

Vigilance and foraging behaviour of female caribou in relation to predation risk

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Abstract: Behaviour of female caribou (*Rangifer tarandus*) was investigated during the calving season on ranges in Alaska and West Greenland with the purpose of determining whether investment in vigilance behaviour differed between areas with and without natural predators of caribou. Female caribou in Alaska foraged in larger groups, displayed a higher rate of vigilance during feeding, spent less time feeding and, when lying, more often adopted a vigilant posture (with head up) than did female caribou in West Greenland. Moreover, a predation-vulnerable posture of lying down flat was observed in West Greenland but not in Alaska. Within Alaska, females with calves spent more time searching the environment than did those without calves. Finally, the amount of time individuals spent searching declined more gradually with group size in Alaska than in West Greenland, suggesting that what caribou perceive as a predator-safe threshold differs in the two areas. These results indicate that caribou, like several other species of ungulates, show behavioural adaptations to the risk of predation which are relaxed when this risk is reduced.

Key words: foraging ecology, predator-prey relationships, *Rangifer tarandus*, wolves, ungulates.

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Introduction

Predation has been a major selective force influencing the evolution of the socioecology and behaviour of ungulates (Geist, 1974; Estes, 1974; Jarman, 1974; Skogland, 1989; Nelson & Mech, 1991). Parturient female ungulates (and their accompanying offspring) are particularly vulnerable to predation (Carbyn & Trottier, 1988; FitzGibbon, 1989; Geist, 1974) and therefore display behavioural adaptations, including vigilance for predators (Clutton-Brock & Guinness, 1975), directed toward

minimizing the risk of predation during the period around parturition (Carl & Robbins, 1988). Within the time-energy budget of the individual, vigilance is considered expensive because it reduces the amount of time available for foraging and involves increased energy expenditure compared to resting (Elgar, 1989). For example, the foraging efficiency of bighorn sheep (*Ovis canadensis*) was observed to decline when they engaged in vigilance behaviour (Berger, 1978). Similarly, female pronghorn antelope (*Antilocapra americana*) accompanied by fawns

devoted less time to feeding and more time to vigilance than did nonparturient females (Lipetz & Bekoff, 1982).

Because predator-avoidance behaviour reduces both time spent foraging and foraging efficiency, its adaptive value should only be realized in situations or environments in which predation represents a threat to survival and reproduction (Carl & Robbins, 1987; Glück, 1987). It can therefore be expected that the display of such behaviours will decline or disappear when the risk of predation is reduced or removed (Abrams, 1990). This relationship has been observed in empirical studies documenting that the rate of vigilance displayed by individual herbivores declines, and the rate of foraging increases, as group size increases because of reduced risk of predation to the individual (Chadwick, 1977; Berger, 1978; Monaghan & Metcalfe, 1985; Lima, 1987; 1992).

In caribou/reindeer (*Rangifer tarandus*), the risk of predation by wolves (*Canis lupus*) has been observed to influence habitat-selection (Bergerud *et al.*, 1984; Ferguson *et al.*, 1988) and sociality (Skogland, 1989). Research on relationships between predation risk and vigilance and foraging behaviour in caribou has, however, been scant (Roby, 1980). Caribou and wolves have co-evolved for approximately 500,000 years (Mech, 1970; Leader-Williams, 1988), during which time caribou have become the primary prey of wolves where the two species co-exist (Skogland, 1989). It should be expected, then, that caribou display vigilance behaviour on ranges where they are hunted by wolves. In contrast, caribou inhabiting ranges where wolves or other predators are not present might be expected to devote less time and energy to vigilance.

The present study tested the hypothesis that female caribou exposed to predation risk would, during the calving season, display behavioural adaptations to that risk, while female caribou existing without predators would display reduced adaptations or no such adaptations. Specifically, we tested the predictions that: (1) female caribou in Alaska would devote more time to searching for predators and less time to feeding than female caribou in West Greenland; (2) as group size increased, female caribou in Alaska would show a decrease in the amount of time spent searching for predators and an increase in the amount of time spent feeding, while among West Greenland caribou the amount of time devoted to searching and feeding would not vary with group size; (3) in Alaska, female caribou with

calves would spend less time feeding, more time searching for predators, and display a higher rate of vigilance than would those with calves in West Greenland or those without calves in Alaska; (4) average size of groups of female caribou would be greater in Alaska than in West Greenland; and (5) the occurrence of single female caribou would be less common in Alaska than in West Greenland.

