ANTI-PREDATOR BEHAVIOUR OF MATERNAL CARIBOU (*Rangifer tarandus*) IN WEST-CENTRAL NEWFOUNDLAND

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Anti-predator behaviour of maternal caribou (*Rangifer tarandus*) in west-central Newfoundland

by

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Abstract

Caribou (*Rangifer tarandus*) calf survival largely depends on the physiological condition and behaviour of the mother, and her resulting ability to provide her calf with nourishment and protect her calf from harm. Calf mortality in Newfoundland's insular herds has increased dramatically in recent years, concurrent with a change in predator guild. Passive (vigilance) and active (response to disturbance) aspects of maternal anti-predator behaviour in the Gaff Topsail herd, west-central Newfoundland, were studied to gain an understanding of their implications for calf survival.

The group-size effect on vigilance was only observed for adult female caribou engaged in foraging behaviour, indicating a foraging-vigilance trade-off exists (foraging increased and vigilance decreased when competition for local resources increased). Time-activity budgets did not differ between females with calves and those without; however, maternal caribou fed more intensely and were less frequently vigilant. When disturbed, maternal caribou were usually the first individuals to run and, particularly during the peri-calving season, separated from and ran further than other group members.

Consistent with other evidence, this study supports the hypothesis that Newfoundland's insular caribou are currently facing nutrient stress. The reduction of vigilance in favour of foraging may additively contribute to predation vulnerability of calves. Aspects of maternal caribou response to disturbance indicate low levels of perceived safety but may increase calf vulnerability to stalking or coursing predators.

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1.0 Introduction

1.1 Background of Study

Recruitment in insular Newfoundland's caribou (*Rangifer tarandus*) herds has declined substantially in recent years due to low calf survival (Mahoney 2000b). Calf survival dropped from 63% to <10% within a decade (Mahoney and Weir 2007), the majority of which is proximately attributable to predation (Norman et al. 2006). Calf survival largely depends on the physiological condition and behaviour of the mother, and her resulting ability to provide her calf with nourishment (milk, access to forage) and protect her calf from harm (predation, accident, separation, disease). Nevertheless, studies of caribou maternal behaviour in the wild are surprisingly scant (but see Bøving and Post 1997, Espmark 1971 and Lent 1964).

Relative to other adult females, maternal caribou should have higher nutritional demands due to lactation and higher predator monitoring demands due to the vulnerability of their young. Very young caribou calves do not discriminate between their own mother and other adults (Espmark 1971, Lent 1964) so, consequently, there may be added behavioural demands on females with calves for maintaining contact with their calves, especially during weeks immediately post-calving. Differences in behaviour between adult females with and without calves are important for understanding the behavioural demands of mothering and may provide insight into the observed decrease in calf survival.

Since calf morality proximately caused by predation is very high relative to starvation and orphaning (Norman et al. 2006), maternal caribou appear to be motivated by nutrient acquisition at the expense of adequate anti-predator behaviour; females may be investing in future reproductive effort at the expense of current reproductive success. Since the 1970's, antler and jawbone size has decreased in adults (Mahoney 2000a), as has the birth weight of calves (Norman et al. 2006), which suggests that forage quality or quantity has become limiting. Calves may be more susceptible to predation due to reduced size, weakness associated with nutrient stress, or reduced maternal vigilance. Vigilance is considered to be an anti-predator behaviour (Roberts 1996, Treves 2000) shaped by an individual's perceived risk of predation. If predation-starvation trade-off exists between vigilance and foraging, the consequences of reduced maternal vigilance may additively contribute to calf vulnerability to predation.

In addition to possible nutritional stress, the predator guild in insular Newfoundland has changed in recent years. Historically, the grey wolf (*Canis lupus*) was likely a major predator of caribou, but was extirpated from insular Newfoundland around 1920. Bergerud (1971) identified lynx (*Lynx canadensis*) as the main predator and black bear (*Ursus americanus*) as a less significant predator of caribou calves between 1958 and 1964. From 1979 to 1984, lynx and black bear were responsible for the majority of predation deaths of caribou calves and red fox (*Vulpes vulpes*) were identified as an incidental predator (Mahoney et al. 1990). Recently, coyote (*Canis latrans*) and bald eagle (*Haliaeetus leucocephalus*) have also been identified as calf predators and black bear predation now extends throughout the fall (Norman et al. 2006). The expanded predator guild and the seasonal extension of predation by black bears may also contribute to the decline in calf recruitment.

Coyote have been implicated as the cause of reduced caribou recruitment in south-eastern Québec, due to predation on calves (Crête and Derosiers 1995). This species colonized insular Newfoundland in 1985 by crossing on ice from the mainland, ending more than 60 years of the absence of a large canine predator. The arrival of coyote and their rapid dispersal across insular Newfoundland is temporally coincident with the decline in recruitment. Lynx and coyote have different hunting styles even in shared habitat (Murray et al. 1995) and, if lynx predation was as intense as estimated by Bergerud (1971) during the years following extirpation of wolves, it is possible that selective pressure on anti-predator behaviour of caribou may have favoured lynx evasion, leaving caribou behaviourally vulnerable to a canid predator.

Calves are most susceptible to predation mortality during the first 6 weeks after birth (Norman et al. 2006, Mahoney 1990, Bergerud 1971), but remain more vulnerable than other age classes throughout the summer because they are smaller, slower, and less experienced than adult and yearling caribou. Observations of actual predation events are rare, but human approaches can be used to estimate their reactionary anti-predator behaviour (Lingle and Wilson 2001, Caro et al. 1995, Caro 1994). Trends related to group and individual characteristics may be consistent between human and other predator disturbance types and can be used to estimate the effect of maternal behaviour on calf vulnerability to predation.

1.2 Overview of Study

This project was conducted as part of a larger research initiative investigating the causes of decline in caribou calf recruitment. This study is intended to:

- determine whether an apparent trade-off between nutrient acquisition and anti-predator behaviour exists for adult females;
- if so, examine whether maternal caribou manage this trade-off differently than other adult females; and,
- quantify the undisturbed and reactionary anti-predator behaviour of maternal caribou.

The research was organized into three parts: group-size effect on vigilance in adult females; undisturbed behaviour of adult females with calves and those without; and, response to disturbance. Study components were designed to give an interconnected assessment of the behavioural characteristics of the mothers which may influence calf predation and are intended to provide information useful in making management decisions and conservation plans appropriate to the behavioural ecology of the caribou.

In social aggregations of mammals and birds, vigilance tends to decline as group size increases (Elgar 1989, Roberts 1996, Beauchamp 2003a), which is referred to as the group-size effect on vigilance. Predominant hypotheses to explain this trend attribute the group-size effect to increased safety or to increased resource competition in large groups. In order to test between these hypotheses, and establish whether an apparent trade-off exists between foraging and vigilance, I compared patterns of vigilance observed in both foraging and resting groups (section 2.0). If adult female caribou display the group-size effect and it is attributable to resource competition rather than safety, it implies a predation-starvation behavioural trade-off exists.

Calf presence is expected to intensify the conflict between vigilance and foraging due to increased behavioural demands on mothers. Time-activity budgets during foraging and observations of vigilance and feeding behaviour were compared between females with and without calves to determine how maternal caribou manage the predation-starvation trade-off (section 3.0). As vigilance is indicative of wariness, and is thought to correspond with predator detection and avoidance, this component allowed for an assessment of undisturbed anti-predator behaviour.

To interpret the relationship between vigilance and reactionary anti-predator behaviour and to quantify and describe predator avoidance tactics of maternal caribou, human approaches were used to elicit a fright response. The disturbed behaviour of maternal caribou and their calves was compared to other group members to assess calf vulnerability and safety with respect to maternal behaviour (section 4.0).

The study was conducted during late spring and early summer, from about the time of the initiation of calving until the caribou dispersed across their late summer range, coinciding with the period when calves are most vulnerable to mortality. Study subjects were social groups and individual caribou of the Gaff Topsail herd in west-central Newfoundland. In 2003 and 2004, the size of this herd was estimated at 3550-4100 individuals, 65% of which were adult females (G. Luther, pers. comm.). The study site was a portion of the calving and early-summer range of the Gaff Topsail herd (Appendix I).

2.0 The Group-size Effect on Vigilance: A Test between Hypotheses

2.1 Introduction

Vigilance behaviour is generally considered to be an anti-predator behaviour (Roberts 1996, Treves 2000) shaped by an individual's perceived risk of predation, though it may be altered by conflicting behavioural needs, such as acquiring sufficient food (Elgar 1989, Beauchamp 2003a). Vigilance allows for information gathering that should improve predator detection: a completely unobservant animal would not detect predators approaching. Other ecologically and biologically significant information is likely obtained concurrently, such as the location of food sources and the behaviour of other individuals within a social group.

The cognitive aspects of vigilance (what animals are looking at or for, and why) are poorly understood (Bekoff 1996) limiting our ability to interpret what information is being gathered (Bekoff 2003). Whether vigilance is primarily motivated by environmental monitoring for predators is uncertain. Nonetheless, studies of vigilance in many mammal and bird species have shown a positive correlation with predation pressure (e.g. Bøving and Post 1997, Hunter and Skinner 1998, Laundré et al. 2001, Childress and Lung 2003) and distance from escape terrain (Frid 1997, Mooring et. al. 2004) or distance from visually obstructive cover (Rolando et al. 2001, Mooring et al. 2004) implying that the perception of risk is related to vigilance behaviour of individuals. Similarly, in controlled experiments, dairy cattle displayed higher vigilance in response to increased levels of danger in their local environment (Welp et al. 2004).

The reduction of individual vigilance with increased social group size is one of the most commonly reported trends of vigilance behaviour in gregarious species of birds and mammals (Elgar 1989, Roberts 1996, Beauchamp 2003a; but see Treves 2000, Barbosa 2002, Roberts 2003). This tendency of individuals to decrease vigilance as group size increases is referred to as the group-size effect on vigilance. Three prevalent hypotheses exist to explain this trend: shared predator detection, dilution of risk, and increased competition for local resources.

The many-eyes hypothesis (Pulliam 1973) suggests that individuals benefit from being in a group because they are able to share vigilance among group members. Predator detection can remain high or improve with many eyes while still allowing individuals to decrease vigilance and apportion more time to other activities. This hypothesis assumes that predator detection influences the risk perceived by individuals and that information about predator presence is transferred among group members. Early detection of predators can reduce the risk of attack or increase the likelihood of escape or defence in the event of an attack.

The anti-predator benefits of forming groups extend beyond shared predator detection and include effects of dilution of individual risk as group size increases. The dilution hypothesis (Roberts 1996) asserts that as group size increases, individual risk declines, thus requirement for vigilance is reduced. Improved or shared predator detection is unnecessary to explain the group-size effect because the simple fact of dilution of risk is enough to produce the decrease in individual vigilance.

These hypotheses rely on increased anti-predator benefits to individuals within a group and, though they are functionally different (improved predator detection and reduced individual risk), they are not expected to differ quantifiably in their effect on vigilance (Beauchamp 2003a). Further, improved predator detection and decreased individual predation risk have interactive effects on safety (Bednekoff and Lima 1998). For the purposes of this study, these were considered together as selfish-herd effect hypotheses.

The third prevalent hypothesis suggests that as group size increases, intra-group competition for limited resources also increases, reducing the amount of time available for vigilance as group members compete to acquire resources (Beauchamp 2003a). The resource-competition hypothesis implies that the group-size effect will exist only in circumstances where local resources are limited. Notably, studies of foraging groups in areas where predators are absent have documented declining individual vigilance with increasing group size (Bøving and Post 1997, Blumstein et al. 2001), which may indicate that the group-size effect is not related to predation risk. Most studies of vigilance documenting the group-size effect have been conducted on foraging animals, which confound selfish-herd effects with resource-competition effects (Elgar 1989). To evaluate the resource-competition hypothesis, it is necessary to observe non-foraging groups (Arnez 2003, Roberts 2003) and groups competing for non-food resources (Burger 2003).

Documentation of the group-size effect exists for waterfowl in sleeping (Gauthier-Clerc et al. 2002, Gauthier-Clerc et al. 2000, Gauthier-Clerc et al. 1998) and preening

(Roberts 1995, Randler 2005) groups. The only mammalian study, to my knowledge, documenting group-size effect in non-foraging groups examined harbour seals (*Phoca vitulina*) during haul out (Terhune and Brillant 1996). The observed group-size effect, however, was attributed to time since haul out, rather than group size *per se*.

Studies of vigilance in non-foraging social groups can be difficult to obtain and require cautious interpretation. Some social foragers rest independently rather than collectively and thus do not afford the opportunity to compare vigilance patterns of foraging and rest; some animals may select resting sites in obstructive cover and are thus difficult to observe. The posture of animals can differ greatly between foraging and resting (e.g. standing to forage and lying down to rest) and the level of risk associated with posture may vary. In some instances, lying down may be associated with reduced detection, particularly if the animal is obscured by vegetation. Under other circumstances, lying down is a more vulnerable posture than standing; visual, olfactory and auditory range may be reduced due to the lower elevation of the head (even when the head is raised), vegetative cover may reduce an individual's ability to observe both the local environment and other group members, and if a predator attacked, the additional time required to stand up before fleeing may increase the chance of capture. Failure to document a group-size effect on vigilance of resting groups may simply indicate a limit on the ability to reduce vigilance due to the high risk of the posture or an inability for group members to assess group size, rather than be attributable the absence of resource competition within the group.

Caribou offer a good opportunity to test between the selfish-herd effect hypotheses and the resource-competition hypothesis. Caribou forage and rest in social aggregations, and their resting postures include both lying and standing. The naturally occurring states of foraging, standing at rest, and lying at rest are seasonally concurrent and observed frequently enough to test between the selfish-herd effect and resource-competition hypotheses by observing the pattern of vigilance with respect to group size in each of these posture-activity states. If the group-size effect is observed only in foraging caribou, there is support for the resource competition hypothesis; if it is observable during rest, there is support for selfish-herd hypotheses. This is the first study, to my knowledge, of the group-size effect in non-foraging ungulates, and the first to compare foraging and non-foraging patterns of vigilance within the same population over the same time period.

2.2 Methods

Behavioural data were collected from undisturbed caribou groups by instantaneous scan sampling (ISS) (Altmann 1974). ISS was conducted between 06h00 and 21h00 local time for groups in which: no individual appeared to be aware of my presence, and the caribou were clearly visible by the naked eye, or with the aid of binoculars or a spotting scope. Groups separated by > 75 m (estimated visually) were considered to be in separate groups. Observations were made at distances of 100-400 m, most commonly 200-350 m.

2.2.1 Subject Selection

Caribou were located by chance encounter; all study subjects were within a 10 km radius from a temporary camp or within a 6 km of either side of an abandoned rail-bed (for study site location and description, see Appendix I). The maximum distance from campsite or rail-bed access in which subjects were found reflects time and mobility constraints of conducting research on foot, rather than distribution of caribou in the immediate area. The direction initially traveled away from camp each morning was decided by a random number table to reduce the possibility of encountering the same caribou on consecutive days, and to minimize the chance of collecting data from the same location at the same times each day.

2.2.2 Instantaneous Scan Sampling

All data were recorded on a hand-held microcassette recorder in order to maintain constant visual contact with a group during a scan. Prior to each scan, I recorded habitat descriptors, weather conditions, group-density, and insect activity (Appendix IV). I scanned groups at 15-min intervals for periods of 15-120 min, providing data sets of 2-9 scans. For each scan, the sex and age class and current behaviour of each individual in the group was recorded as soon as the individual was looked at. Scan direction (left to right or right to left) was decided by random number table. Sampling periods ended: after 120 min; if the caribou moved out of sight and could not be re-sighted within 30 min; or, if individuals appeared to become aware of my presence. I considered caribou aware of my presence if any of the following occurred: a stare directed at my location; alert postures (ears and tail erect, head up, may be accompanied by modified urination pose) directed toward me or elsewhere with no apparent alternative cause of alarm; or, an individual sniffing the air and walking toward me.

Behaviour was recorded as indicated in Appendix II. All behaviour performed with the head held at or above the shoulders was considered to be vigilant. Apparent visual scanning of the environment was not required for vigilance, nor did other behaviour need be interrupted (for example, feeding with the head up was considered a vigilant form of feeding). I chose this broadly inclusive definition of vigilance due to the increased sensory benefits of raising the head, to allow for comparisons between foraging and non-foraging animals, and to acknowledge the potential function of the head-up posture as a signal to predators (see 2.4.1).

For the category Stand Head Up (SU), I distinguished inactive SU from active SU by watching the animal for a few seconds to see whether it resumed an active behaviour (Appendix III); if so, SU was assumed to have been interruptive of other activity. When no behavioural change was observed, the decision of interruptive SU or inactive SU was made based on the behaviour of the individual's nearest neighbours. Caribou display high intra-group synchrony of behaviour (Maier and White, 1999) so an individual surrounded by inactive individuals is more likely to be inactive than active. When the nearest neighbours on all or most sides were inactive (Appendix III), the individual was considered to be inactive.

Data from tapes were transcribed to data sheets (Appendix V). A random subsample (62 of 617 scans) was transcribed two weeks after completion of the first transcriptions. The subsample was inspected visually against the matching originals; only three discrepancies were found, so the original set was accepted.

2.2.3 Statistical analysis

Each adult female was classified by general posture (Standing or Lying) and level of activity (Active or Inactive) and assigned one of: Standing-Active, Standing-Inactive or Lying-Inactive. Foragers in open social groups, like caribou, show little evidence of coordinated vigilance (Fernández-Juricic et al. 2004). Theoretical models also predict a lack of coordinated vigilance between group members when their common predators are attentive to prey behaviour (Bednekoff and Lima 1998, Scanell et al. 2001). Vigilance of individuals should be independent at 15-min intervals, so the mean proportion vigilant in each posture-activity category within each scan was used as the unit for analysis.

To determine effects on vigilance, a general linear model (GLM) ANOVA was constructed using group size, posture-activity category, year, season, calf presence, distance to cover, and average nearest-neighbour distance as explanatory variables. For each posture-activity category, a GLM ANOVA was constructed with proportion individuals vigilant as the response variable and group size as the explanatory variable to test the relationship between vigilance and group size.

Data were not transformed to approximate a normal distribution because data transformations create artificial and potentially meaningless disassociation between observed activities and interpretation. Initially, tests were performed twice, once treating Proportion Vigilant, the response variable, as an ordinal variable during analysis to approximate a non-parametric test, and once treating Proportion Vigilant as a continuous variable. Actual F-values differed between these methods but there were no discrepancies in decisions of significance; parametric tests lend themselves better to *post hoc* evaluations of significant explanatory variables, so the results presented are those of the parametric tests.

Weather variables, biting insect activity, and season (peri-calving and early summer) are potentially confounding variables as they are expected to correlate with each other (Mörschel 1999). Few scans were collected in unusual weather conditions (e.g. light snow, severe rain) or those that hindered my ability maintain visual contact (e.g. dense fog, high winds). Ease of observation was restricted by visibility and subject to existing weather conditions on each day; the data collected do not yield enough variation in weather conditions to maintain sufficient statistical power, so weather variables were not considered. The presence of nasal bot and warble flies (both Oestridae) are best determined by the behaviour caribou themselves (Mörschel and Klein 1997) rather than by direct observation. To avoid circular analysis, insect activity was not considered.

All statistical tests were performed using JMP IN 5.1 (SAS Institute 2003).

