23	F	4	275	58	55	50
CT	5	24	U	4	200	47	43	5
WT	5	27	F	1	176	142	111	35
WB	5	27	FC	5	312	77	44	20
CB	5	28	F	3	244	145	130	5
CT	5	28	M	1	214	115	55	2
WT	5	28	M	1	211	84	80	13
WT	5	30	FC	9	435	416	126	
WB	6	1	U	2	290	266	219	3
CB	6	1	U	3	480	257	245	12
CT	6	5	FC	27	217	191	153	2
CB	6	5	F	2	255	68	65	5
WT	6	5	FC	2	523	185	47	
WB	6	5	F	3	350	109	84	10
CT	6	5	FC	9	135	120	86	5
WT	6	5	F	1	135	50	40	20
CB	6	6	FC	19	266	215	185	5
WB	6	6	F	10	211	168	105	10
CT	6	7	FC	17	381	305	305	70
WT	6	7	FC	21	360	198	177	50
CB	6	7	F	1	240	91	87	10
WB	6	7	FC	7	137	131	129	20
CT	6	8	FC	6	190	94	90	20
CB	6	8	F	4	347	274	265	20
CT	6	8	FC	13	279	162	81	60
WB	6	9	FC	13	322	118	110	5
WB	6	9	FC	4	289	220	211	999
CB	6	9	FC	25	327	254	251	30
WT	6	9	FC	4	160	114	106	30
CT	6	10	FC	6	271	157	123	5
CB	6	10	FC	33	274	160	158	5
WB	6	10	FC	11	430	285	235	15

CT	6	10	FC	31	288	253	231	10
WT	6	10	FC	6	128	86	76	30
CT	6	11	FC	6	210	133	128	10
WB	6	11	FC	11	349		237	999
CB	6	11	FC	39	394	297	297	100
WB	6	12	F	2	246	142	129	10
CT	6	12	FC	10				
CB	6	12	FC	3	311	203	203	999
WT	6	13	F	5	394	223	63	5
CT	6	13	FC	11	451	250	173	3
WB	6	13	FC	17	361	173	161	5
WT	6	16	FC	15	200	95	42	20
CB	6	17	M	1	151	110	92	10
CT	6	17	FC	5	185	152	60	50
WB	6	18	F	1	211	140	132	20
WT	6	18	F	1	306	73	59	50
CB	6	18	FMC	9	314	74	65	20
CT	6	19	FM	2	381	55	53	3
WB	6	19	FM	9	245	151	97	1
WT	6	19	F	2	246	172	134	5
CB	6	19	M	1	175	85	70	2
CB	6	20	FC	7	168	87	85	999
CT	6	20	F	5	233	135	100	2
WT	6	21	FMC	35	188	158	139	20
WB	6	21	F	1	130	93	78	10
WT	6	21	F	1	288			3
CB	6	21	FC	16	432	126	116	999
CT	6	21	FC	9	232	40	36	10
WB	6	24	F	11	270	195	171	2
CB	6	24	F	1	199	135	115	100
WT	6	24	F	1	212	20	20	40
WT	6	25	FC	11	550	67	53	5
WB	6	25	FC	55	346	184	164	3
CT	6	25	F	2	234	63	58	50
WB	6	27	FMC	10	140	106	97	999
CT	6	27	FC	15	293	213	120	5
CB	6	27	FMC	12	184	131	121	3
WB	6	28	FC	26	325	127	118	10
CT	6	28	FMC	78	285	86	50	15
CB	6	29	FMC	13	190	153	136	8
WT	6	29	F	1	350	137	116	10

CB	6	30	FMC	25	333	117	112	2
WB	6	30	FMC	50	417	258	186	4
WT	6	30	FMC	73	312	75	30	3
CT	6	30	FMC	15	160	131	103	10
WB	6	30	FMC	29	197	123	103	
WT	7	1	FMC	31	169	40	32	10
CB	7	1	FC	22	264	140	128	3
CT	7	1	FMC	9	260	159		3
CT	7	1	FMC	33	209	70	40	5
CT	7	1	F	1	188	87	74	3
WB	7	2	FC	19	390	98	53	5
WT	7	2	FC	26	457	150	72	5
CB	7	2	FMC	33	190	122	58	5
CT	7	3	F	1	255	150	140	8
WB	7	3	M	2	230	218	212	10
CB	7	3	FMC	175	237	194	91	3
CT	7	4	F	4	183	58	37	3
WT	7	4	FC	9	217	95	51	10
WB	7	4	FC	13	235	162	106	10
CT	7	4	F	2	272	58	58	8
CB	7	4	F	1	169	147	141	8
WB	7	5	FC	2	156	146	131	8
WT	7	5	FM	5	321		21	
CT	7	6	FC	19	215	121	32	3
CB	7	6	FC	7	199	51	45	4
WT	7	6	FMC	195	370	98	44	3
WB	7	6	FMC	9	200	87	62	3
CB	7	6	FMC	33	222	67	49	67
WT	7	7	FMC	13	219	127	71	20
CT	7	7	FC	13	261	118	53	5
WB	7	7	FC	20	217	163	123	10
CB	7	7	FC	42	160	96	45	10
CT	7	8	FC	9	287	61	39	10
WT	7	8	FC	32	469	78	40	10
WB	7	8	FMC	74	458	199	72	5
WT	7	8	FMC	103	166	83	20	5
CB	7	8	FMC	175	273	80	49	5
CT	7	12	FC	16	127	62	55	10
WB	7	12	FC	14	240	165	121	5
CB	7	12	FC	7	151	97	97	25
CT	7	12	FC	3	153	133	121	80