Methods

Study Areas and Herds

The Southern Alaska Peninsula Caribou Herd (SAPCH) occupies the tip of the Alaska Peninsula, Alaska, USA (55°45'N, 161°30'W) (Fig. 1). The SAPCH range is influenced by a strong maritime climate with frequent high winds and mild winters with little snow accumulation (Pitcher *et al.*, 1990). The area is treeless, dotted with lakes and crossed by watercourses. Vegetation communities consist of flat, saturated, sedge meadows in low-lying areas (dominated by *Carex nesophila* and *Potentilla palustris*), mesic and riparian meadows in mid-elevation zones (dominated by *C. nesophila* and *Eriophorum angustifolium*) and well-drained uplands (dominated by *Empetrum nigrum* and *Betula nana*) (Post, 1995). Topographical relief varies from sea-level flood plains to volcanoes and mountains of volcanic origin rising to 1,500 m - 2,500 m in elevation. Mean daily minimum and maximum ambient temperatures for May, June, and July are 5.8°C and 14.6°C respectively (United States Weather Service). Carnivores inhabiting the Southern Alaska Peninsula that are known predators of caribou include wolves, brown bears (*Ursus arctos*), lynx (*Lynx canadensis*), golden eagles (*Aquila chrysaetos*), wolverines (*Gulo gulo*), and coyotes (*Canis latrans*) (Post, 1995). Additionally, caribou of the SAPCH have been hunted by humans on their winter range as recently as 1992.

The Kangerlussuaq-Sisimiut Caribou Herd (KSH) ranges over that portion of West Greenland bounded on the west by Davis Strait, on the east by the Inland Ice, on the north by the Nordre Isortoq River valley, and on the south by Sukkertoppen Icecap (66-67°N, 50-52°W) (Thing, 1984) (Fig. 1). Our study focused on the calving area (Thing, 1984) located approximately 10 km south of Isortoq River and 3 km west of the Inland Ice. The KSH calving range has a continental climate with low annual precipitation and mean daily minimum and maximum ambient temperatures for May, June,