2.3 Results

In total, 3217 individual behavioural observations were made within 617 instantaneous scans of 78 groups of caribou. Thirty-six groups were observed during the peri-calving season and 42 were observed in early summer. Thirty-nine groups contained calves, 39 groups did not. Exclusion of males, yearlings, and calves and summary of vigilance by posture and activity category for each scan resulted in a sample size of 513.

2.3.1 Predictors of vigilance

Posture and activity category was related to proportional vigilance ($F_{(7,240)}$ = 86.16, p = <0.001) (Figure 2.1). Females Standing Active had the lowest levels of vigilance ($\bar{x}$ = 0.13 ± 0.016, n = 265); those Lying Inactive had the highest levels ($\bar{x}$ = 0.70 ± 0.030, n = 142); those Standing Inactive were slightly more vigilant than foraging females ($\bar{x}$ = 0.25 ± 0.037, n = 106). Mean vigilance of posture and activity categories all differed (Tukey HSD: q = 2.35, p < 0.001). Group size was negatively related to proportional vigilance of combined data ($F_{(7,240)}$ = 3.94, p = 0.048) but, though statistically significant, was not strongly explanatory ($r^2 < 0.01$).

2.3.2 Group-size effect within posture-activity categories

The pattern of proportional vigilance relative to group size differed between active and inactive caribou. Females Standing Active displayed lower vigilance in larger groups ($t_{(1,263)}$ = -2.80, p = 0.005); for those Standing-Inactive or Lying-Inactive, vigilance was not affected by group size (Standing-Inactive: $t_{(1,104)}$ = 0.29, p = 0.771; Lying-Inactive: $t_{(1, 140)}$ = 17.8, p = 0.441) (Figure 2.2).

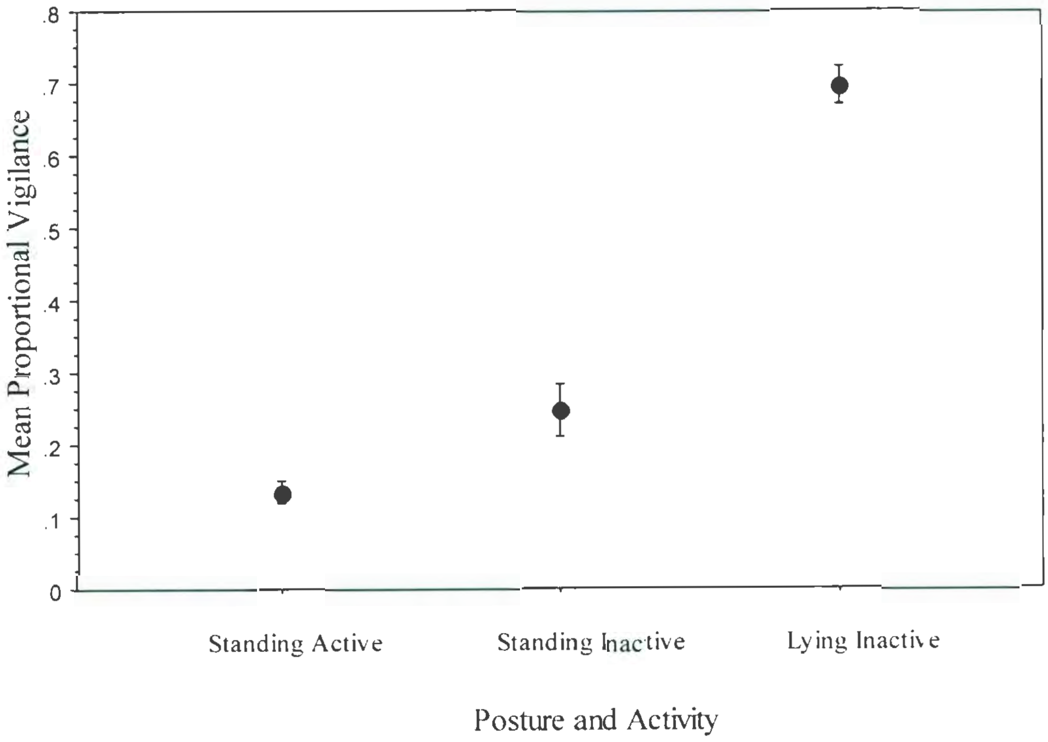
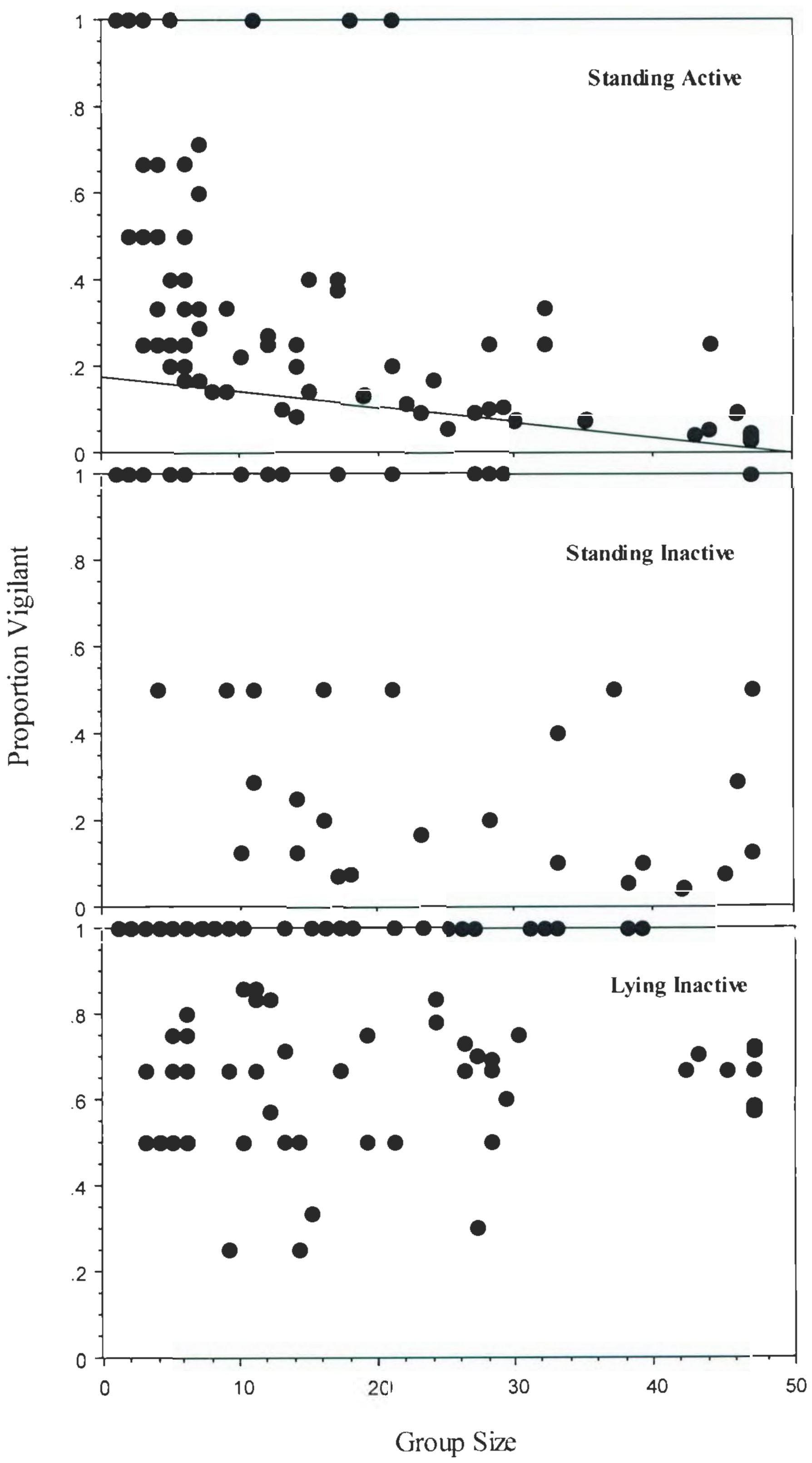


Figure 2.1 Observed proportional vigilance by female caribou relative to posture and activity category. Adult females were least vigilant during active periods and most vigilant when lying at rest. Mean vigilance is differed significantly between each category. Means are shown ± SE.


Standing Active
Standing Inactive
Lying Inactive
Proportion Vigilant
Group Size
1
.8
.6
.4
.2
0
0
10
20
30
40
50

2.4 Discussion

2.4.1 On Recognizing Vigilance

There is inconsistency among published studies in defining behaviour as vigilant, even within group, such as ungulates. Shorrocks and Cokayne (2005) defined vigilance in impalas (*Aepyceros melanmpus*) as "when the head was raised, and [the impala] appeared to be looking around, for any amount of time" (p. 92). Cameron and duToit (2005) used a similar definition but qualified it by requiring it to last "at least 1 s without chewing" (p. 1339), presumably to measure costly vigilance only. Frid (1997) defined vigilance for Dall's sheep (*Ovis dalli*) as an interruption of "food searching or handling to stand with the head raised above the shoulders" (p. 803), not requiring overt looking around. Childress and Lung (2003) defined vigilance in elk (*Cervus canadensis*) as standing with the head at or above shoulder level, whether it was an interruption of foraging or not, and considered all lying postures to be non-vigilant whether the head was raised or not (p. 391). Mooring et al. (2004) classified all observed behaviour in a five-category vigilance hierarchy[1]. Bøving and Post (1997) distinguished between caribou standing with the head erect and observing the environment, and the interruption of a feeding bout to raise the head (preceded and followed by feeding); although only the

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[1] The hierarchy weighed relative attentiveness to the environment, from least to most vigilant: feeding with the head down; lying or moving with the head down; feeding head up or standing head down; moving head up; standing or lying head up; standing alert (Mooring et al. 2004, p. 522)

latter behaviour was labelled vigilance (p. 58), they considered both to be anti-predator behaviour.

Much attention has been paid to whether and to what extent vigilance is costly (Illius and Fitzgibbon 1994, Cowlishaw et al. 2004, Fortin et al. 2004), which is relevant to the interpretation of what vigilance implies about both the behavioural requirements of the animals studied and the theoretical framework within which hypotheses and predictions about vigilance are developed. In a time-energy analysis, only vigilance can be costly, but in a time-activity analysis the extent to which vigilance is costly to foraging is not distinguishable from the extent to which foraging is costly to vigilance. If vigilance and foraging reflect a predation-starvation trade-off, either behaviour can incur costs to the other. Additionally, vigilant behaviour is not necessarily interruptive of other behaviour. For example, animals may forage from tall shrubs or handle food with the head elevated, improving environmental monitoring without interrupting foraging. In resting ruminants, the head may be elevated without interrupting the process of rumination or decreasing the benefits of inactive periods. To compare vigilance between foraging and non-foraging groups, the definition of vigilance must be applicable to both situations. Restricting definitions of vigilance to costly-only circumstances inhibits our ability to detect patterns necessary to test hypotheses about the extent to which vigilance is costly; it also implies that vigilance is only ecologically and biologically interesting when it is at the expense of other behaviour.

Our inability to fully recognize the relative importance of visual, olfactory, and auditory information gathering also makes defining vigilance difficult; overt visual scanning is only one component of how animals can monitor their surroundings. What animals are looking at or for during overt visual scanning is difficult to assess (Bekoff 1996, Treves 2000, Beauchamp 2003b). To further complicate this, valuable visual information about predators can be acquired in a head-down posture (Fernández-Juricic et al. 2005, Bednekoff and Lima 2005) and some species are capable of detecting predators when not overtly vigilant (Lima and Bednekoff 1999).

In the study of vigilance, the behaviour traditionally measured and interpreted is the act of raising the head (but see Treves 2000, Blumstein et al. 2003). Although vigilance is possible from head-down postures, defining vigilance operationally by a head-up posture is not arbitrary: 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. Head-up postures increase the range at which predators are detected relative to head-down postures (Lima and Bednekoff 1999, Cresswell et al. 2003a). For many ungulate species, the highest visual acuity in the eye corresponds with the horizon when the head is lifted (Cronin 2006).

Head-up postures are useful to understand even if they make up only a portion of an individual's vigilance. Head-up behaviour increases after a disturbance to a group (Duschesne et. al 1992, Roberts 1995). Overt vigilance might be partly motivated by the need to verify a stimulus detected while the head was down. Anecdotally, during my field observations, an individual detecting my presence would often snort loudly. In response to the snorting, most group members would lift their heads but often resumed their previous behaviour within seconds, regardless of the continued alert posture of the snorter. Bighorn sheep (*Ovis canadensis*) react with a head-up posture to olfactory stimuli likely perceived while the head is down (R. Sayre, pers. comm.).

Apart from monitoring and verification, head lifting may have a function in predator deterrence. Fitzgibbon (1989) observed that cheetahs (*Acinonyx jubatus*) preferentially attacked less vigilant Thompson's gazelles (*Gazella thomsonii*). Scheel (1993) suggested that African lions (*Panthera leo*) selectively choose prey based on seasonal lows in their vigilance and noted that stalking lions delay movement until all prey group members have their heads down. If predators can assess and respond to prey vigilance, prey might use overt vigilance as a signal to potential predators thereby deterring predation attempts. Given the evidence of the increased vulnerability of less vigilant individuals and the reaction of predators to overt signs of vigilance, vigilance might reflect an individual's perceived risk of predation but relate inversely to the actual risk of predation.

2.4.2 Vigilance in the Gaff Topsail Caribou Herd

In this study, all behaviour in which individuals were observed in a head-up position was considered vigilant (Appendix III). I chose this definition to acknowledge the increased sensory benefits of raising the head, the potential function of the head-up posture as a signal to predators, and to allow for comparisons between foraging and non-foraging animals.

Vigilance was lowest for standing caribou, and lower for those foraging than those standing at rest, indicating that a trade-off between foraging and vigilance exists.

Vigilance was highest for caribou lying at rest, which is consistent with the increased vulnerability of this posture.

I observed higher vigilance levels than that reported for Alaska or Greenland (Bøving and Post 1997). This may be partly due to considering all head-up behaviour vigilant in this study, but even in comparing lying behaviour exclusively, the Gaff Topsail caribou spend a greater proportion of time with their heads elevated (Gaff Topsails: 0.70 ± 0.03; Alaska: 0.37 ± 0.01; Greenland: 0.21 ± 0.01). In a lying posture, discrepancies in vigilance levels are not attributable to differences in forage availability or quality. Bøving and Post (1997) suggested that caribou were more vigilant in Alaska due to higher predation risk; caribou predators were varied and abundant in Alaska and were absent from the study area in Greenland.

Similar to the Gaff Topsail herd, during their study, the Alaskan herd was experiencing a population decline due to low recruitment. The Alaskan decline is primarily attributed to nutrient stress (Stephenson et al. 1999) but predation by wolves and brown bear (*Ursus arctos*) proximately contributed to low calf survival (Sellers et al. 2003). Differences in vigilance rates may be due to differences in current or historic predation risk or differences caribou ecology.

Predator diversity was greater for the Alaskan herd; in the Alaskan field site, caribou predators included wolves, brown bear, coyote, lynx, golden eagle (*Aquila chrysaetos*), and wolverines (*Gulo gulo*) (Bøving and Post 1997). There is insufficient information available to evaluate differences in predator abundance. Calf predation in insular Newfoundland has recently changed with the arrival of coyote, predation by bald eagles, and an extended season of predation by black bears (Norman et al. 2006); a relatively novel predator guild or recently increased predation pressure may be sufficient to increase wariness above that in a more stable predator-prey system. Alternatively, Newfoundland's caribou may have a tendency toward high rates of vigilance because of historic predation pressure; due to low prey diversity, insular Newfoundland's small predators may have traditionally relied more heavily on caribou calves than mainland predators.

Differences in ecology may also account for observed differences in vigilance and have a substantial effect on predation risk. Alaskan caribou migrate over great distances, which may allow them to leave predators behind, or space away (Seip 1991) from predators more easily than the relatively sedentary caribou in Newfoundland. Additionally, caribou aggregations in Alaska were much larger than those in this study; although no group-size effect was observed in resting groups, group size may still contribute to perceived predation risk. Bøving and Post (1997) observed groups of up to 900 individuals; in the Gaff Topsail herd, groups in excess of 90 individuals were rarely seen. Barren-ground caribou groups are typically larger than those of woodland caribou; dilution of individual risk may affect vigilance in groups at a scale I was unable to measure.

2.4.3 The Group-size Effect

The group-size effect was observed in adult females only during active periods, which are overwhelmingly characterized by foraging behaviour. Adult females showed lower levels of vigilance and higher levels of foraging in larger groups; results which support the resource-competition hypothesis.

Not all studies of vigilance and group size have documented the group-size effect during foraging, but foraging tactic may influence vigilance behaviour. Both the ability and utility of decreasing vigilance with increasing group size may be important in accounting for the group-size effect (Barbosa 2002). If, for example, searching for forage requires a head-up posture, decreased head-up behaviour should not be expected in larger groups. Robinette and Ha (2001) found that in kleptoparasitic Northwestern crows (*Corvus caurinus*), vigilance increased with increasing group size as a result of monitoring conspecifics for opportunities to rob food and to protect acquired food. If caribou use foraging interruptions, such as searching for forage or moving between sites, opportunistically for vigilance, changes in the duration of foraging bouts or frequency of searching with either increased competition for local resources or social facilitation of feeding might be responsible for the trend observed.

Lazarus (2003) maintains that social facilitation itself may be sufficient to explain the appearance of increased resource competition in larger groups. Blumstein et al. (2002) found that food availability had no effect on time allocated to foraging in tammar wallabies (*Macropus eugenii*). Social facilitation may require closer inspection through studies designed to separate the effects of facilitation from those of resource competition.

Differences in foraging tactics and social facilitation of feeding cannot, however, explain differences in the non-foraging vigilance behaviour between species. In this study, individuals at rest did not show a relationship between vigilance and group size regardless of posture, suggesting that selfish herd anti-predator effects are not sufficient to cause the group-size effect. These results are contrary to those found in non-foraging birds (Roberts 2003) and non-foraging harbour seal (Terhune and Brillant 1996). With few studies of vigilance in non-foraging animals, it is difficult to interpret why the Gaff Topsail caribou herd shows a different pattern of vigilance during rest than these other populations. Better information about the behaviour of the specific predators to these populations may help explain these differences.

Theoretically, observant predators might be best discouraged from attack if vigilant bouts by prey are either unpredictable (Scannell et al. 2001) or constant. Both Fitzgibbon (1989) and Scheel (1993) provided evidence of stalking predators attending to vigilance behaviour of their prey. This implies that prey can use vigilance as a signal of alertness to predators, thereby reducing predation risk. If an individual's best strategy is to be more vigilant than its neighbours, vigilance might be expected to increase with group size. Yet, if head lifting is costly, due to loss of available foraging time or to increased energy expenditure in holding the head erect, some upper threshold on vigilance may exist. With more neighbours, an individual may be able to reduce vigilance to be minimally more vigilant than the least vigilant neighbour, allowing the group-size effect to occur.

If the most common predators are opportunistic or unobservant, limits to and requirements of vigilance would be expected to be different. Though their results are difficult to interpret, Cresswell et al. (2003b) found that opportunistically foraging Eurasian sparrowhawks (*Accipiter nisus*) did not show preference for either vigilant or non-vigilant prey models. Ambush predators should be as or almost as successful attacking either vigilant or non-vigilant prey that wanders within an appropriate range.