WT	7	12	FC	2	155	75	51	40
WB	7	13	FC	16	370	206	136	10
WT	7	13	FMC	15	396	102	62	5
WT	7	13	FMC	28	159	108	101	4
CB	7	13	FM	5	166	133	116	999
CT	7	13	FMC	37	298	36	25	3
CB	7	13	FMC	83	230	181	104	4
WT	7	14	FMC	18	196	46	35	5
WB	7	14	F	1	150	140	123	3
CB	7	14	FC	3	175	133	120	10
WT	7	14	FMC	11	220	153	64	5
WB	7	18	FMC	8	198	153	123	5
CT	7	18	FMC	19	287	83	45	10

Appendix IV: Flight initiation distances in other studies

Flight initiation distance means (or medians where italicized) for caribou and reindeer displaced by humans on foot. Standard deviation is included where available. Studies referenced in table: 1) this study, 2) Soulliere 2008, 3) Aastrup 2000, 4) Reimers et al. 2009, 5) Reimers and Eftestol 2012, 6) Baskin and Skogland 2000, 7) Nieminen 2013, 8) Reimers et al. 2006.

Subspecies	**Study region**	**Comments**	**FID (m)**
Caribou	Gaff Topsails, Newfoundland[2]	**Large predators**, insular, food limitation, hunting, summer data (2004)	**93** ± 55.26
	Middle Ridge, Newfoundland[1]	**Large predators**, insular, food limitation, hunting, summer data (2011), walking or crawling approaches	**103.1** ± 60.69 78.8 ± 52.39 (tan cue) 127.1 ± 59.08 (black cue)
	Akia and Tasersuaq, Greenland[3]	**No predation**, hunting, summer and fall data (1997-98)	**103.6** ± 76.26
	Kangerlussuaq, Greenland[3]	**No predation**, frequent summer hikers, hunting, summer and fall data (1997-98)	**129.5** ± 108.23
Wild reindeer	Norefjell–Reinsjøfjell, Norway[4]	High recreational activity, no hunting, summer data (1992), walking or skiiing	**22**
		High recreational activity, hunting, winter, summer data (2002-2006), walking or skiing approaches	**43**
	Spitsbergen, Svalbard[6]	Insular, **no significant predation**, hunting	***150*** *(median)*
	Edgeøya, Svalbard[5]	Insular, **polar bears**, no tourism, no hunting, summer data (2006)	**152.1** ± 90.9 92 ± 81.22 (dark clothes, upright walking posture) 231± 43.36 (white clothes, leaning amble posture)
	Kuhmo and Suomenselka, Finland[7]	**Large predators**, excellent pastures, extensive road and agriculture development, no hunting, all seasons data (2010-12), approaches in dark clothes, and snowshoes	**192** ± 62.61
	Dovre Mountains, Norway[6]	**Significant predation**, extremely intensive hunting	***409*** *(median)*
Feral reindeer	Forolhogna, Norway[8]	Good recruitment, excellent pastures, low recreational activity, hunting, winter, summer and autumn data (1996) walking or skiing (in dark clothes)	***95-120*** *(median)*

	Forelhogna Mountains, Norway [6]	**Significant predation**, extremely intensive hunting	***178*** *(median)*
	Wrangel Island, Russia[6]	Insular, **no significant predation**, hunting	***216*** *(median)*
Semi-domestic reindeer	Various herding cooperatives, Finland[7]	**Large predators**, worn pastures, supplementary feeding, extensive road and agriculture development, all seasons data (2010-12) walking (in dark clothes, snowshoes)	**68** ± 28.28
Domestic reindeer	Bol’shezemal’skaya tundra, Russia[6]	Frequent human interaction (with herders)	***49*** *(median)*
	Chukotka, Russia[6]	**Significant predation**, frequent human interaction (with herders)	***60*** *(median)*
	Vaigach Island, Russia[6]	Infrequent human interaction	***114*** *(median)*
	Lapland, Sweden[6]	Infrequent human interaction	***147*** *(median)*