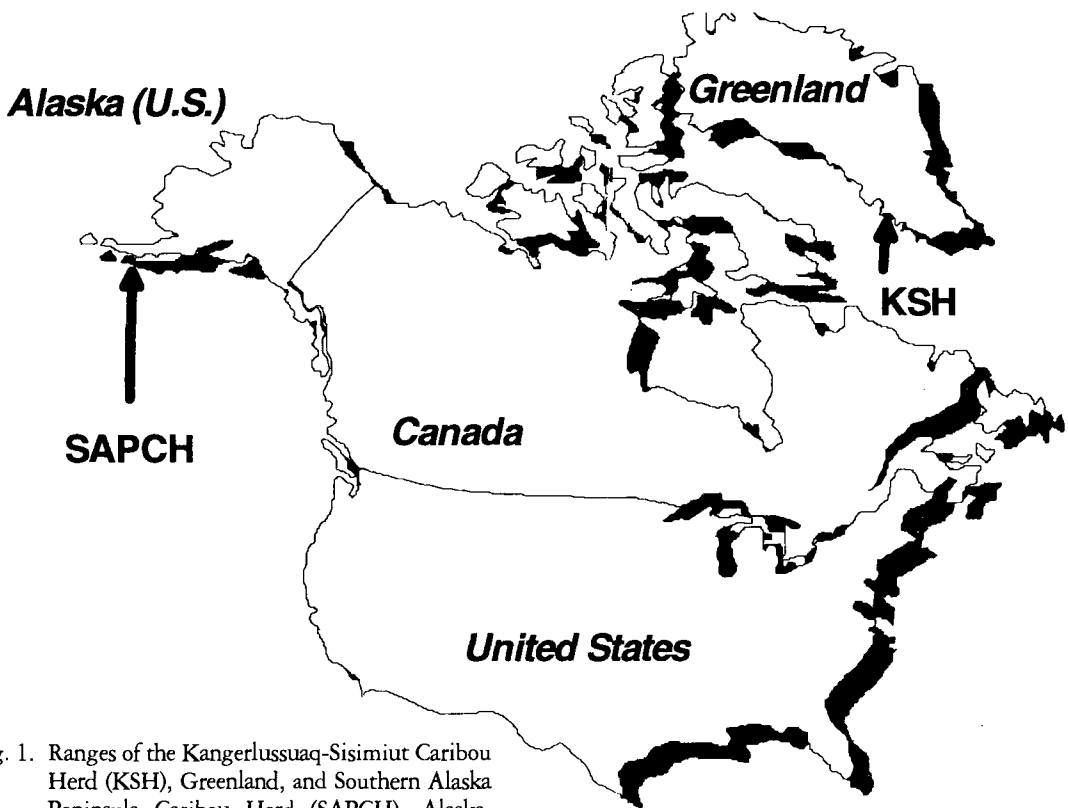


Fig. 1. Ranges of the Kangerlussuaq-Sisimiut Caribou Herd (KSH), Greenland, and Southern Alaska Peninsula Caribou Herd (SAPCH), Alaska, United States.

and July of 1.6°C and 12.5°C respectively (Danish Meteorological Institute). Winters in the area are dry with low snow cover (Thing, 1984). The study area consists of low mountain ridges running east-west with arid south-facing slopes characterized by mosaics of xerophyllic graminoids and *S. glauca* shrubs, and north-facing slopes covered by moss, *Ledum palustre*, and *B. nana* (Thing, 1984). Wolves have been absent from West Greenland for approximately 4,000 years (Dawes *et al.*, 1986; Klein *et al.*, 1987), and there are no known predators of caribou on the KSH calving range. The KSH had been hunted by humans on its winter range until 1967.

Both the SAPCH and the KSH have declined from peak densities in the early 1980s and late 1960s respectively, due to forage limitation (Strandgaard *et al.*, 1983; Thing & Thing, 1983; Meldgaard, 1986; Post, 1995). At the time the present study was undertaken, densities of the two herds were approximately 0.57 caribou/km² (SAPCH) (Post, 1995) and 0.16 caribou/km² (KSH) (Greenland Homerule Government, pers. comm.), the lowest reported values for either herd since their recent peaks.

Data Collection

Groups consisting mostly of female caribou and their calves were observed from 30 May - 13 July 1992 in Alaska and from 5 June - 20 June 1993 in West Greenland, periods including, but not limited to, the calving seasons on both ranges. Although we intended to observe exclusively the behaviour of female caribou, on occasion groups in both areas contained yearling males. Caribou groups were located by foot in both study areas and additionally by boat in Alaska. We defined a group as consisting of at least two adult or yearling caribou separated by at most 100 m. Upon locating a group, we quantified the numbers of adult and yearling females and males as well as the numbers of calves. Observations of groups were made from approximately 100 - 500 m using 2 observers equipped with binoculars (8x and 10x) and a spotting scope (30x).

Altmann's (1974) scan sampling technique was used to quantify the behaviour of all group members (excluding calves) at intervals of 15 minutes. Categories of behaviour recorded in each sampling interval included: feeding, searching, lying head-up, lying head-down, and lying flat. *Feeding* was

defined as the act of ingesting forage with the muzzle down, rather than as the act of searching for and ingesting forage (*sensu* Lipetz & Bekoff, 1982) because time spent searching for forage can vary with the distribution of forage within feeding sites (Underwood, 1982). *Searching* (Berger & Cunningham, 1988) was defined as the act of standing with head held erect and observing the environment (presumably olfactorily, audially, and/or visually), and was distinct from standing associated with harassment by parasitic flies (Oestridae) (*cf.* Downes *et al.*, 1986). Searching was considered to be a form of vigilance for predators because it allows an individual to scan the environment for predators as well as to observe conspecifics for signals indicating the presence of predators (Berger, 1978; Underwood, 1982; Monaghan & Metcalfe, 1985). *Lying head-up* was defined as lying down with head raised above the level of the shoulders, a position from which an individual can observe its surroundings while ruminating and/or resting, particularly in low-growth vegetation characteristic of Arctic and sub-Arctic caribou ranges. We have drawn distinctions between lying head-up, lying head-down, and lying flat because although the primary function of lying in caribou is probably for resting and ruminating (Roby & Thing, 1985), we believe that the position in which caribou lie either allows them to be vigilant for predators or leaves them vulnerable to predation. Thus, lying head-up was considered a vigilant form of lying. *Lying head-down* was defined as lying with the mandible resting on the ground and was considered a predation-vulnerable posture because caribou in this position are presumably less able to detect predators. *Lying flat* was defined as lying on the side with legs stretched out and head resting flat on one side on the ground. Lying flat was considered a predation-vulnerable posture. Scans of groups of caribou were conducted for as long as it appeared that none of the animals were aware of our presence.