For the Gaff Topsail herd, in 2003 and 2004, ambush predators (lynx and black bear) accounted for 8%, stalking predators (coyote) accounted for 36%, and avian predators (bald eagle) accounted for 36% of calf mortality due to predation (Norman et al. 2006). Adult mortality due to predation in this herd is unknown for the period of study, but thought to be uncommon.

When caribou are at rest, they are stationary and risk of predation from ambush predators should be constant. Foraging caribou tend to walk past or through obstructive cover and face an elevated and inconsistent risk of predation from ambush predators. Caribou do not retreat to cover for rest, so during both active and rest periods, risk of predation from stalking and avian predators is likely similar.

Wolves have historically been caribou's most important predator across their range, and are implicated in shaping their anti-predator behaviour (Seip 1991). The historic relationship between caribou and wolves in insular Newfoundland and the recent arrival of coyote may select for anti-predator behaviour specific to observant predators and explain the absence of the group-size effect during rest. During foraging, when there is a trade-off between nutrient acquisition and vigilance, and predation risk is higher only for ambush predators, individual risk might be best managed by maintaining only a minimally higher vigilance than nearest neighbours within the group.

More studies about the behavioural responsiveness of predators and prey to each other, though often difficult to observe directly, may be crucial to our understanding of vigilance patterns, providing a richer understanding of the ecological and evolutionary relationships in predator-prey systems and behaviour. Empirical evidence of how predators and their prey respond behaviourally to each other and which combined responses increase or decrease the likelihood of successful attack by predators is scarce, limiting our ability to create realistic models to predict prey behaviour (Lima 2002). Without sound modeling, testing our theoretical constructs or interpreting our empirical evidence of behaviour such as vigilance and aggregation is difficult at best.

3.0 Activity Budgets, Foraging, and Vigilance in Maternal Caribou

3.1 Introduction

During the peri-calving season and early summer, caribou have high nutritional demands due to replacing winter loss of body reserves and, in the case of parturient females, lactational demands (Chan-MacLeod et al. 1999). Coincident with the physiological need for foraging, calves are most vulnerable in the few weeks following birth (Bergerud 1971, Mahoney et al. 1990, Norman et al. 2006). Females with calves, therefore, face behavioural demands to restore their own body reserves, prepare nutritionally for a successive pregnancy through winter, provide adequate nourishment to calves, and to obtain sufficient environmental information to adequately protect calves from predation; yet, increasing foraging can reduce the ability to increase vigilance and *vice versa.*

If time spent vigilant is limited by nutritional demands, lactating females may be less vigilant than non-lactating females. If time spent vigilant is limited by predation risk, females with young may increase vigilance in order to adequately protect their young from harm (Toïgo 1999). How maternal caribou behave relative to their non-mother counterparts can provide important information about the demands of mothering; the way maternal caribou manage this trade-off should indicate whether they are more limited by obtaining sufficient nutrients or by monitoring the environment for danger.

Under circumstances of increased resource competition, adult female caribou in the Gaff Topsail herd reduce vigilance (head-up behaviour) in favour of foraging (section

2.0), suggesting that increased foraging requirements would result in reduced vigilance. However, females with calves should have greater need for both behaviours and may manage the starvation-predation trade-off differently than their non-mother counterparts. Despite the demands of lactation, female caribou with calves displayed higher vigilance than those without in both Alaska and Greenland (Bøving and Post 1997); similarly, in impala and wildebeest (*Connochaetes taurinus*), females with young are always the most vigilant in a group (Hunter and Skinner 1998).

The Gaff Topsail caribou herd is sexually segregated during calving. Females aggregate on the calving grounds and form nursery bands consisting primarily of adult females and calves; yearlings are sometimes present in these groups. Three to 4 weeks after calving, males arrive on the calving grounds and join the female groups. As these mixed groups begin to form, the caribou depart the calving grounds for their early summer range. Due to group composition changes and high intra-group synchrony of activity (Maier and White 1998, Collins and Smith 1989), behaviour of all females during the early summer may change due to the influence of males in the groups. As calves gain experience, vigilance requirements of their mothers should decrease. Additionally, as body reserves are restored, the feeding requirements for females without calves should decrease. Females with calves, however, may take longer to replenish reserves, continue to have added nutritional demands to support lactation and should thus maintain high nutritional requirements throughout the summer.

In this study, I examine time-activity budgets of maternal and non-maternal females during periods of activity, which are predominantly characterized by foraging activity. In addition to the proportion of time dedicated to foraging and vigilance, and to analyse more subtle maternal behaviour, I compare feeding intensity (the portion of foraging time spent handling and ingesting food, relative to the total time spent foraging), and the frequency and length of Feeding and Searching bouts, and the frequency and length of vigilant behaviours. How maternal caribou manipulate their foraging and vigilance can provide insight into nutritional demands, perceived risk, and calf monitoring. High predation risk and high calf-monitoring demands may result in greater time spent vigilant and reduced foraging. High foraging demands may result in more time spent foraging or higher Feeding Intensity; the former would be expected to result in lower vigilance.

3.2 Methods

To investigate differences in behaviour between females with and without calves, continuous focal observations (Altmann 1974) were used. Focal females were selected only from groups containing at least one female with a calf and at least one female without, to be able to interpret maternal behaviours which exist despite social facilitation; since caribou are social, I was interested in maternal behaviour which exists despite possible influence of non-maternal group members. Observations were conducted between 06h00 and 21h00 local time for individuals in groups where: no group member appeared to be aware of my presence, and the focal individual was clearly visible with the aid of binoculars or a spotting scope. Focal females were chosen from active group members with the aid of a random number table.

3.2.1 Data Collection

Prior to beginning each observation and again at completion, I recorded habitat, weather, group density, group size and group composition variables (Appendix IV). Focal samples for each selected female ended either: at 30 min; when the individual moved out of sight; or, if the individual apparently became aware of my presence, whichever came first.

Observations less than 20 minutes in length were discarded. I intended to collect focal samples only during active periods, but if a female became inactive during the observations, I continued to record her behaviour. Periods of inactivity >3 min were excluded from the sample as was the behaviour preceding the inactive period; inactivity for <3 min followed by a resumption of active behaviour (like Walking or Feeding) was considered to be part of the active period. The maximum observed length of inactive behaviour that was both preceded and succeeded by active behaviours was 42 seconds.

Focal individuals were watched continuously; all changes in behaviour (Appendix II) were recorded on a microcassette tape running continuously, and recordings were transcribed to data sheets (Appendix V), using a stopwatch. A random subsample (10 of 98 focal samples) was transcribed a second time, to assess the repeatability of measuring behavioural intervals. The subsample and originals were inspected visually; durations rarely (less than 4 per sample) differed by more than 0.5 seconds and the sequence of behaviour recorded did not differ between transcriptions, so the originals were accepted.

3.2.2 Statistical Analysis

Weather variables, insect activity, and season (peri-calving and early summer) are potentially confounding variables as they are expected to correlate with each other (Mörschel 1999). As in section 2.2.3, weather variables and insect activity were not considered in the analysis.

All statistical tests were performed using JMP IN 5.1 (SAS Institute 2003).

Activity Budgets

Proportion of time dedicated to each Behaviour Category (Column III, Appendix III) was used as the unit of analysis for activity budgets, each focal observation period yielding one measurement per Behaviour Category. Preliminary analysis of Behaviour Categories by univariate GLM ANOVA was conducted wherein proportional data were treated in separate analyses as ordinal (to approximate a non-parametric test) and as continuous response variables. Observed trends and decisions of significance did not differ between the methods; since the data are correlated by nature of representing portions of the activity budget, and parametric statistics allow for GLM multivariate analysis, a GLM MANOVA was constructed to analyse the activity budget of female caribou during active periods.

A GLM MANOVA was used to analyse the activity budget of female caribou during active periods. Explanatory variables included in the MANOVA analysis were presence of accompanying calf, season, group size and all 2-way interactions. *Post hoc* tests were incorporated *a priori* into the MANOVA model to appropriately distribute degrees of freedom.

Foraging

As a Behaviour Category, foraging consists of Feeding (handling and ingesting food) and Searching (looking for food); Feeding Intensity was described by the proportion of Feeding relative to the sum of Foraging behaviours. GLM ANOVAs were used to test for differences in Feeding Intensity and to analyse the rate and duration of Feed and Search behaviour. Three of 5 focal observations where <10% of the observation period was dedicated to foraging were identified as obvious outliers during visual inspection of plotted Feeding Intensity data; all 5 were thus excluded from analysis of foraging behaviour.

Feed and Search patterns were compared between females with and without calves. Mean proportion, mean duration (s), and mean frequency (bouts per minute) were response variables in GLM MANOVAs; explanatory variables included were presence of accompanying calf, season, group size and all 2-way interactions.

Vigilance

All behaviour performed with the head elevated was considered vigilant behaviour (Appendix III). The proportion of time spent vigilant, mean duration of vigilant bouts (s), and mean frequency of vigilant behaviour (bouts per minute) were analysed in a GLM MANOVA. The MANOVA model included season, calf presence, group size, and all 2-way interactions as explanatory variables. *Post hoc* univariate tests were performed for each response.

3.3 Results

A total of 2155 minutes of focal observations were collected for 98 adult female caribou (55 with calves). Fifty-five samples were obtained during peri-calving (31 with calves); 43 samples were obtained during the summer (24 with calves).

3.3.1 Activity Budgets

Activity budgets of females with and without calves did not differ ($F_{(7,90)} = 1.78$, $p = 0.092$) (Figure 3.1). Females spent less time Foraging ($F_{(1,94)} = 12.73$, $p = 0.001$), more time Walking ($F_{(1,94)} = 6.87$, $p = 0.010$), and more time Standing ($F_{(1,94)} = 5.52$, $p = 0.021$) during summer (Figure 3.2).

Although the overall activity budgets were the same for maternal and non-maternal females, it is notable that in *post hoc* univariate tests the only significant finding was that time spent Lying during active periods differed ($F_{(1,94)} = 3.96$, $p = 0.049$); females without calves occasionally interrupted Foraging to lie down, but females with calves were never observed to do so.

The activity budget for all females was related to the interaction of season with group size ($F_{(7,90)} = 3.00$, $p = 0.005$). The amount of time spent Walking was lower in larger groups ($F_{(1,94)} = 4.11$, $p= 0.046$) and the proportion of time spent Foraging was higher in larger groups ($F_{(1,94)} = 5.41$, $p = 0.022$) (Figure 3.3). The relationship between activity budgets and group size was more pronounced in the summer.

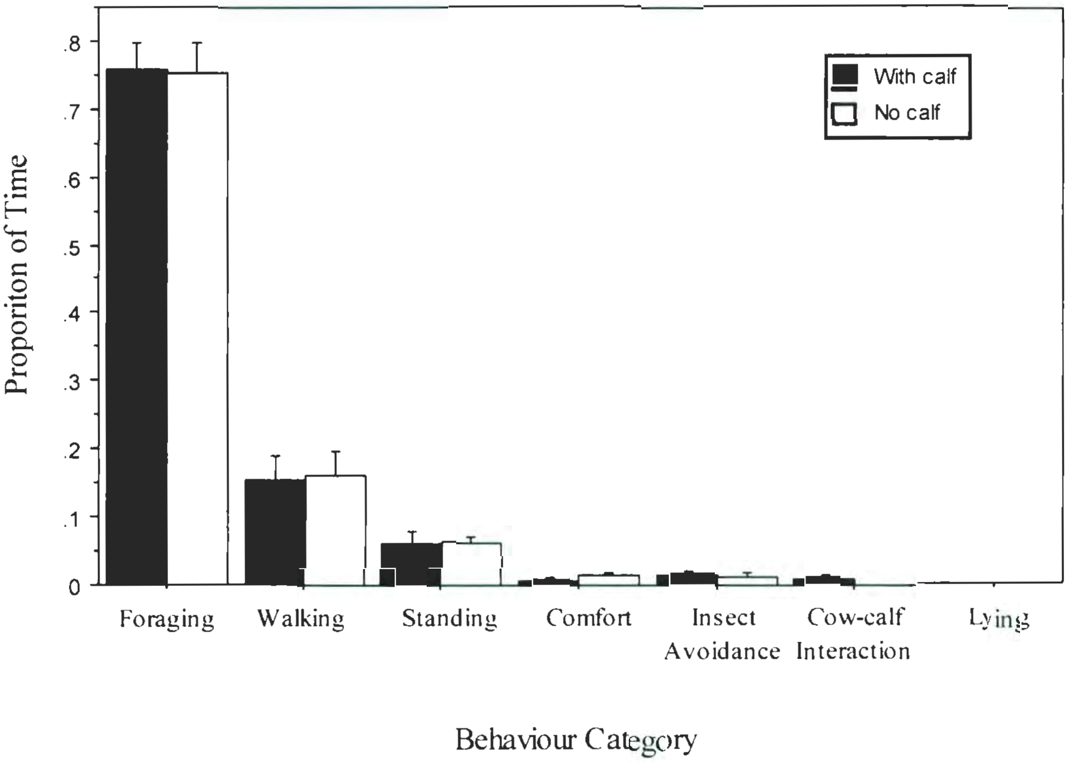


Figure 3.1 Comparison of time-activity budgets of females with calves and those without. Data were collected by continuous observation of individuals during periods of activity. Maternal caribou do not apportion time differently than their non-maternal counterparts. Error bars indicate ± SE.

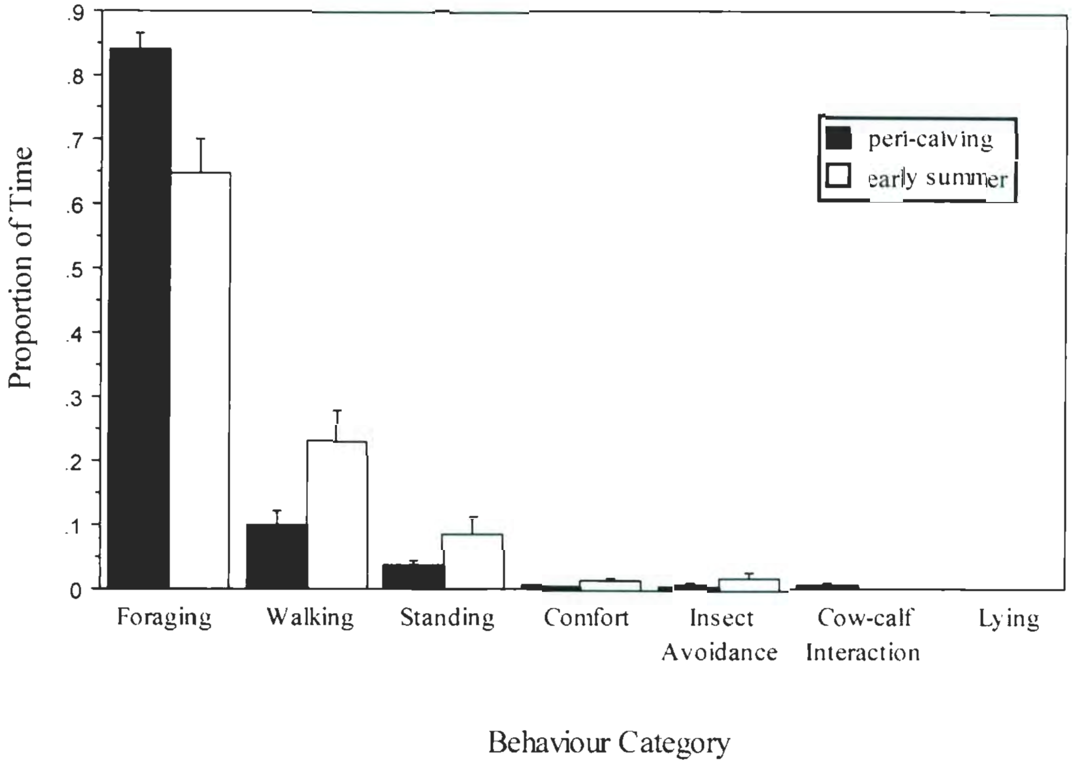


Figure 3.2 Comparison of time-activity budgets between peri-calving and early summer seasons for all adult females. Foraging was significantly lower during summer; Walking and Standing were significantly higher during summer. Error bars indicate ± SE.

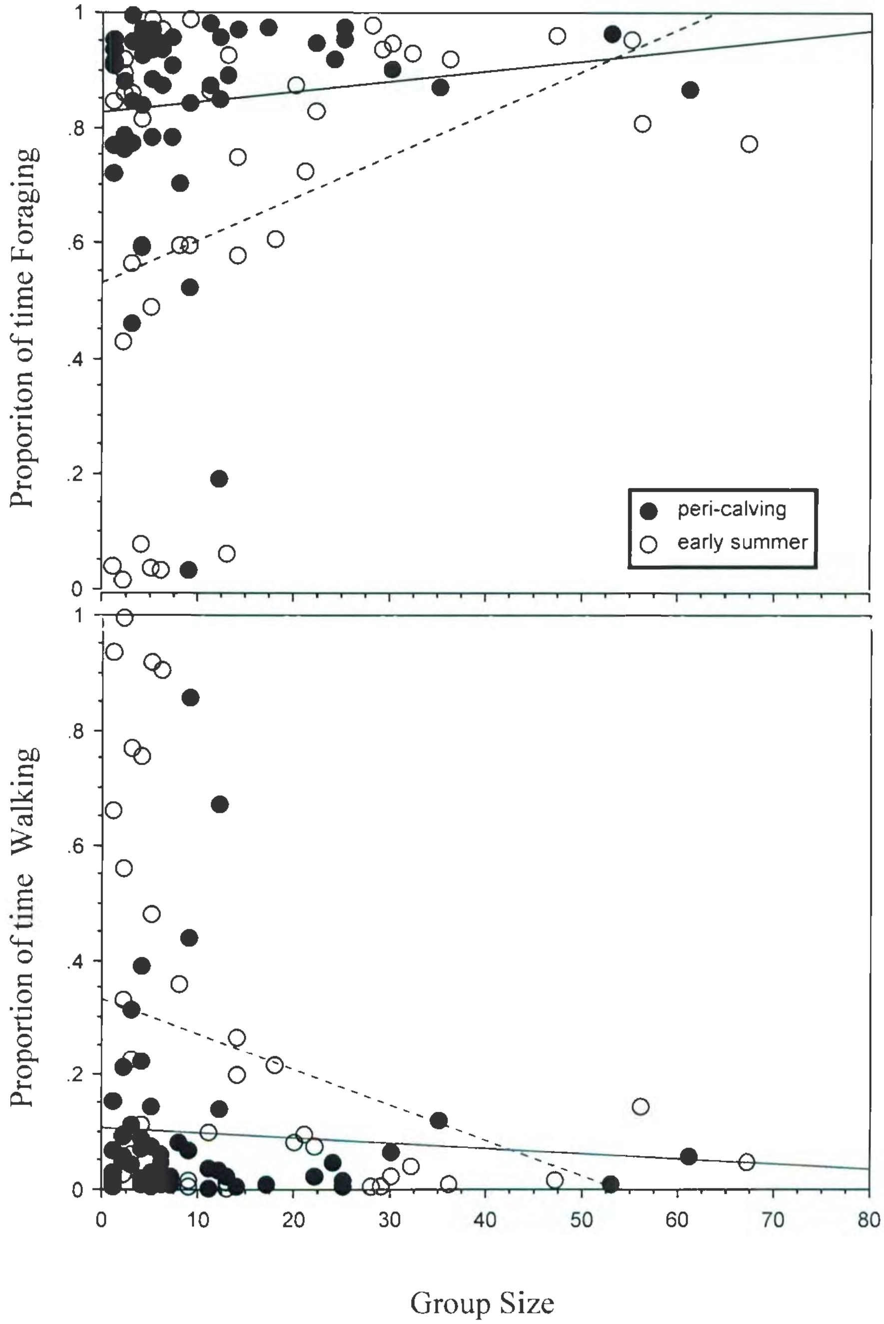


Figure 3.3 Proportion of active periods spent Foraging and Walking relative to group size and season for focal individuals. Group size influenced both Foraging and Walking more strongly during summer than during the peri-calving season. Regression lines are shown for peri-calving (solid) and early summer (dashed).

3.3.2 Foraging

Females with calves had a higher Feeding Intensity than those without ($F_{(5,92)}$ = 20.45, $p < 0.001$). Feeding Intensity for all females was lower in summer ($F_{(5,92)}$ = 6.45, $p = 0.013$), although maternal caribou reduced Feeding Intensity less substantially (Figure 3.4).

The set of measures (proportion of time, bout frequency, bout duration) to describe Feeding differed between females with calves and without ($F_{(2,88)}$ = 8.57, $p < 0.001$) and was related to group size ($F_{(2,88)}$ = 4.18, $p = 0.008$). Feeding bouts were longer in larger groups ($F_{(2,90)}$ = 6.08, $p = 0.016$, $r^2 = 0.048$) for all adult females pooled (Figure 3.5). Females with calves initiated Feeding less frequently ($F_{(2,89)}$ = 24.10, $p < 0.001$) and fed for longer periods ($F_{(2,89)}$ = 15.39, $p < 0.001$) than those without calves (Figure 3.6). The set of Searching measures differed between females with and without calves ($F_{(2, 89)}$ = 5.04, $p = 0.003$). Females with calves Searched less frequently ($F_{(2,90)}$ = 13.24, $p < 0.001$) for shorter periods ($F_{(2,89)}$ = 6.10, $p = 0.015$) than those without.

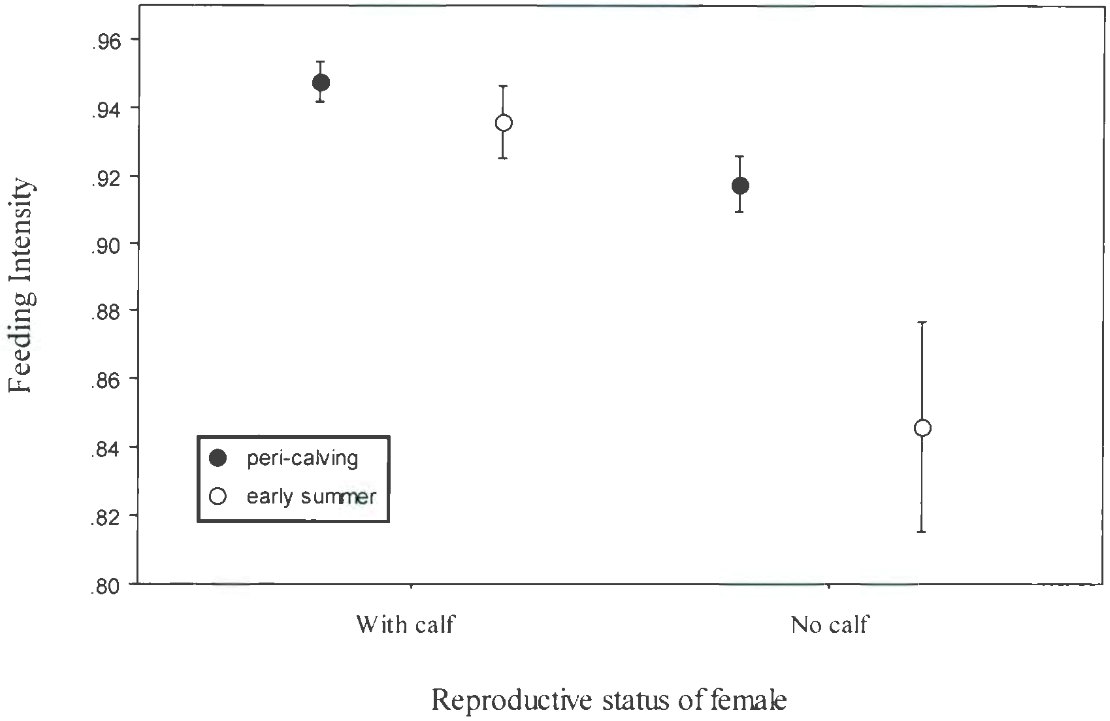


Figure 3.4 Comparison of Feeding Intensity between females with calves and those without, by season. Maternal females feed more intensely. In non-maternal females, Feeding Intensity is reduced much more substantially in early summer relative to the peri-calving season. Error bars indicate ± SE.

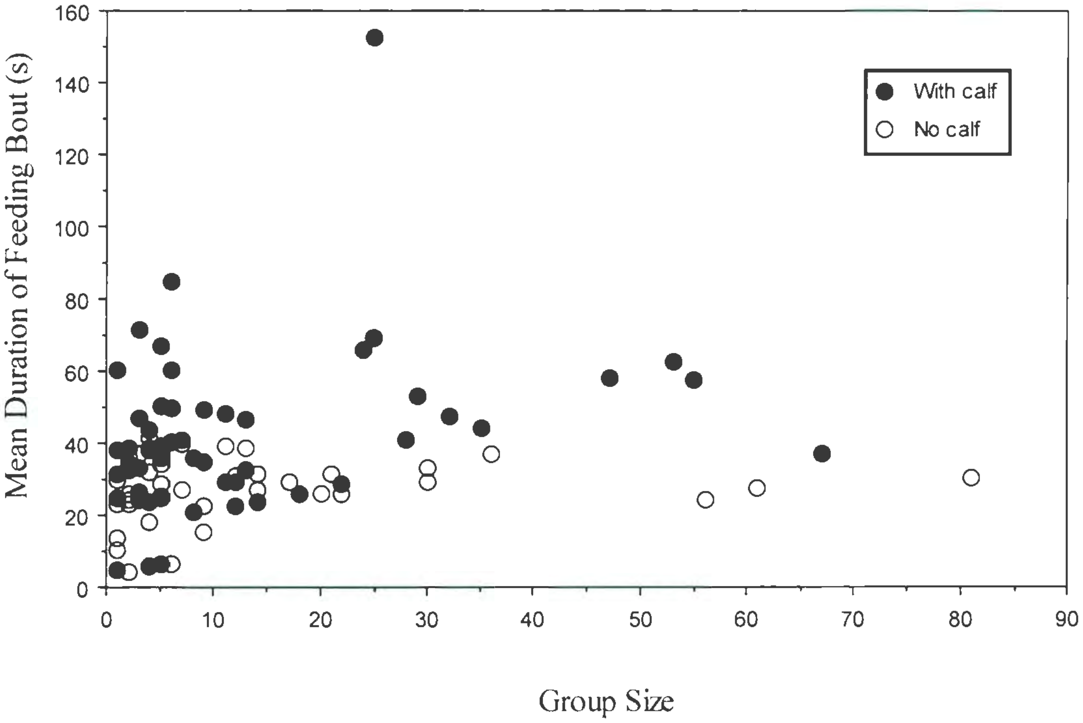


Figure 3.5 Mean duration of feeding bouts for adult females without and with calves relative to group size. Females with calves feed for longer uninterrupted bouts than females without calves regardless of group size. Feeding bout duration is longer in larger groups.

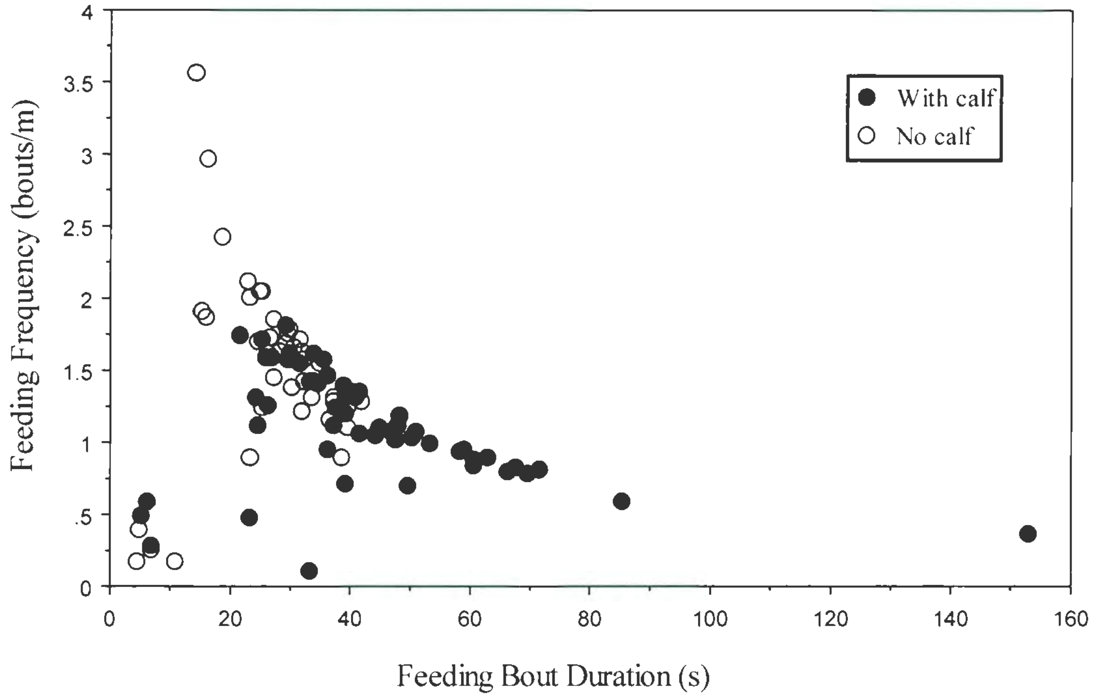


Figure 3.6 Frequency and duration of feeding bouts in adult females without and with calves. Females with calves tend to feed for longer periods of time and initiate feeding bouts less frequently.

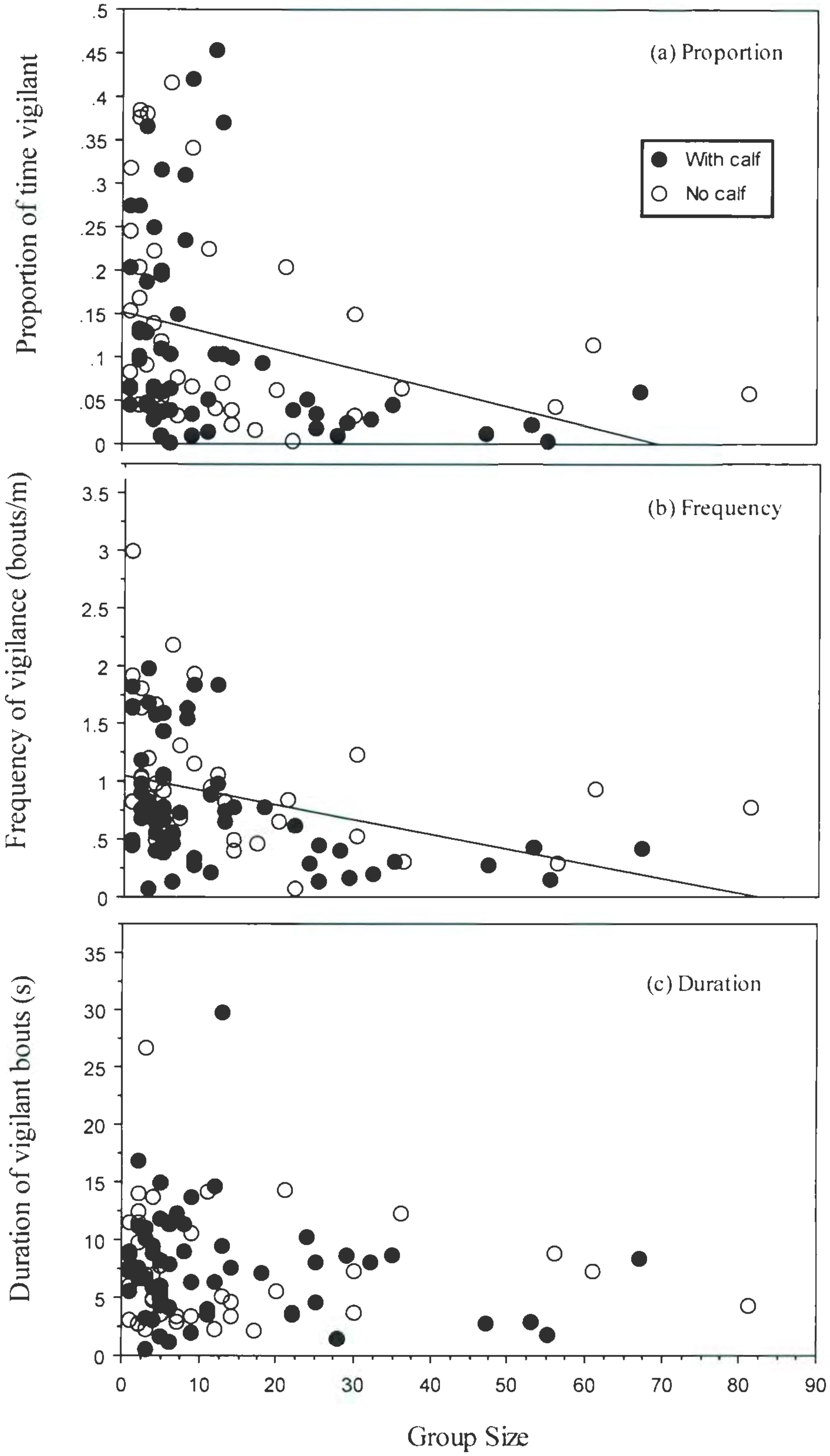
3.3.3 Vigilance

Results from MANOVA indicate that vigilance differed between females with calves and those without ($F_{(2,88)} = 3.82$, $p = 0.013$) (Table 3.1) and differed with group size ($F_{(2,88)} = 3.76$, d.f. = 90, $p = 0.014$) (Figure 3.7). Females with calves were vigilant less frequently than those without ($F_{(2,87)} = 9.42$, $p = 0.003$). There was no difference in the mean duration of vigilant bouts. *Post hoc* univariate tests indicated that both the proportion of time spent vigilant and the frequency of vigilant bouts was lower in larger groups (proportion of time: $F_{(2,87)} = 7.06$, $p = 0.009$; frequency: $F_{(2,87)} = 11.23$, $p = 0.001$). The interaction between group size and calf presence is not significant.

Table 3.1 Observed vigilance in adult females with and without calves. Vigilance is described by duration and frequency of vigilant bouts and the proportion of time spent vigilant during continuous observation. Females with and without calves only differ in their pattern of vigilance by the frequency with which they adopt vigilant posture (as indicated with an asterisk). Data are presented ±SE.

Statistical Population	**n**	**Mean Duration (sec)**	**Mean frequency (number of vigilant events/min)**	**Mean proportion of time spent vigilant (proportion)**
All Females	100	7.6 ± 0.47	0.9 ± 0.06	0.12 ± 0.01
With Calf	56	7.7 ± 0.64	0.8 ± 0.07*	0.12 ± 0.02
No Calf	44	7.4 ± 0.72	1.0 ± 0.09*	0.13 ± 0.02

Figure 3.7 Vigilance of adult females with and without calves in relation to group size, as estimated by continuous focal observations. Maternal caribou display vigilant behaviours less often, but spend as much time vigilant overall and per bout as those without calves. Regression lines are shown for significant relationships with group size.


(a) Proportion
Proportion of time vigilant
.5
.45
.4
.35
.3
.25
.2
.15
.1
.05
0
● With calf
○ No calf
(b) Frequency
Frequency of vigilance (bouts/m)
3.5
3
2.5
2
1.5
1
.5
0
(c) Duration
Duration of vigilant bouts (s)
35
30
25
20
15
10
5
0
0
10
20
30
40
50
60
70
80
90
Group Size

3.4 Discussion

3.4.1 Activity Budgets and Foraging

The time-activity budgets of females with and without calves did not differ. Given the increased nutritional demands on lactating females, it is surprising that they do not dedicate more time to foraging than their non-lactating counterparts. Similarly, Barten et al. (2001) hypothesized a trade-off between forage acquisition and predator avoidance in parturient females, but found no quantifiable difference in habitat choice between females with and without calves. Females with calves may be unable to forage more than lone females if rumen capacity, which would be similar, is limiting. Focal individuals were not observed for long enough to determine whether the active/rest cycles are of different lengths between females with and without calves; behavioural differences, such as longer active periods or shorter resting periods for females with calves were not detectable in this study.

Despite dedicating the same amount of time to foraging, patterns of foraging behaviour differed between females with and without calves. Females with calves fed more intensely and interrupted Feeding less frequently to Search. With high nutritional demands, filling the rumen quickly by being less selective may be advantageous, but only if there was no substantial loss associated with the digestion of lower-quality forage. Alternatively, the observed pattern may suggest that females with calves have access to better foraging patches, allowing higher nutritional demands to be met with greater foraging efficiency rather than increasing time dedicated to Foraging.

The observed feeding patterns might simply demonstrate that those females who are the best foragers are more likely to produce and maintain calves. Maternal body mass is positively correlated with calf survival (Fauchald et al. 2004), as is maternal age (Weladji et al. 2003) and, thus, experience. Larger females may either be better foragers or need to feed more intensely because of a larger rumen capacity; due to their likelihood of maintaining calves, they may have contributed a disproportionately to the focal samples as time since calving increased. The striking difference in the reduction of Feeding Intensity in early summer between those with and without calves may be interactively caused by continued high nutritional demands and increasing sampling bias toward larger females. To test whether maternal foraging patterns affect the probability of maintaining a calf through the early summer, known adult females with known calf retention would need to be observed repeatedly through the season.

Holand et al. (2004) showed a correlation between adult female dominance and body mass in penned reindeer groups. Kojola (1989) observed that female social dominance in semi-domestic reindeer groups predicts the over-winter weight gain of calves; the higher the mother is in social hierarchy, the heavier her calf will be at winter's end. It is not clear, however, whether these females are larger because they are socially dominant and have access to preferred forage sites or whether they are socially dominant because of their size. Social hierarchies have rarely been noted in wild populations of caribou; hierarchies may form only under artificially high densities or around scarce but defensible food patches (Barrette and Vandal 1986).

Lent (1964) commented on the rarity and subtlety of agonistic behaviour in barren ground caribou, and suggested that the openness and fluidity of caribou aggregations do not create an environment wherein individual dominance would be expected to form. In his analysis of the few agonistic events observed, he proposed a social hierarchy for caribou based on social class. Like Lent (1964), I frequently observed caribou joining and leaving groups as individuals or in small groups. For hierarchies based on individual dominance to be maintained, caribou would need to recognize many individuals or agonistic behaviour would be common, especially when groups merge. If access to forage is correlated with dominance, as would be expected, and Feeding Intensity is a good measure of access, this study supports a social hierarchy like that described by Lent (1964): adult females with calves dominant to adult males dominant to adult females without calves dominant to yearlings. Feeding Intensity was higher for females with calves than those without, but is similar between all adult females and adult males (Appendix VI), suggesting that females without calves have lower Feeding Intensity than adult males. Yearlings were encountered rarely making it difficult to assess their Feeding Intensity, but it appears to be lower than that of adults (Appendix VI, Figure VI-i).