Whenever possible, a focal animal was selected from the group under observation. Focal animals were distinguishable females, either with or without a calf, and were observed continuously. Behaviour of focal animals was quantified according to the same categories of behaviour used in scans of groups, plus an additional category termed «vigilance». *Vigilance* was defined as the act of interrupting a feeding bout to lift the head above the shoulders and briefly observe the surroundings before returning to feeding. Vigilance was considered an

anti-predator behaviour according to the same rationale used to define searching.

Analyses

Data were analyzed to test for differences in the proportions of time spent feeding, searching, lying head-up, lying head-down, and lying flat between: (1) females observed in group scans in Alaska and West Greenland, using the Mann-Whitney *U*-test (Siegel & Castellan, 1988); (2) females with calves observed as focal animals in Alaska and West Greenland, using the Chi-square test (Zar, 1984) or the *G*-test of independence (Sokal & Rohlf, 1995); and (3) females with and without calves observed as focal animals in Alaska, using the Chi-square test or the *G*-test of independence. Furthermore, to determine whether the proportion of time spent searching declined, and whether the proportion of time feeding increased, with increasing group size in Alaska and West Greenland, we used non-linear regression analysis (SYSTAT, Inc., 1992) between these two variables and group size on each range using data from group scans. To determine whether the relationship between group size and time spent searching differed between Alaska and West Greenland, we used the *t*-test of regression coefficients (Zar, 1984). We tested for relationships between group size and frequency of vigilance by females with calves from focal animal observations in Alaska and West Greenland, using linear regression (SYSTAT, Inc., 1992). We tested for differences in the frequency of vigilance by: (1) females with calves (focal animals) in Alaska and West Greenland, and (2) females with and without calves (focal animals) in Alaska using the *Z*-test for Poisson counts (Zar, 1984). Finally, we tested for differences in sizes of foraging groups in Alaska and West Greenland, using the *t*-test (Zar, 1984); and differences in frequency of occurrence of single animals in Alaska and West Greenland, using the *G*-test of log-likelihood ratios (Zar, 1984).

The proportion of the total activity budget devoted to each behaviour was derived from group scan data by dividing the number of animals engaged in each behaviour during a scan by the total number of animals observed in the scan. These proportions were averaged over the total number of scans within groups for comparisons. The proportion of time spent in each behaviour by focal animals was calculated as the number of minutes devoted to each behaviour divided by the total number of minutes of observation. These proportions were averaged

Table 1. Activity budgets of caribou of the Southern Alaska Peninsula, Alaska, USA, and Kangerlussuaq-Sisimiut, West Greenland, herds based on scans of groups during the calving seasons in 1992 and 1993 respectively. The proportion of time devoted to each activity is given as the mean proportions (± 1 SD) of the total number of caribou engaged in each activity in each scan averaged over the total number (n) of scans.

RANGE	YEAR	n	FEEDING	SEARCHING	LYING HEAD-UP	LYING HEAD-DOWN	LYING FLAT
Alaska	1992	154	0.53 \pm 0.2	0.02 \pm 0.01	0.37 \pm 0.1	0.01 \pm 0.001	0
West Greenland	1993	132	0.59 \pm 0.1	0.07 \pm 0.04	0.21 \pm 0.1	0.01 \pm 0.001	0.01 \pm 0.001

Note: proportions do not sum to unity because of time devoted to other behaviours (e.g. walking) which were not included in analysis.

Table 2. Activity budgets of female caribou (with and without calves) of the Southern Alaska Peninsula, Alaska, USA, and Kangerlussuaq-Sisimiut, West Greenland, herds based on observations of focal animals during calving seasons in 1992 and 1993 respectively. The proportion of time devoted to each activity is given as the mean (± 1 SD) of the total number of minutes devoted to each activity averaged over total number (n) of caribou observed.