A social hierarchy based on reproductive status can be beneficial for gregarious mammals with open and temporary group membership. In many species, lactating females are commonly documented to display higher levels of aggression than their non-lactating counterparts (Blaffer Hrdy 1999). Allowing maternal caribou unchallenged access to prime foraging sites may reduce the amount of energy expended in conflict, compensating for the potential loss of resources from these foraging patches. Body size is an adequate mechanism to maintain hierarchical order between the remaining social classes.

3.4.2 Vigilance and Foraging

Females with calves were less vigilant than those without, but only in the frequency of initiating vigilant posture. The proportion of time dedicated to vigilance and the length of vigilant bouts were the same between the groups. Longer bouts are thought to provide more information and are useful for monitoring predators whereas shorter bouts are useful for monitoring other group members (Desportes et al. 1991). The length of vigilant bouts did not differ between those with and without calves, suggesting no difference in the type of information acquired.

I did not explicitly measure sequential behaviour during foraging to identify temporal patterns of vigilance and foraging, but vigilance trends are consistent with foraging in adult females; maternal caribou initiate Feeding, Searching and Vigilant bouts less frequently than other females. In chaffinches (*Fringilla coelebs*), vigilance during foraging is opportunistically related to foraging patterns (Cresswell et al. 2003a), such that whenever a seed is obtained, the head is raised for handling. Female caribou with calves may have fewer opportunities to lift their heads due to the length of Feeding bouts.

Given the high predation risk faced by calves, it is notable that females with calves are less vigilant than their lone counterparts. This is inconsistent with published studies comparing the vigilance behaviour of breeding and non-breeding female ungulates (Bøving and Post 1997, Hunter and Skinner 1998, Toïgo 1999, Childress and

Lung 2003), suggesting that the Gaff Topsail caribou are either limited by nutrient acquisition, do not perceive a relatively high predation risk to their calves, or do not respond with increased vigilance to this increased risk.

Hunter and Skinner (1998) found a time-lag between predator introduction into an area and responsive increased vigilance by impala and wildebeest. The Gaff Topsail caribou may not have yet adjusted behaviourally to the recent change in predator guild, which may itself contribute to the very high rates of calf mortality in recent years.

Alternatively, females with calves may not rely on vigilance to reduce predation risk to their young. During the peri-calving season, nursery bands form consisting almost entirely of cow-calf pairs. Lent (1964) suggested that nursery bands form passively as females equally hindered by the mobility of their calves and tend to get left behind as lone females travel at a faster rate. Kojola's (1990) study of social association in semi-domestic reindeer suggests, however, that there is a capacity to actively choose groups or individuals with which to associate. I once observed an adult male on the calving grounds early in the season, attempting to forage with a nursery group; each time the male joined the periphery of the group, those females nearest to him moved away, appearing intolerant to his presence. Although this behaviour was observed only once, it supports the idea that free-ranging caribou groups, despite their open and fluid nature, might form as a result of active rather than passive choices by individuals. Maternal caribou choosing to associate with other cow-calf pairs dilute predation risk to their calves more evenly than forming groups with lone adults.

Although females with and without calves all experience similar range quality, maternal females compensate for their increased nutritional demands by foraging more intensely at the apparent cost of vigilant behaviour. Additionally, in opportunistic field observations during this study, calf suckling normally concluded by cessation of nursing by the mother (Appendix VII), indicating that calves were not feeding to satiation. Concurrent with the recent decline in calf survival, Newfoundland's insular caribou herds have experienced decreases in calf weight, adult body size, and antler size (Mahoney and Weir 2007). The combination of these observations suggests strongly that Newfoundland's caribou are under nutrient stress. The smaller size of calves increases their predation risk, but the reduced vigilance of maternal may additively affect calf vulnerability.

4.0 Behavioural Response to Threat

4.1 Introduction

Vigilance improves predator detection (Lima and Bednekoff 1999) and may contribute to predator deterrence and avoidance. Alert distance (the distance at which an individual reacts overtly to an approaching threat) has been used in other studies as a proxy for vigilance (Baskin and Scogland 2000) or detection distance (Lingle and Wilson 2001, Aastrup 2000). Groups which display higher vigilance are expected to respond more quickly to a threatening disturbance, such as an approaching predator, than less vigilant groups. Vigilance assesses the undisturbed anti-predator behaviour of caribou and can be used to evaluate perceived levels of risk; predator avoidance tactics as observed in active response to threat can be used to evaluate perceived safety and behavioural vulnerability to predation.

This study component was designed to examine the relationship between vigilance and response to threat, and to assess the threat response and predator avoidance behaviour of maternal caribou. Trends in behavioural response of maternal caribou (both behaviour specific to maternal caribou and that relative to other social group members) to a threatening disturbance may have implications for the vulnerability and safety of calves.

Caribou calves in the Gaff Topsail herd are subject to predation by bald eagle, black bear, lynx, and coyote (Norman et al. 2006). These predators have varied hunting styles: bald eagles are aerial predators; black bear have been observed to act as ambush predators when targeting caribou calves but may also be coursing predators (S. Mahoney, pers. comm.); lynx are primarily ambush predators (Murray et al. 2005); and coyote have been observed both stalking and coursing (Lingle and Pellis 2002) when hunting large ungulates. Newfoundland's insular caribou may have predator avoidance behaviour specific to particular predators or to different hunting styles.

In both years of study during peri-calving season, bald eagles were sighted almost daily, black bears were observed twice, and coyote and lynx were never directly observed. In the early summer season, coyote tracks and fresh bear scat were observed infrequently, a bear was sighted once, and coyote and lynx were never directly observed. In 2003 and 2004, coyote and bald eagle were each responsible for 36% of known predation of radio-collared calves in the Gaff Topsail herd; black bear and lynx were predators of lesser effect (Norman et al. 2006).

In addition to natural predators, the Gaff Topsail herd is subject to hunting pressure outside of the studied field season. Human presence was typically absent in the study area during the peri-calving season, moderate during late spring and early summer, and was usually associated with machinery. I was only twice aware of other people on the calving grounds; in both cases a float plane landed on a pond and two men were observed fishing. In other parts of the spring range, there is all-terrain vehicle (ATV) traffic on an abandoned railway (Appendix I), which is used for recreational access. In the study area used during the early summer season, there is daily traffic on the wood roads associated with forest harvesting. The wood roads also provide access for occasional pedestrian berry pickers and recreational ATV traffic. The caribou most commonly occupy bogs and unused wood roads (pers. obs.) during this time; berry pickers were occasionally observed in bogs and ATV users sometimes used roads within visual range of caribou groups but were never seen to approach the animals.

Human approaches have been used to measure the reaction of ungulates to human disturbance (Fortin and Adruskiw 2003, Aastrup 2000, Baskin and Scogland, 2000, Andersen et al.1996, MacArthur et al. 1982) and to estimate their predator avoidance behaviour (Lingle and Wilson 2001, Caro et al. 1995, Caro 1994). Caribou and other ungulates are expected to perceive humans as predators, particularly when approached by pedestrians (Webster 1997). Alert distances of white tail deer (*Odocoileus viginianus*) and mule deer (*O. hemionus*) are similar whether approached by humans or by coyote (Lingle and Wilson 2001). Moose (*Alces alces*) respond with a longer run distance and a greater physiological response when approached on foot than when approached by machinery (Andersen et al. 1996) implying that pedestrians are perceived as a greater threat.

Using human approaches limits the ability to generalize results of the study to other predators, but actual predation events are difficult to observe predictably or reliably. Human approach is a practical and controllable way of eliciting a reaction to threat. In this study, I approached caribou groups directly and on foot in habitat with high visibility; the reaction of caribou to this type of approach is best interpreted as a proxy for the reaction to coursing (due to visibility) or stalking (due to quiet approach) predators. In white tail deer which, like caribou, rely on outrunning predators for avoidance, coyote attacks are most likely to escalate to kills if the group fails to stay together while fleeing

(Lingle 2001). Lent (1964) noted that caribou with calves tend to move away from their group before others when disturbed by human approach. If early fleeing results in separation rather than increased distance from the predator, caribou calves may face a disproportionate vulnerability to stalking and coursing predators.

Although this study has a limited ability to address predator avoidance behaviour of maternal caribou to other types of calf predators, some observed trends may be consistent regardless of predator type. The relative risk for individuals in a group is similar despite predator type; dilution of individual risk is dependent on group size, not the threat itself; individuals lacking experience or physical competence relative to other group members will be similarly disadvantaged regardless of the type of predator.

4.2 Methods

I conducted disturbance trials from 10 June - 23 July 2004, avoiding early calving season to minimize the risk of causing permanent cow-calf separations. The start date was chosen based on field observations of cow-calf interactions: before 9 June of 2004, some calves displayed non-recognition of their mothers; by 9 and 10 June, all calves appeared to be capable of responding to their own mother's vocalizations and seeking out their own mother without error (I no longer observed suckling refusal by one female followed with suckling acceptance by another female).

4.2.1 Subject Selection

Groups of caribou were located on foot by chance encounter in habitats with high visibility (bogs, fens, barrens, and wood road sections with vegetation <0.5m high on either side). Open habitats were chosen in order to ensure the caribou's visibility of my approach and *vice versa*. Prior to approach, I watched the group to ensure the caribou were not aware of my presence or already alert in response to other stimuli. Groups in which any individual appeared to be agitated (standing or walking with ears and tail erect; engaging in running or trotting; performing an excitation leap) or in which any individual appeared aware of my presence were not used for trials.

4.2.2 Natural Pre-Disturbance Behaviour

Prior to beginning an approach, I conducted two instantaneous scans of the whole group (as described in 2.2.2) at 10-min intervals to estimate group activity, group posture, and group vigilance. Activity was classified as Active or Inactive (Appendix III) for the whole group by the Activity displayed by the majority of group members. Posture was determined similarly, and classified as Standing or Lying. Vigilance was measured by mean number and mean proportion individuals Vigilant (any behaviour in which an individual's head was elevated at or above the shoulders was considered Vigilant; see Appendix III).

4.2.3 Approaches

To elicit a fright response from caribou, I directly approached the center of the group on foot at ≈ 4 km/hr. All groups were approached from a distance > 350 m. Directions of approach, wind direction and the slope of approach (walking uphill, downhill or level) were also recorded.

A laser rangefinder (Bushnell Yardage Pro 1000) was used to measure Alert Distance (AD), Flight Distance (FD), and Run Distance (RD) (Taylor and Knight 2003); Flight Lag (FL) was calculated as the distance moved by the researcher between AD and FD (Table 4.1). Qualitative measurements of disturbance response were recorded as follows: the sex and age category and reproductive status (if female) of: first individual alert; first individual to flee; and last individual to flee. Presence or absence of curiosity return and behavioural response of the group during and after flight (moving together, spreading, splitting, no change) (Table 4.1) were also noted.

Table 4.1 Definition of terms used to describe behavioural response to disturbance. Despite the prevalence of human disturbance trials in behavioural research studies, there is considerable inconsistency in how studies are conducted and in the terminology used to describe measures of animal reactions to humans (Taylor and Knight 2003). Alert distance, flight distance and run distance follow the recommendations of Taylor and Knight (2003). The descriptors of group behavioural response are adapted from Lingle (2001).

Term	**Definition**
alert reaction	recognized by overt alert behaviour including any of the following: standing alert, head-bobbing toward approaching person, and snorting or vocalization accompanied by a display of erect ears and tail; usually a standing alert posture (Appendix II) precedes other overt behaviour
alert distance (AD)	the distance between the approaching person and the nearest caribou of the group at the point where any individual of the group displayed an alert reaction
flight distance (FD)	the distance between the approaching person and the nearest caribou of the group at the point where any individual in the group initiates flight (running or trotting) or performs an excitation leap; excitation leaps were always immediately followed by flight but were not always performed
flight lag (FL)	the difference between alert and flight distance; a measure of how far the approaching person moved toward the caribou group between the first alert reaction and the initiation of flight
run distance (RD)	the distance moved by the caribou away from the approaching person before the caribou stopped running or trotting for the first time after flight initiation; calculated as the difference between the distance from the stationary person to the nearest caribou at the first stop and the flight distance
curiosity return	behaviour wherein one or more caribou from a group decreased the distance between themselves and the stationary person by approaching the person after stopping flight
moving together	decrease in average nearest-neighbour distance during flight or at the first stop location relative to pre-disturbance group arrangement; group remains as one unit
spreading	increase in average nearest-neighbour distance during flight or at the first stop location relative to the pre-disturbance group arrangement; group remains as one unit (nearest-neighbour distances are less than 75 m)
splitting	formation, during flight, of 2 or more sub-groups, separated by more than 75 m at the locations of the respective first stops

During approaches, I paused briefly during the measurement of AD and stopped my approach at FD. I maintained visual contact with the caribou group after disturbance only as long as necessary to determine RD, sex and age of each group member, and to record qualitative group behaviours during flight. Group size was recorded as total number of adults and yearlings in the group. Group composition was classified as in Table 4.2.

All data were recorded on a hand held microcassette recorder to allow the observer to maintain visual contact with the group. Data were transcribed to data sheets (Appendix V).

Table 4.2 Classification of group types by sex and age composition.

Group Type	**Code**	**Composition**
Females	F	*adults*: female only *yearlings*: variably present *calves*: none
Females with Calves	FC	*adults*: female only *yearlings*: variably present *calves*: at least one present
Males	M	*adults*: male only *yearlings*: variably present *calves*: none
Mixed Adults	MX	*adults*: at least one of each female and male *yearlings*: variably present *calves*: none
Mixed Adults with Calves	MXC	*adults*: at least one of each female and male *yearlings*: variably present *calves*: at least one present

4.2.4 Statistical Analysis

Based on patterns evident during visual inspection of AD and FD plotted against group size, group size was analysed as a categorical variable and divided into small ($\leq$ 15) and large (>15) groups. Sample size was too small to refine group-size categories further or make statistically meaningful inferences from using group size as a continuous variable. AD, FD and FL were inspected for correlation.

T-tests were used to compare AD, FL, FD, and RD between group size, calf presence, adult male presence and season categories. Since vigilance is theoretically related to detection distance, regression analysis was used to determine whether mean number vigilant or mean proportion vigilant affected AD.

When RD was plotted in relation to group composition (Table 4.2), it was evident that FC groups behaved differently than all other group types. A t-test was used to compare RD between FC groups and all other groups.

The behaviour of individuals within groups was analysed using chi-square tests to test for trends in behavioural response according to sex, age, and reproductive status of adult females. The expected frequency was calculated as the sum of the proportional representation of each sex and age class in each trial group. The observed frequency was calculated as the sum of individuals by sex and age class recorded as first alert, first to run and last to run. Curiosity returns were summarized by frequency and the sex and age classes of individuals.

The run behaviour of groups was summarized by the frequency of response type (move together, spreading, splitting, and no change). FC groups showed a different trend than observed in other group types; results were summarized to compare FC groups to all other group types. Calf behaviour recorded during flight was summarized qualitatively.

All statistical tests were performed with StatView 5 (Haycock et al. 1992).

4.3 Results

Thirty-nine disturbance trials were performed from 10-20 June (peri-calving) and 11-23 July 2004 (early summer). Groups used for trials ranged in size from 2 to 91 individuals; 24 groups were small (2 – 15 adults and yearlings) and 13 were large (16 – 91 adults and yearlings). Most large were MXC groups encountered mainly during July, after the caribou had left the calving grounds.

4.3.1 Alert Distance, Flight Distance, Flight Lag and Run Distance

Small groups displayed greater AD than large groups ($t = -3.775$, d.f. = 34, $p < 0.001$) (Figure 4.1(a)) but were more variable in their response; despite the larger sample size (small groups: $\bar{x} = 146.83 \pm 12.62$ m, $n = 24$; large groups: $\bar{x} = 78.69 \pm 6.22$ m, $n = 13$). Groups containing calves had a shorter AD than those without ($t = 3.092$, d.f. = 35, $p < 0.005$), while the presence of males had no effect on AD ($t = -0.24$, d.f. = 34, $p = 0.981$). AD was greater during calving season than during early summer ($t = 3.032$, d.f. = 33, $p < 0.005$).

Neither proportional vigilance nor total vigilance of groups was related to AD (Figure 4.2). AD was shorter for groups which were Standing Inactive relative to Standing Active or Lying Inactive groups ($F_{(2,32)} = 3.383$, $p = 0.047$).

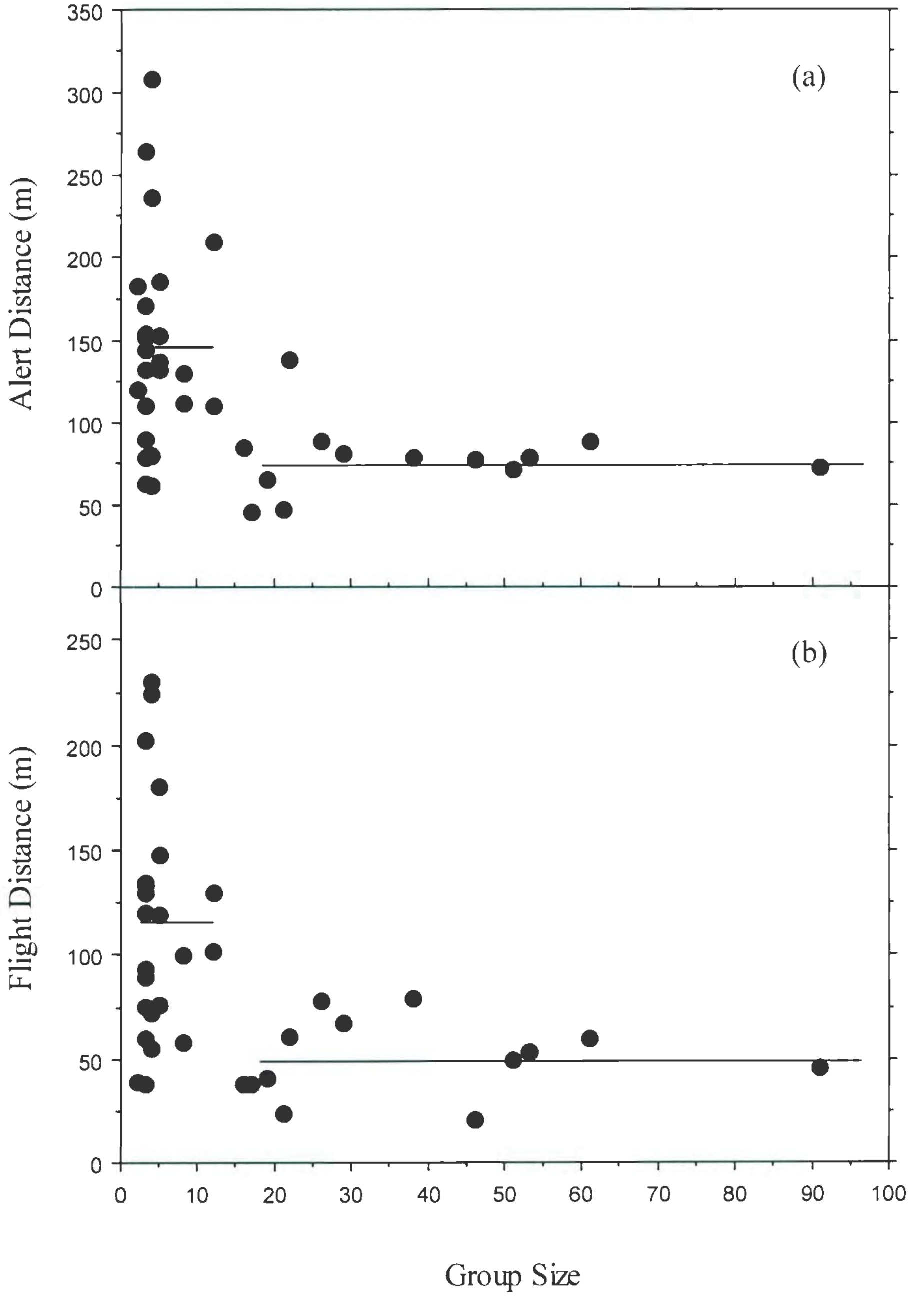


Figure 4.1 Alert and flight distances in relation to group size. (a) Alert and (b) flight distances were longer for small (< 15 adults and yearlings) groups; means for small and large groups are shown by horizontal lines. Small groups showed greater variation in both AD and FD.

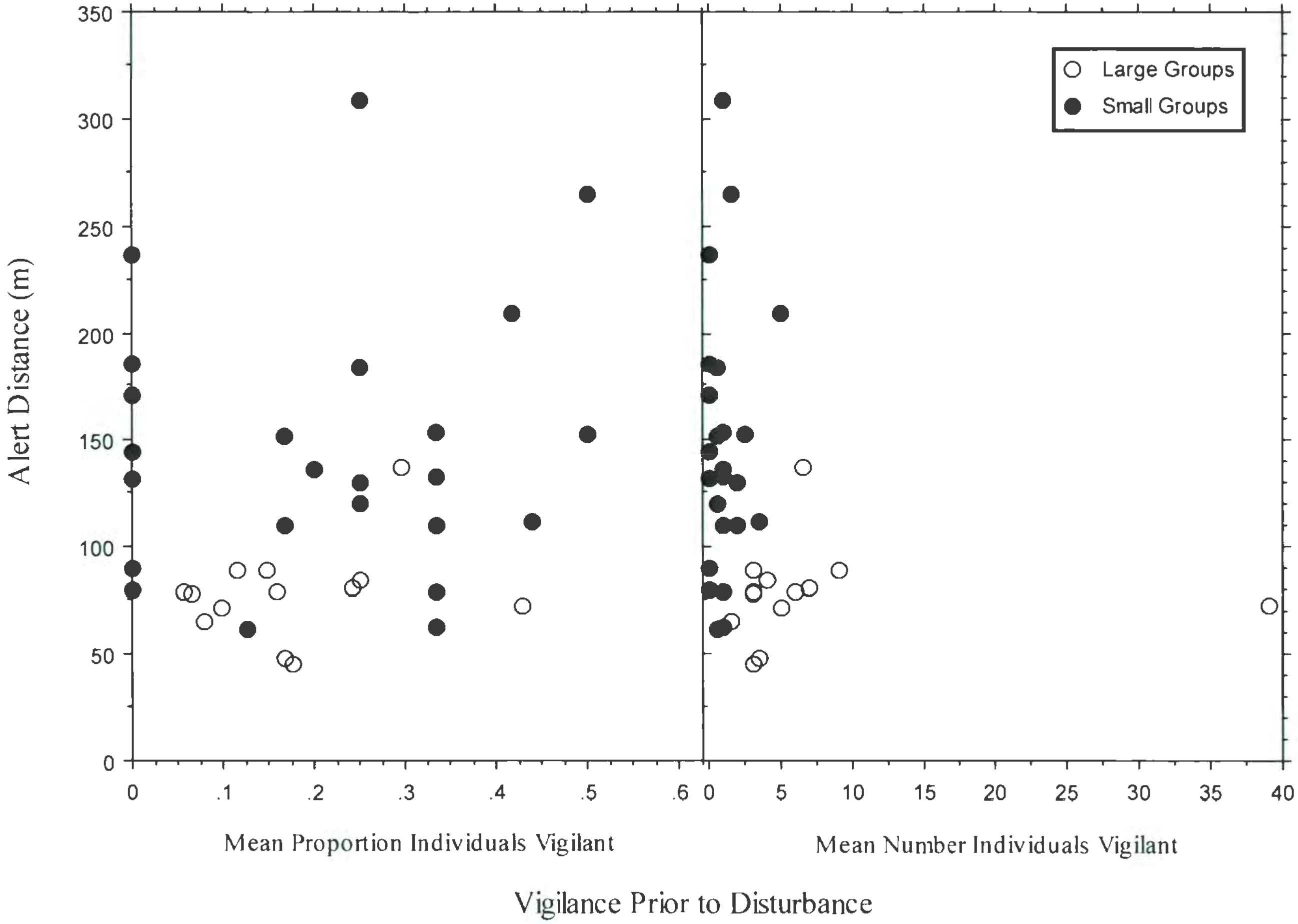


Figure 4.2 The relationship between Alert Distance and vigilance. Alert Distances were unrelated to either mean proportion vigilance or the mean number of vigilant individuals in a group. This indicates that either vigilance is unrelated to early detection or that early detection is unrelated to alert distance.

The greatest AD observed was 309 m and the majority of alert distances measured were less than 150 m. All groups were approached from a minimum distance of 350 m, so it is unlikely that approach distance affected AD (caribou did not adopt alert posture as soon as the approach began, it occurred sometime later).

FD was highly correlated with AD ($r = 0.952$, $Z = 8.669$, $p < 0.001$) and showed the same trends as described for AD (Table 4.3). Small groups responded more variably (Figure 4.1(b)) and had a greater FD ($t = -4.026$, d.f. = 33, $p < 0.001$). Groups containing calves had a lower FD than those without ($t = 4.126$, d.f. = 34, $p < 0.001$).

The mean FL was 30.39 ± 4.272 m ($n = 36$). Small and large groups did not differ in FL ($t = -0.389$, d.f. = 34, $p = 0.700$) nor did FL differ between seasons ($t = -0.463$, d.f. = 33, $p = 0.646$).

RD was not correlated with AD ($r = 0.071$, $Z = -0.028$, $p = 0.978$) or FD ($r = 0.237$, $Z = 0.309$, $p = 0.757$). RD did not differ between seasons ($t = 1.719$, d.f. = 33, $p = 0.095$). The most striking predictor of RD was group composition; FC groups ran further than all other group types (FC groups: 195 ± 69.10 m, other groups: 45 ± 5.76 m; $t = 2.935$, d.f. = 32, $p = 0.006$).

Table 4.3 Mean alert and flight distances. Distances are shown as the overall mean distances and sub-divided by selected categorizations of groups. The results of t-tests comparing sub-groups are also included.

Sub-group Characteristics	**Alert Distance (m)**			**Flight Distance (m)**		
	n	**Mean ± SE**	**t (p)**	**n**	**Mean ± SE**	**t (p)**
All groups	37	122 ± 10.28		36	93 ± 9.21	
Groups with calves	25	104 ± 8.580	3.092 (0.004)	24	69 ± 33.6	4.126 (<0.001)
Groups without calves	12	163 ± 21.38		12	135 ± 18.15	
Peri-calving groups	18	151 ± 16.46	3.032 (0.005)	18	123 ± 13.92	4.274 (<0.001)
Early summer groups	19	96 ± 8.12		18	59 ± 5.26	
Small groups (≤15)	23	148 ± 13.17	-3.775 (<0.001)	22	115 ± 11.92	-4.026 (<0.001)
Large groups (>15)	13	79 ± 6.22		13	50 ± 5.11	

4.3.2 Behaviour of Individuals within Groups

The sex, age, and reproductive classification of the first individual to adopt an alert posture did not differ from that expected by chance ($X^2 = 3.198$, d.f. = 4, p = 0.525) (Figure 4.4(a)). However, adult females with calves were the first to run more than twice as often as expected and adult females without calves were the first runners much less often than expected ($X^2 = 14.78$, d.f. = 4, p = 0.005) (Figure 4.4(b)). Females with calves were rarely the last individuals to run and females without calves were usually the last to run, but observations of last runners were not different from the expected ($X^2 = 3.725$, d.f. = 4, p = 0.444) (Figure 4.4(c)).

Curiosity returns were observed in 26% (9/35) of trials. No curiosity returns were observed prior to 16 June 2004, and no calves participated in curiosity returns prior to 13 July 2004. In half (6/12) of the large groups, at least some members exhibited a curiosity return; compared to 3 of 23 trials of smaller groups.

4.3.5 Group Behaviour During Flight

In 55% (21/38) of trials, groups responded by moving together. In 34% (13) trials, the disturbed group split; in 8 of these splitting events, at least one subgroup contained only a cow-calf pair. In 9% (3) of trials, the individuals of the groups spread out, and in 1 trial, the group did not run at all, but instead Walked Head Up without pausing approximately 300 m across open bog and into dense cover. (Table 4.4)

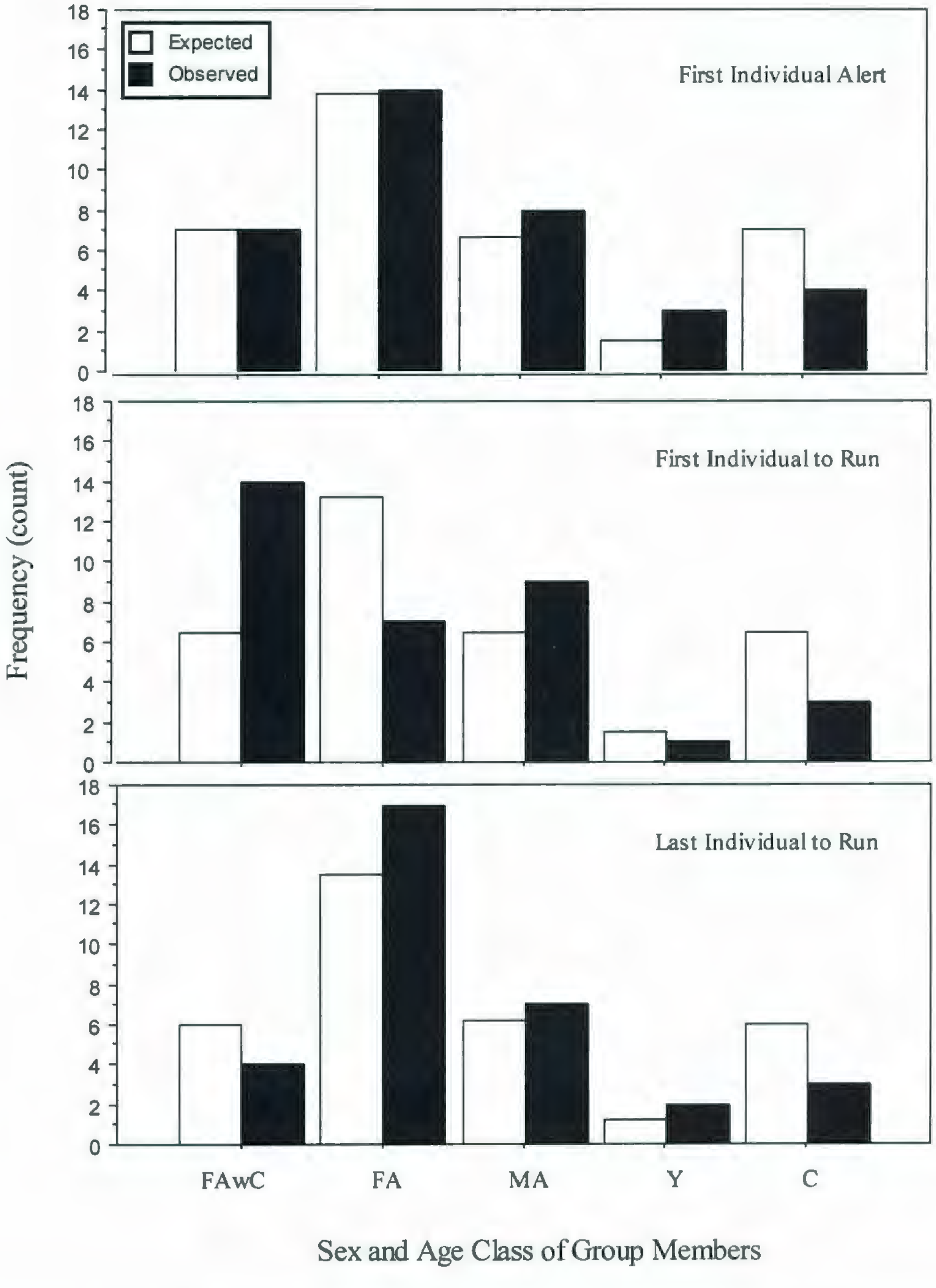


Figure 4.3 Expected and observed frequencies of sex and age classes response to disturbance. (FAwC: adult females with calves; FA: adult females without calves; MA: adult males; Y: yearlings; C: calves). Expected distributions are the sum of the proportional representation of each sex and age class in each group for which identification was made for the variable (first alert, first to run, last to run); observed distributions are counts.

Trends observed within the FC groups were different from groups either lacking calves or containing males ($X^2 = 8.02$, d.f. = 2, p = 0.018) (Table 4.4). In all (3/3) disturbance trials with F groups, the group moved together during flight. In FC groups, the most common response was to split during flight (7/13 or 54% of trials). During calving season, splitting usually involved all females with calves staying together but becoming physically separated from the rest of the group by running farther than the other group members (3 of 4 splitting responses). Anecdotally, when groups were accidentally disturbed during the peri-calving season, females with calves almost always separated as a group from females without calves. This was never observed during early summer.

Table 4.4 Summary of the frequency and proportion of observed group arrangement as a response to disturbance. The distribution of responses displayed by FC groups differed from that of other group types. Post-disturbance arrangement categories are relative to pre-disturbance arrangement and are described in Table 4.1.

Post-disturbance arrangement of group	**All groups n = 38**		**FC groups n = 13**		**Other groups n = 25**	
	Frequency	**Proportion**	**Frequency**	**Proportion**	**Frequency**	**Proportion**
Moving together	21	0.55	4	0.30	17[1]	0.68
Splitting	13	0.34	7	0.54	6	0.24
Spreading	3	0.09	1	0.08	2	0.08
Other	1	0.02	1	0.08	0	0.00

[1] All (3/3) F groups moved together during flight.

During the peri-calving season, calves were never seen separated from their mothers while running, but in the summer trials calves occasionally split, either individually or in small calf groups, from the rest of the group. On one of these occasions, 8 calves initially ran into vegetative cover, approximately 100 m away from their pre-disturbance position. They later ran, in groups of 2, 1, 2 and 3 calves, from the cover to the group, crossing a distance of approximately 150 m of open bog. Calves split, without accompanying adults, from the rest of the group during two other trials, both in late July. In the first instance one calf stayed behind in vegetative cover when the rest of the group ran; this calf remained for 23 minutes, until a female returned and called for it. In second instance, a calf was the first individual to run and was not followed by the remainder of the group, which ran in a different direction. Seven minutes after beginning to run, the calf reunited with the rest of the group, having to cross more than 350 m of open bog by itself.

4.4 Discussion

4.4.1 Comparison to other Disturbance Studies

Fright behaviour measured by alert, flight, and run distances for *Rangifer* (Table 4.5) in other studies indicate some common trends. As in this study, Aastrup (2000) found that caribou became alert to human approach at longer distances during the calving season than later in the year; Lent (1964) also noted that caribou were particularly wary during calving. Surprisingly, groups containing calves consistently allow a closer approach before becoming alert than those without (this study, Baskin and Scogland 2000), even when approached by snowmobile (Mahoney et al. 2001) in winter. Similar to this study, Baskin and Scogland (2000) observed that larger groups had shorter alert distances although no such relationship was reported by Reimers et al. (2003), Mahoney et al. (2001) or Aastrup (2000).

Among *Rangifer* studies reviewed, I documented the closest alert distances but these are not substantially different than those of caribou in Greenland (Aastrup 2000) and the semi-domestic reindeer in Scandinavia (Baskin and Scogland 2000) approached on foot, or of groups with calves approached by snowmobile in Gros Morne National Park in Newfoundland (Mahoney et al. 2001). Wild reindeer become alert much earlier when approached, but semi-domestic reindeer respond similarly to caribou.

The similarities in the patterns of disturbance response might indicate the responses are particular to a human threat, and the differences in actual distances reported provide indications of relative perceptions of risk among these herds. Run distances recorded in this study are shorter than reported for caribou approached by snowmobile (Mahoney et al. 2001), suggesting that snowmobiles are perceived as a greater threat. However, the alert distance of reindeer is not different when approached by a snowmobile or a skier (Reimers et al. 2003) and, similarly, the disturbance response of bison (*Bos bison*) is similar whether they are approached by snowmobiles or pedestrians (Fortin and Andruskiw 2003).

Table 4.5 Comparison of Gaff Topsail Herd alert, flight and run distances with selected studies. Studies represent caribou (*Rangifer tarandus caribou*) and reindeer (*Rangifer tarandus tarandus*) human approach trials. Lingle and Wilson's (2001) study of white-tail deer (*Odocoileus viginianus*) are included for comparison; though smaller than caribou, white-tail deer also rely on their ability to outrun predators in order to evade attack.

Population (authors)	**Species**	**Approach Type**	**Comments**	**Alert Distance (m) ± SD**	**Flight Distance (m) ± SD**	**Run Distance (m) ± SD**
Gaff Topsails, Newfoundland (this study)	Caribou	Walking	High calf mortality; hunting	122 ± 61.66	93 ± 56.0	98 ± 157
Isotroq, Greenland (Aastrup 2000)	Caribou	Walking	Low predation; some hunting	190 ± 10.56	130 ± 8.920	
Akia, Greenland (Aastrup, 2000)	Caribou	Walking	Low predation; low hunting	156 ± 12.19	103 ± 7.550	
Dovre Mountains, Norway (Baskin & Skogland 2000)	Reindeer	Walking	High predation; high hunting	471 ± 64.6		409 ± 36.3
Spitsbergen, Svalbard (Baskin & Skogland 2000)	Reindeer	Walking	Low predation	270 ± 21.0		150 ± 21.5
Lapland, Sweden (Baskin & Skogland 2000)	Reindeer	Walking	Semi-domestic herd	178 ± 22.5		147 ± 14.5
Gros Morne, Newfoundland (Mahoney et al. 2001)	Caribou	Snowmobile (winter)	No calves in group	240 ± 212	186 ± 198	161 ± 316
			Calves present	174 ± 123	123 ± 122	116 ± 203
Southern Alberta (Lingle & Wilson 2001)	White-tail deer	Walking (winter)	High coyote presence in area	50-70		

Mahoney et al. (2001) conducted their study in winter, and, although no hunting is permitted within the boundaries of Gros Morne National Park, some of the caribou encountered in that study may have some experience with hunters outside the park boundaries. When approaching reindeer on foot, Baskin and Scogland (2000) found that reindeer herds subject to intense hunting pressure became alert sooner and ran further than those subject to little or no hunting. Aastrup (2000) reported that caribou in Greenland had longer alert distances just after hunting season than during the calving season.

The Gaff Topsail caribou appear to perceive a level of threat from an approaching human similarly to other caribou, but lower than wild reindeer. If alert distances were reflective of an underlying predation risk, Newfoundland's caribou should show alert distances intermediate between Alaska (high predation) and Greenland (very low predation). Manipulated encounters using additional threat models (trained dogs or other predator models like disguised humans) could confirm whether the type of threat elicits different fright reactions in caribou.