RANGE	n	MINUTES OF OBSERVATION	FEEDING	SEARCHING	LYING HEAD-UP
Alaska					
with calf	4	1047	0.48 \pm 0.2	0.02 \pm 0.01	0.48 \pm 0.2
no calf	2	342	0.38 \pm 0.2	0.004 \pm 0.001	0.59 \pm 0.1
West Greenland					
with calf	3	426	0.77 \pm 0.2	0.04 \pm 0.03	0.17 \pm 0.2

Note: proportions do not sum to unity because of time devoted to other behaviours (e.g. walking) which were not included in analysis.

over the total number of animals in each class of focal animal (Alaska or West Greenland, with or without calf). For the non-linear regression analyses of proportions of time spent searching and feeding as functions of group size, we used data from group scan observations that were averaged for each group, because data from each scan are not independent and therefore not appropriate for regression analysis (Neter *et al.*, 1990). Proportions used in regression analyses were normalized with the arcsine transformation (Sokal & Rohlf, 1995). Frequency of vigilance was calculated as the number of vigilance bouts per hour of observation per focal animal, and comparisons of frequencies of vigilance were based on mean rates averaged over the total number of focal animals in each class.

Results

Female caribou in Alaska spent significantly less time feeding than did female caribou in West Greenland ($P=0.04$) (Table 1). The amount of time

female caribou spent searching did not, however, differ between Alaska and West Greenland ($P=0.09$). In Alaska, lying head-up was observed more often ($P<0.001$) and lying flat less often ($\chi^2=4.4$, $P<0.05$) than in West Greenland. Indeed, caribou in Alaska were never observed to lie flat. The amount of time devoted to lying head-down did not differ between Alaska and West Greenland ($P>0.05$).

Female caribou accompanied by a calf allocated less time to feeding in Alaska than in West Greenland ($\chi^2=75.5$, $P<0.001$) (Table 2). Time spent searching by females with calves did not differ between Alaska and West Greenland ($G=2$, $P>0.05$). Females with calves were observed to lie head-up more often in Alaska than in West Greenland ($\chi^2=3.9$, $P>0.05$).

In Alaska, time spent feeding did not differ between female caribou with and without calves ($\chi^2=2.64$, $P>0.10$) (Table 2). The presence of a calf was, however, associated with more time spent searching by female caribou in Alaska ($\chi^2=6.79$,

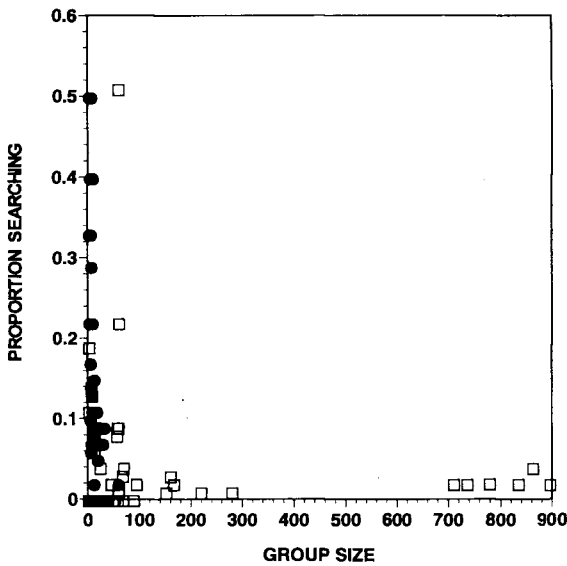


Fig. 2. Relationships between caribou group size and proportion of the group searching in the Southern Alaska Peninsula Caribou Herd, Alaska, USA, 1992 (open squares), and Kangerlussuaq-Sisimiut Caribou Herd, West Greenland, 1993 (solid circles).

$P < 0.05$). In contrast, females without calves spent more time lying head-up than those with calves ($\chi^2 = 4.45$, $P < 0.05$).

The proportion of the total activity budget devoted to searching by female caribou decreased exponentially with increasing group size in both Alaska ($Y = 0.2e^{(-0.001X)}$, $R^2 = 0.33$, $P < 0.001$) and West Greenland ($Y = 0.36e^{(-0.014X)}$, $R^2 = 0.23$, $P < 0.001$) (Fig. 2). A t -test comparing the coefficients of both functions indicated that the curve fitting the Alaska data declined more gradually than that fitting the data from West Greenland ($t = 3.87$, $P < 0.0005$, $df = 165$). To confirm that this difference was not due solely to the fact that group sizes in Alaska covered a much greater range of values than did those in West Greenland, we re-analyzed the data, restricting our analysis to group sizes less than 100 animals for both ranges. Over this range of values, the curve fitting the Alaska data still declined more gradually than did the curve for the West Greenland data ($t = 6.08$, $P < 0.0005$, $df = 153$). Finally, the amount of time allocated to feeding was independent of group size in both Alaska ($R^2 = 0.007$, $P = 0.5$) and West Greenland ($P^2 = 0.013$, $P = 0.26$).