4.4.2 Detection, Alert Response, and Flight Onset

No correlation was found between measured vigilance and alert distance, suggesting that either vigilance does not improve detection, or detection is not appropriately described by alert behaviour. Some researchers have measured detection by other behavioural cues, like a direct stare from the animal to the researcher (Reimers et al. 2003, Mahoney et al. 2001, Lent 1964), which can occur at a substantial distance prior to alert posture (pers. obs.) but still does not capture the ability of an animal to detect and identify human presence by smell, sound or peripheral vision without showing any outward response.

An alert posture cannot be elicited before threat is detected; this detection constraint on alertness may explain the large variation of alert distances observed in small caribou groups. Individual risk of predation in smaller groups is higher than that of larger groups, so smaller groups would be expected to become alert sooner than larger groups. However, with fewer individuals to monitor the surroundings there may be gaps in time and field of view allowing approach before detection. The inconsistent alert distances observed in smaller groups may be due to high perceived risk sometimes constrained by poor detection.

Alert postures require the prey species to stop other behaviour like feeding, resting, or ruminating and so can be costly if they are preformed frequently or for long durations. Caribou flee from predators and may most effectively manage their time by reacting to an approach only when it becomes threatening. White-tail deer alert distance was not correlated to the probability of a successful attack by coyote, but for mule deer, which tend to physically defend themselves against predators, successful attacks were most common when alert distances were short (Lingle and Wilson 2001). Mule deer alert distance was highly correlated with approach distance (the mule deer alerted to the approaching researcher as soon as the approach started) but white-tail deer alerted later and did not show a pattern correlated with approach distance. Running prey may only show alertness at a minimal distance from which it is able to outrun a predator; waiting to display alertness until a predator is closer than when first detected could increase time available for feeding or other activities, reducing the cost of alert behaviour.

If alert distances indicate perceived risk, the high correlation of alert and flight distances is not surprising for a running prey species like caribou. All individuals within a group, regardless of sex, age or reproductive status were equally likely to be the first to assume an alert posture. The first individual to begin to run was, more often than expected, a female with a calf. Lent (1964) also noted a tendency for females with accompanying calves to be the first move away from a group, sometimes without overtly alerting the rest of the group, when approached. The observed differences in alertness and flight onset, however, suggest that risk and safety are perceived differently by maternal caribou or that risk, relative to other group members, changes once a threat is detected. Females with calves appear to perceive lower safety when threatened than do other group members.

4.4.3 Run Distance and Group Behaviour during Flight

Females with calves were not only usually the first to run, but also tended to run further than other individuals, particularly during the peri-calving season. Aastrup (2000) also found that run distances were longest during calving season. Though caribou calves can keep up with running adults by 3-5 days old (pers. obs., Lent 1964) they are smaller and may tire more quickly; the energetic cost of running long distances might be high, but outweighed by the benefit of creating a large enough separation to dissuade predators from pursuit.

Moving together while running and during pauses in running was the most common reaction of caribou groups during flight, but was seen in only about half of the trials. Splitting into two or more groups was also common, and spreading out was occasionally observed. It is possible that as long as the caribou are fast enough, the arrangement of the group during and after flight is unimportant, or that the variety of response the Gaff Topsail caribou displayed could reflect a history of avoiding multiple predator types (stalking, ambushing, aerial), and their displayed preference for moving together specific to experience with humans.

During the peri-calving season, splitting was the most common flight response of groups containing calves. In most splitting events, females with calves remained together and separated from females without calves by running sooner and further. By separating from less vulnerable individuals and remaining with similarly vulnerable individuals, this particular pattern may reduce individual risk for the calves. Curiously, cow-calf pairs often split independently from their group on both calving and summer grounds, a behaviour also noted by Lent (1964). Alternatively, the tendency of maternal caribou to run first and run far may allow other group members to choose to remain separated from females with calves. Females without calves, adult males, and yearlings may all reduce their own predation risk by avoiding association with calves which may be highly attractive to predators due to their vulnerability.

Lingle (2001) found that coyote hunts of deer were most successful if group members either split up or failed to move together; or if individuals separated independently from the group. Both standing ground and fleeing are effective strategies against coyote predation, as long as all group members behave the same way (Lingle and Pellis 2002). If this is typical of coyote success, trends observed in this study have implications for calf survival; females with calves were most likely to separate independently from a group, calves were also observed separating from the group during flight and groups consisting of only females and calves were more likely to split into subgroups than other group types. Lingle (2001) also found, however, the further white-tail deer ran, the less likely they were to be killed. The long run distances observed by FC groups in the Gaff Topsails during the peri-calving season could help protect calves, but once the calves were more independent (early summer) there were fewer long run distances observed. Female with calves appear to use a mixed strategy of putting large distances between themselves and an approaching threat and reducing their calves' vulnerability by maintaining similarly vulnerable neighbours.

Coyote have been of particular interest in the insular Newfoundland circumstance because their arrival has been coincident with the recent decline in calf recruitment. Coyote were responsible for additive mortality resulting in the decline of caribou calf recruitment in south-eastern Québec (Crête and Desrosiers 1995). Calf recruitment in the Gaff Topsail herd is similar to that in other herds on insular Newfoundland; these other herds, however are less substantially affected by coyote predation (Norman et al. 2006), implying that behavioural vulnerability to coyote is insufficient to explain the recent increase in predation mortality. Other predators may take advantage of the same behaviours, but observations of predation events will be necessary to determine whether this is so.

The reaction of caribou to humans may show different patterns beyond alert, flight and run distances, than would be elicited by predators. Bergerud (1971) suggested that females may defend their young from attack on occasion; he noted that twice, while crawling, he was aggressively approached by a female that had a calf. He also once observed a female caribou charge a black bear in defence of her calf. Once, while photographing a dead calf, a female approached within 20 m of my position, head-bobbing towards me. I interpreted this as an attempt to entice her calf to get up and run away rather than aggression directed toward me. Bergerud, by crawling, seemed to have elicited an entirely different behaviour than has been recorded by anyone approaching caribou by walking upright. Detailed observations of predation attempts and studies using better predator models than humans, such as trained dogs or a disguised human would be beneficial to improving our understanding of disturbed anti-predator behaviour.

5.0 Conclusion

5.1 Summary of Results

Adult females in the Gaff Topsail caribou herd displayed a starvation-predation trade-off between foraging and vigilance behaviours. Individuals were more vigilant during rest than while engaged in active behaviour, which is primarily dedicated to foraging. Due to the relative vulnerability of the lying posture, higher vigilance is expected when caribou are lying at rest, but even those females standing at rest were more vigilant than those foraging. The group-size effect on vigilance (reduced individual vigilance in larger groups) was only documented when females were engaged in active behaviours, supporting the resource-competition hypothesis: female caribou decreased vigilance during foraging and decreased vigilance further when local resource competition increased.

Time-activity budgets of females with calves did not differ from those of females without calves. Maternal caribou dedicated the same amount of time to each Behaviour Category (Appendix II) as their non-mother counterparts; however, aspects of how they managed their time differed. Maternal caribou fed more intensely at all times and maintained high feeding intensity into early summer when non-maternal caribou showed a decrease in feeding intensity. Females with calves were vigilant less frequently despite the ability to compensate for added nutritional demands without increasing foraging time. Maternal caribou forage at the cost of the ability to increase vigilance, despite high predation pressure on calves.

During the peri-calving season, caribou groups reacted more quickly to a human approach than later in the summer, which is consistent with greater vulnerability of calves in the weeks immediately following birth. Maternal caribou were no more likely to be the first individual in a group to become alert during a disturbance, but were more than twice as likely as expected by chance to be the first individual to run. Caribou with calves, particularly during the peri-calving season, showed a tendency to split from their groups (either in a cow-calf pair or a sub-group consisting exclusively of cow-calf pairs) and ran further than other group members.

5.2 Implications of Maternal Behaviour for Calf Survival

Vigilance of adult females in the Gaff Topsail herd is generally high relative to that reported in other herds (Bøving and Post 1997). Assuming vigilance is correlated with perceived predation risk, this wariness is consistent with the known high level of predation. However, vigilance is unrelated to the distance at which the Gaff Topsail caribou become alert to a threat; so, although vigilance may be a good measure of predation anxiety, it appears to be a poor measure of safety. Maternal caribou are less vigilant than females without calves, but react more strongly to disturbance, indicating a lower perception of safety when threatened.

The observed increased foraging and decreased vigilance of maternal caribou is consistent with other evidence (Mahoney and Weir 2007) that insular caribou herds in Newfoundland and Labrador are currently facing nutrient stress. Predation is the largest proximate cause of calf mortality in the Gaff Topsail herd during the time between calving and the onset of winter (Norman et al. 2006), but whether predation mortality is additive or compensatory is unknown. Tveraa et al. (2003) found that in a group of semi-domestic reindeer, the calves which died of starvation while in a predator-free enclosure had mothers of the same size and condition as the calves which died due to predation mortality outside of the enclosure. Their conclusion was that in that herd, predation mortality was compensatory, targeting the calves that would have otherwise died of starvation. Calves which are smaller and weaker are at the highest risk of predation, but the reduced vigilance of mothers in the Gaff Topsail herd, during a period of nutrient stress, may additively increase the vulnerability of all calves.

Maternal caribou moderate calf vulnerability in the peri-calving period by associating with other females and calves rather than with less vulnerable individuals. This is especially evident when they are faced with a threat; females with calves tend to separate themselves from other individuals but remain a cohesive sub-group while fleeing from disturbance. They also tend to run relatively long distances from a threatening disturbance which is likely a predator-deterrent. However, their tendency to be the first individuals to run, to separate with their calf from the rest of the social group, and to allow a close approach before running may put them at particular risk of predation from coursing or stalking predators, like coyote. These behaviours, when observed in white-tail deer (another species which relies on its ability to outrun predators), have all been identified as increasing the risk of successful attack by coyote (Lingle and Pellis 2002, Lingle 2001).

The evolutionary history of Newfoundland's insular caribou's anti-predator behaviour has been influenced by the historic presence of wolves prior to the recent arrival of coyote; the caribou may be behaviourally predisposed toward avoidance of predation by canids. However, in the 80 years with no canid predator, lynx (Bergerud 1971) and black bear (Mahoney et al. 1990) were major predators of caribou and both species may have been important predators prior to wolf extirpation. Additionally, caribou of insular Newfoundland have been hunted by humans since about 4500 BP (Renouf 1999). This history of varied and changing predators may have selected for a generalized anti-predator behaviour or for many predator-specific avoidance behaviours; a generalized behaviour may result in increased vulnerability to particular predators. Improved understanding of the interactions between caribou and their predators will help to better assess the actual risk of the current and future predator guild to the insular caribou herds of Newfoundland.

5.3 Recommendations for Future Work

Many knowledge gaps continue to exist regarding the life history, density, and range of the predators, and the reliance of the predator populations on the caribou as a food source. Further gaps exist in our understanding of how predator-prey interactions have shaped and will shape the behaviour of both caribou and their predators in Newfoundland. Management decisions will be best informed by a dynamic understanding of caribou and their predators and competitors. Increasing our knowledge regarding predator behaviour and caribou-predator interactions is vital in predicting the impact of the current predator guild on calf survival and population dynamics.

Observations of actual predation attempts should be well documented and recorded. In the absence of reliably observable predation attempts, a useful extension of this study would be to conduct disturbance trials using different threat models. Trained dogs could be used to elicit canid-specific fright responses; a human disguised in such a way as to neither look nor smell human might remove human-specific response from the reaction. Approaches done by crawling may illicit different responses even if the experimenter is clearly human (Bergerud 1971). Understanding the range of available fright response and the limitations of this will improve evaluations of caribou vulnerability.

Repeating the vigilance assessment and disturbance trials both over time (to monitor change) and between herds known to have different relative exposure to the common predators (to give insight into predator-specificity and generality in anti-predation behaviour) will increase our understanding of community dynamics. Effective means of predator deterrence and effective escape behaviour are both components of survival, and ultimately, fitness (Lind and Cresswell 2005). Clear understanding of how both prey and predators manipulate their behaviour in response to each other will strengthen the ability of managers to implement measures, when necessary and feasible, either to control predators or to manipulate prey vulnerability.

Continued behavioural monitoring of Newfoundland's insular caribou herds is recommended to detect changes in behavioural patterns which may result from selective pressure by predators, and to understand how changes in nutrient availability affect behaviours related to calf survival and maternal investment in both current and resources for future offspring. In this study, individual females whose calves survived through the study period likely contributed disproportionately to data as time since calving increased.

This study component would have been strengthened by the ability to observe known individuals throughout the season. Repeated behavioural observation of known females would increase our understanding of which behaviours promote, and which are detrimental to, calf survival, since the ability of individuals to maintain their calves could be correlated with behavioural aspects.

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Appendices

Appendix I: Study Area

The study was conducted on the late spring and early summer range of the Gaff Topsail herd in west-central Newfoundland (Figure I-i). During the late spring, female and some yearling caribou aggregate on the herd's traditional calving grounds in the vicinity of Eclipse Pond (49°00N, 56°48W) for the period encompassing the calving and post-calving season (peri-calving). The calving grounds range from 360 m to 560 m in elevation and are characterized by scrub and shrub barrens mixed with large bog and fen complexes interspersed with krummholz tucks and patches of spruce and fir forest (Figure I-ii and I-iii). During peri-calving, single and occasional calving female, male, and some yearling caribou tend to aggregate in an area northeast of the calving grounds. The area occupied by these individuals is at a slightly lower elevation (240-400 m) than the calving grounds but contains similar habitat, dominated by bog, fen and barrens, but with larger and more numerous patches of spruce and fir forest. In the early summer, all the sex and age classes of caribou tend to mix together and aggregate further northeast (49°12N, 56°15W), in an area lower in elevation (160-320 m) and with a flatter topography than the areas frequented during peri-calving. A mixture of peat bogs, fens, dense forested areas and wooded areas in various stages of post-logging regrowth, characterizes the habitat of the early summer range (Figure I-iv).

The field site was accessed mainly by helicopter, or by vehicle from an abandoned rail bed. Three remote campsites were used in each of 2003 and 2004. A cabin was used when caribou were aggregated within walking access from the rail bed. 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) and by the location of sources of fresh water and suitable ground for erecting tents.

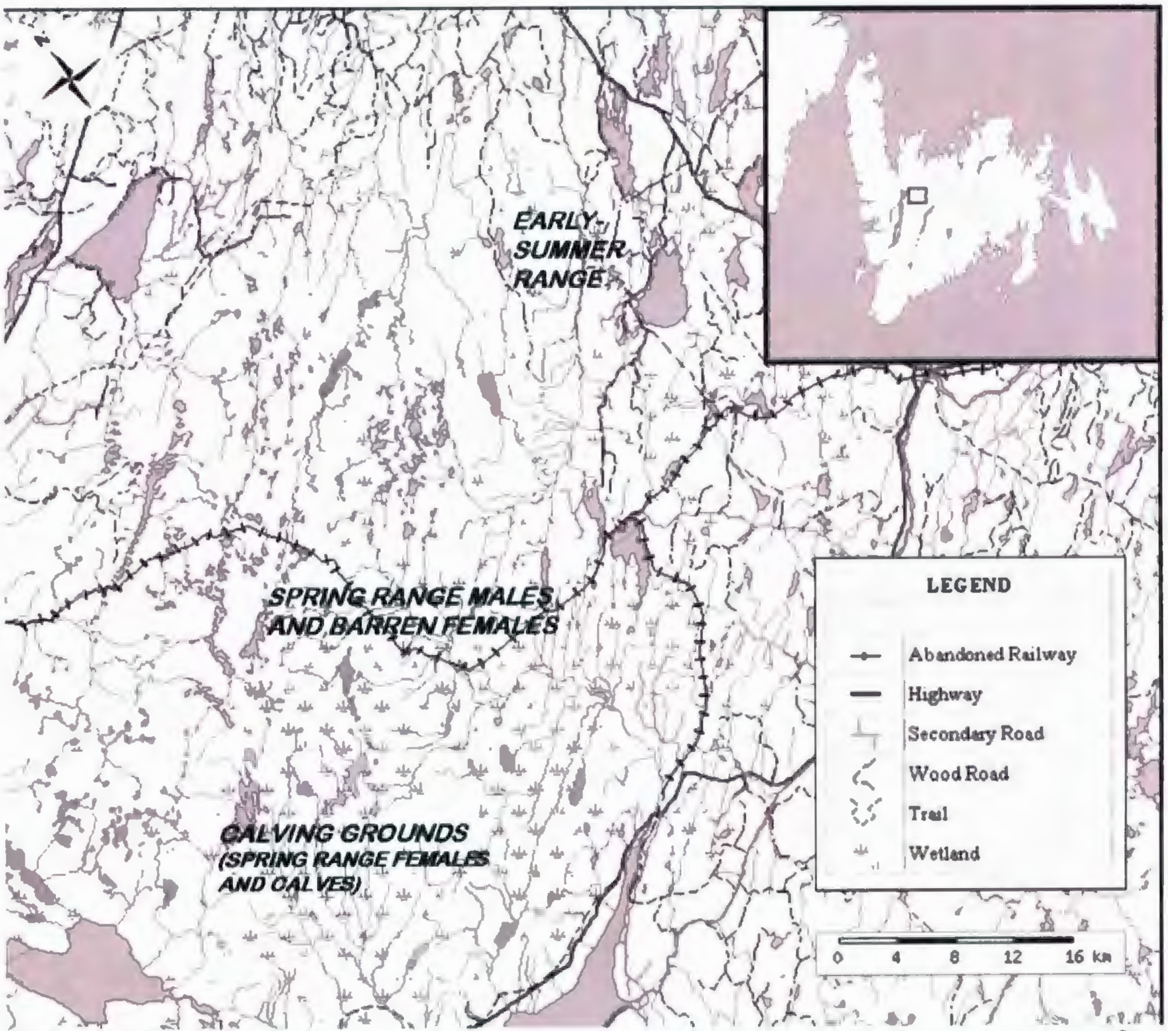

Figure I-i. Map of the study area. This area encompasses the late spring/early summer range of the Gaff Topsail Caribou Herd in west-central Newfoundland. The calving grounds and early summer range are indicated.

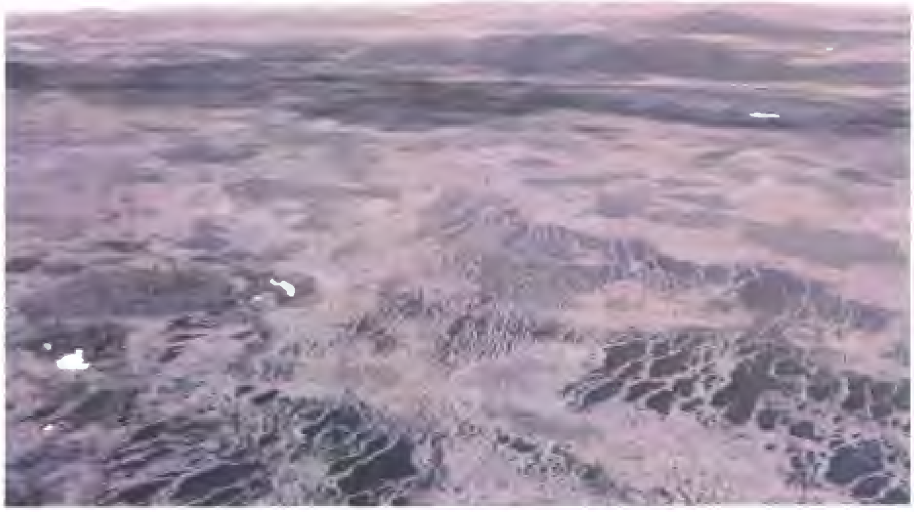

Figure I-ii. Aerial view of the calving grounds showing typical habitat features.

Figure I-iii. Typical habitat occupied during peri-calving: water-saturated soil mixed with scrub and shrub barrens and krummholz patches.

Figure I-iii Typical habitat of early summer range: water saturated soil surrounded by forest patches.

Appendix II: Identified behaviours and operational definitions as used in the Gaff Topsail study.

Behaviour (Code)	**Description**
Feed Head Down (FD)	The act of feeding with head lower than shoulders; head typically moves vertically during forage-gathering; biting, chewing and swallowing were easily visible with spotting scope or binoculars
Search (Se)	Head was lowered with snout directed toward the ground; typically the individual walks slowly with head swaying laterally or stands stationary moving head slowly over vegetation
Feed Head Up (FU)	Gathering or ingesting forage with head elevated at or above shoulders (e.g. stripping leaves from tall shrubs)
Walk Head Down (WD)	Walking, head held lower than shoulder, snout typically directed forward and parallel to the ground; excludes walking while feeding or apparently searching for food
Walk Head Up (WU)	Walking with head held at or above shoulders, snout typically directed forward and parallel to the ground or tilted slightly upward
Groom Self (Gr)	In a standing posture, licking, nibbling self; using hoof or antlers to scratch self
Stretch (ST)	Stretching, in a standing posture; usually an exaggerated walking motion
Urinate (UD)	One or both hind legs outstretched, pelvis tilted forward, head held above shoulders; urination stream usually visible
Groom Calf (GrC)	Licking or other grooming of calf by mother (or, rarely, by another individual); excludes grooming of calf while suckling
Nurse Head Down (ND)	Female's head below shoulders while calf to suckles; includes grooming calf while suckling
Nurse Head Up (NU)	Female's head at or above shoulders while calf to suckles
Attraction Pose (Att)	Mother head-bobbing or vocalizing toward calf while head at approximate level of calf's head
Calf Contact (CC)	Attempts by calf to find or identify mother; vocalization, approaching adult females with head held low; nursing attempts toward females showing no obvious response to calf; rubbing top of head against lower jaw of female; other physical contact between calf and female not including successful nursing/suckling or grooming as described above
Suckle (SK)	calf suckling

Aggression (AG)	Any agonistic behaviour; includes antler threats, sparring, chasing, fleeing from aggressive action, displacement, submission to displacement
Insect Avoidance (IH)	Reactions to insect harassment, including ear flicking, tail flicking, body shaking, nose dropping, head shaking, stomping or running/trotting in response to insect harassment (Mörschel and Klein 1997); **only recorded when interruptive of other behaviour**
Stand Head Up Interruptive (SUI)	Standing still with head held at or above the shoulders, snout directed parallel to the ground or slightly upward; preceded and followed by active behaviour such as foraging or walking
Stand Alert Interruptive (SAI)	Standing in alert posture, head, ears and tail held up and one hind leg outstretched; may include sniffing or urinating; preceded by active behaviour such as foraging or walking
Stand Head Down (SD)	Standing still with head held below the shoulders, snout directed downward
Stand Head Up (SU)	Standing still with head held at or above the shoulders, snout directed parallel to the ground or slightly upward
Stand Alert (SA)	Standing in alert posture, head, ears and tail held up and one hind leg outstretched; may include sniffing or urinating; preceded by other inactive behaviour
Lie Head Down (LD)	Lying on ground with head held below the shoulders, legs tucked under body; may include grooming self
Lie Flat (LF)	Lying flat on side, both head and body on ground, legs outstretched
Lie Head Up (LU)	Lying, with head raised at or above the shoulders
Head Bob (HB)	Head bob directed at source of disturbance, precipitous terrain, unknown object or unidentified stimulus
Play (PI or PE)	Interactive play or exploratory behaviour; usually by calves (as described by Lent 1966)
Others (O)	Any behaviour not listed above or not classifiable as defined above

Appendix III: Categorization of behaviour for analysis

I. Posture	**II. Activity**	**III. Behaviour Category**	**IV. Vigilance**	**V. Behaviour**
Standing Posture	Active	Foraging	non-vigilant	Feed Head Down (FD)
				Search (Se)
			vigilant	Feed Head Up (FU)
		Walking	non-vigilant	Walk Head Down (WD)
			vigilant	Walk Head Up (WU)
		Comfort	non-vigilant	Groom Self (Gr)
			unclassified*	Stretch (ST)
				Urination (UD)
		Cow-calf Interaction	non-vigilant	Groom Calf (GrC)
				Nurse Head Down (ND)
			vigilant	Nurse Head Up (NU)
			directed attention**	Attraction Pose (Att)
				Calf Contact (CC)
				Suckling (SK)
		Aggression	directed attention**	Aggression (AG)
		Insect Avoidance	non-vigilant	Insect Avoidance (IH)
		Interruptive		Stand Head Up Interruptive (SUI)

		Standing	vigilant	Stand Alert Interruptive (SAI)
	Inactive	Non-interruptive Standing	non-vigilant	Stand Head Down (SD)
			vigilant	Stand Head Up (SU)
				Stand Alert (SA)
Lying Posture	Inactive	Lying	non-vigilant	Lie Head Down (LD)
				Lie Flat (LF)
			vigilant	Lie Head Up (LU)
Unclassified Posture*	Activity unclassified*	Other	unclassified*	Head Bobbing (HB)
				Play (PI or PE)
				Others (O)

*unclassified: either not able to be classified under categorical level and/or excluded from analyses performed at that scale

**directed attention: attention directed toward a conspecific group member; excluded from analyses performed at that scale

Appendix IV: Variable Descriptions and Instructions for Coding

Instructions and Coding Information

Beaufort Force	WMO Description	Land Indicators
0	Calm	Calm; smoke rises vertically
1	Light Air	Smoke drift indicates wind direction; vanes do not move
2	Light Breeze	Wind felt on face; leaves rustle; vanes begin to move
3	Gentle Breeze	Leaves and small twigs in motion; light flags extend
4	Moderate Breeze	Leaves and loose paper raised up; flags flap; small branches move
5	Fresh Breeze	Small trees begin to sway; flags flap & ripple
6	Strong Breeze	Large branches in motion; whistling heard in wires
7	Near Gale	Whole trees in motion; resistance felt in walking against wind
8	Gale	Whole trees in motion; strong resistance felt in walking against wind
9	Strong Gale	Slight structural damage occurs; twigs break off trees; shingles blow off roofs
10	Storm	Trees broken or uprooted; considerable structural damage occurs
11	Violent Storm	Widespread damage to trees and buildings
12	Hurricane	Severe and extensive damage

Precipitation

Type refers to the kind of precipitation; rain, snow, hail, sleet, etc.

1 No detectable precipitation
2 Air is wet, misty; trace precipitation
3 Drizzle or light precipitation
4 Moderate steady fall of precipitation; puddles may form slowly
5 Heavy precipitation; puddles form quickly, snow accumulates

Temperature

Measure ambient temperature in shadow or shade; degrees Celsius

Cloud Cover

Choose from: mostly clear, partly overcast, mostly overcast, fog

Description of caribou groups:

The group are those obviously in a social aggregation, not separated from each other (usually) by more than 75 m and distinct from other groups in the area. Composition refers to the number of individuals in each age/sex class.

Avg nr neighbour (NND) is the average nearest-neighbour distance between these individuals (excluding calf-cow pair distances). Estimated by sight in meters, intervals as follows: <u><</u>5, 6-10, 11-15, 16-20, 21-30, 31-40, 41-50, 51-75, 76-100, 101-150

Avg dist cow/calf is the average distance between calves and their mothers, if the mother of a calf is not obvious, make note of this on the data sheet and estimate it's nearest-neighbour distance.

Dist to cover is the distance from the geometric center of the group to nearest obstructive cover, estimated by sight, intervals as for NND.

Insects 1-5+ (mosquitos & blackflies: count the number resting on your forearms + spotting scope; divide by two, round up to nearest integer) (tabanids: count the number resting on forearms + spotting scope; use that number) botflies & warble flies; simply note whether or not the caribou are behaving as though these are present (nose dropping, stomping)

Slope to be described is that which is occupied by the majority of the group or by geometrically central members when the group is distributed across a large area:
1 flat 2 slight incline 3 moderate incline 4 steep incline 5 vertical or near vertical incline

Exposure is the direction the slope is facing (use a compass); flat slope will have no exposure so choose 1 flat.
Shape refers to the area of slope occupied by the group (bottom/top of hill, etc.)
Topography: choose the best description of the GENERAL topography of the area

Appendix V: Data Recording Sheets

Focal Individual Behaviour Data Sheet

Caribou Behaviour Data Sheet: Instantaneous Scan

Caribou Behaviour Data Sheet: Fright Response

Focal Individual Behaviour Data Sheet
(transcription from recording)

Date (d/m/y):____________________ Initials:____________________

Description Focal Animal: M F A Y C Ear tag#: ________ Collar Freq: ________

Location: ____

Time Start: ____________________ Time End: __________________

Weather Start: **Weather End:**

Wind: 0 1 2 3 4 5 6 7 8 9 10 Dir:______ Wind: 0 1 2 3 4 5 6 7 8 9 10 Dir:______

Temp:____________ Temp: ____________

Precipitation none 1 2 3 4 5 heavy Precipitation none 1 2 3 4 5 heavy

Precipitation type:________________ Precipitation type:________________

Insects: Mosq 1 2 3 4 5 Mosq 1 2 3 4 5

B.F. 1 2 3 4 5 B.F. 1 2 3 4 5

Tab 1 2 3 4 5 Tab 1 2 3 4 5

NB/War__________________ NB/Warble____________________

Habitat Description (topo/type/dist cover, etc.)____________________________________

____

Interval	Behaviour			Interval	Behaviour		
	watch time	behaviour	comments		watch time	behaviour	comments

Interval	Behaviour			Interval	Behaviour		
	watch time	behaviour	comments		watch time	behaviour	comments

Caribou Behaviour Data Sheet: Instantaneous Scan

Date (d/m/y):______________
Initials:__________________
Time: ___________________

Sunrise:____________
Sunset :____________
Time Since Sunrise:__________

UTM
E:_________________
N:_________________

#Adults+yearlings:________

Avg nr.neighbour:________

#Calves:__________

Avg dist cow/calf:______

Dist to cover:
C:__________
Other groups nearby? Y N

Group Movement:

Direction: _____________

Slope: + 0 -

Habitat Type:
__Closed Forest
__Open Forest
__Cladonia barren
__Kalimia barren
__Bog
__Fen
__Bog/fen complex
__Marsh
__Other_________________

Elevation:______________

Insects:
Mosq. 1 2 3 4 5
Bl. F. 1 2 3 4 5
NoseB 1 2 3 4 5
Warble 1 2 3 4 5

Slope:
(flat) 1 2 3 4 5 (steep)
exposure: N NE E SE S SW W NW flat
shape: plain lower mid upper ridge
topography: flat moderate steep

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: MO PO MC Fog
Precip type:
Precip rate 1 2 3 4 5

Comments/Notes:

individuals	Foraging			Standing			Walking			Lying			Comfort			Disturbance			Play		Agression		Other
	FD	FU	Se	SD	SU*	SA	WD	WU	TR	LD	LF	LU	GR	ST	UD	IH	FL	HB	EX	IN	AG	DT**	
FA																							
MA																							
UA																							
FY																							
MY																							
UY																							
C																							
T																							

*indicate I (interruptive) or R (rest); **sex and age AG directed toward

Caribou Behaviour Data Sheet: Fright Response

Date (d/m/y):______________
Initials:____________________
Approach: H A

Time: __________________
Sunrise :________________
Time Since Sunrise:_________

UTM
E:________________
N:________________

Reference Sheets: Group Scans ________________ Focal Behaviour ___________________

Group Description

#		Proportion
_____	FA	______
	FwC	______
_____	MA	______
_____	UA	______
_____	Y	______
_____	C	______

Avg nr.neighbour:_______
Avg dist cow/calf:______

Dist to cover: C:_________
Other groups nearby? Y N

Insects:

Mosq.	1	2	3	4	5
Bl. F.	1	2	3	4	5
NoseB	1	2	3	4	5
Warble	1	2	3	4	5

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: MO PO MC Fog
Precip type:
Precip rate 1 2 3 4 5

Habitat Type:

__ Barren
__ Bog/Fen
__Open Forest
__Closed Forest
__Other_______________

Elevation:_____________

Slope:
(flat) 1 2 3 4 5 (steep)
exposure: N NE E SE S SW W NW flat
shape: plain lower mid upper ridge
topography: flat moderate steep

Comments/Notes:

Dir of Approach: N NE E SE S SW W NW

Dir of Flight: N NE E SE S SW W NW

Alert Distance ___________

Flight Distance ___________

Flight Lag ___________

Run Distance ___________

Curiousity Return Y N

First Fright: FA (C__) MA UA Y C U

First Flier: FA (C__) MA UA Y C U

Last Flier: FA (C__) MA UA Y C U

Group

Prior Vigilance: avg number vig _________ avg proportion vig _________

Group Response: move together scatter split other ______________________

Comments:

Focal Individual

Classification: FA (C__) MA UA Y C

Prior activity: ________________________ Fright-flight time lag: _______________________

Prior position: central peripheral

Flight position: central peripheral separated other _____________________

Calf: at heel separated n/a other _____________________

Comments:

Appendix VI: Feeding Intensity for adult females, males, yearlings, and calves.

Methods

Data were collected by instantaneous scan sampling (section 2.2.2). Feeding Intensity was calculated as the proportion of Foraging observations dedicated to handling and ingesting forage (Feed Head Down and Feed Head Up). A GLM ANOVA was performed using the Feeding Intensity of individuals belonging to each sex and age class within each group as the unit of analysis. Explanatory variables included in the analysis were season, sex and age class, group size, and all 2-way interactions.

Results

Feeding Intensity differed between sex and age classes (F= 8.81, d.f. = 124, p< 0.001). Calves displayed a lower Feeding Intensity than adult females or adult males. There was no difference in Feeding Intensity between calves and yearlings.

The interaction of sex and age class with season was related to Feeding Intensity (F= 7.84, d.f.= 124, p= 0.013). Calves had a higher Feeding Intensity in summer but no other sex and age class significantly changed Feeding Intensity between seasons (Figure 3.8).

Feeding Intensity was greater in larger groups (F= 4.10, d.f. =124, p= 0.017); this relationship was observed for adult males and calves but not for adult females or yearlings (interaction of sex and age class with group size: F= 4.48, d.f.= 124, p= 0.005), both of which show little or no change in Feeding Intensity in larger groups. Despite significance of the relationship between Feeding Intensity and group size for adult males, very little of the variation is explained by the regression (r^2=0.007). The relationship between Feeding Intensity and group size is stronger for calves (r^2=0.128), but is confounded with season as group size tended to be larger during summer.

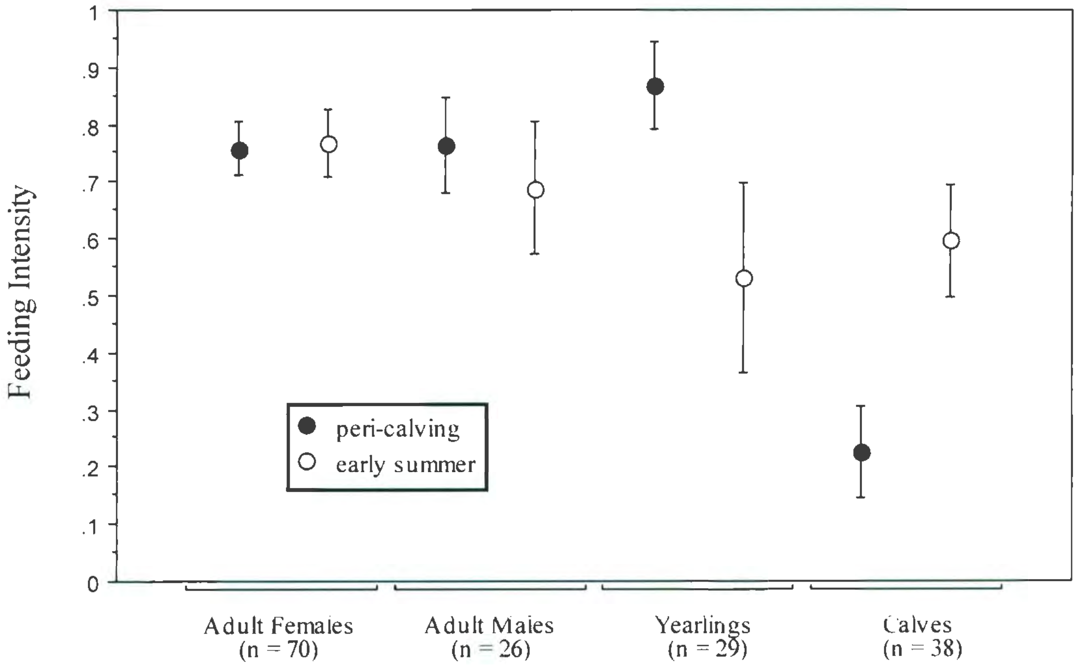

Figure VII-i Feeding Intensity as estimated from instantaneous scan sampling for adult females, adult males, yearlings, and calves during the peri-calving and early summer seasons. Females with calves could not be distinguished from those without during instantaneous scans. Feeding intensity is the proportion of foraging observations handling food. Error bars indicate one standard error of the mean.

Appendix VII: Summary of Suckling Observations Gaff Topsail Herd 2003-2004

Date (d/m/y)	Duration (seconds)	Position of Calf Relative to Female	Cessation By	Grooming	Bunting
2/6/2004	13	front	adult	no	no
2/6/2004	81	side	adult	yes	yes
7/6/2004	27	front	adult	no	yes
9/6/2004	68	back	calf	no	no
10/6/2004	8	side	calf	no	yes
12/6/2004	117	side	adult	yes	no
12/6/2004	34	front	adult	yes	no
12/6/2004	141	side	adult	yes	yes
12/6/2004	127	side	adult	no	no
12/6/2004	36	side	calf	no	yes
21/6/2004	22	side	unknown	no	no
20/6/2004	7	side	adult	no	no
21/6/2004	21	side	adult	no	yes
22/6/2004	45	side	adult	yes	yes
24/6/2004	36	side	calf	yes	no
5/7/2004	33	side	adult	yes	yes
5/7/2004	18	side	adult	no	yes
9/7/2004	42	side	adult	yes	yes
9/7/2004	44	side	adult	no	yes
14/7/2004	8	side	adult	no	yes
14/7/2004	40	side	adult	no	yes
16/7/2004	48	side	adult	no	yes
8/6/2003	52	front	calf	no	no
10/6/2003	22	side	adult	yes	no
10/6/2003	19	side	adult	no	no
22/6/2003	5	back	adult	no	no
22/6/2003	16	side	adult	no	no
24/6/2003	16	side	adult	no	yes
25/6/2003	38	unknown	adult	no	no
25/6/2003	36	side	adult	yes	no