The frequency of vigilance displayed by female caribou with calves was independent of group size in both Alaska ($P = 0.25$, $df = 2$) and West Greenland ($P = 0.18$, $df = 1$). The mean rate of vigilance display-

ed by females with calves was, however, greater in Alaska (7.8 bouts/hr) than in West Greenland (1.2 bouts/hr) ($Z = 2.2$, $P < 0.05$). There was no significant difference between rates of vigilance by females with calves (7.8 bouts/hr) and without calves (6.6 bouts/hr) in Alaska ($Z = 0.32$, $P > 0.05$).

The mean size of groups in which female caribou foraged was larger in Alaska (83.5 ± 13 SD) than in West Greenland (8.4 ± 3.0 SD) ($t = 23$, $P < 0.0005$, $df = 10.7$). Single animals did not, however, occur more frequently in West Greenland than in Alaska ($\chi^2 = 0.02$, $P > 0.05$, $df = 1$).

Discussion

Previous studies of the behaviour of ungulates have documented that the risk of predation influences the allocation of activity budgets of ungulates among the categories of feeding, standing, and lying (or resting) (Roby, 1980; Lipetz & Bekoff, 1982). Our data indicate that predation risk also influences the level of vigilance displayed by caribou while feeding, standing, and lying. Thus, female caribou in Alaska were more vigilant while foraging and *while* lying than were their conspecifics in West Greenland (Tables 1 and 2). Furthermore, female caribou under the risk of predation avoided a predation-vulnerable posture (lying flat) that was displayed by caribou foraging where predators were absent (Table 1).

That caribou in West Greenland displayed vigilance approximately six times less often per hour of foraging than did caribou in Alaska suggests that vigilance has a cost and is reduced when the risk of predation is reduced or removed (*sensu* Treisman, 1975; Berger, 1978). Previous assertions that vigilance is engaged in at the expense of feeding and resting (Chadwick, 1977; Berger, 1978; Glöck, 1987; Elgar, 1989; Desportes et al., 1991; McNamara & Houston, 1992; Caro *et al.*, 1995), are supported by our observations that caribou in Alaska spent less time feeding than those in West Greenland (Table 1) and that, in Alaska, female caribou with calves devoted less time to lying than those without calves (Table 2). It is important to note, however, that the intensity with which ruminants feed and the amount of time they spend lying are also influenced by quality of forage, insect harassment, and physical condition of the animals (Roby, 1980; Roby & Thing, 1985; Langer, 1987; Post & Klein, 1996). Even so, while lying, caribou in Alaska were more likely to adopt a vigilant post-

ure (head-up) than were those in West Greenland (Table 1).

The prediction that female caribou free from the risk of predation would abandon completely their investment in vigilance behaviour was not supported by our observations. That caribou in West Greenland displayed vigilance indicates that behavioural adaptations persist long after the environmental stimulus to which they are directed is removed (Krumbiegel, 1954; Geist, 1974). Similarly, that caribou spent equal amounts of time searching in Alaska and West Greenland (Table 1), and that there was an effect of group size on searching time in both Alaska and West Greenland (Fig. 2) may be attributed to the fact that caribou in West Greenland have been hunted until recently (cf. Berger *et al.*, 1983, for influence of hunting on vigilance in pronghorn antelope). Roby & Thing (1985) observed that caribou in the KSH allocated more of the activity budget to standing when in areas where they were hunted than they did when in areas where they were not hunted. Other studies, however, have noted that the amount of time spent searching by ungulates does not decrease when the threat of predation is removed (Berger & Cunningham, 1988), and that, compared to the cost of being attacked by a predator, vigilance is relatively inexpensive and may be worth investing in even when predators are absent (Underwood, 1982). Alternatively, searching may also be important as a means of locating forage either directly or by observing the movements of conspecifics (Berger, 1978; Underwood, 1982).

Our comparisons of the behaviour of female caribou with and without calves in Alaska as well as of females with calves in Alaska and West Greenland indicate that investment in vigilance behaviour by caribou varies with parturition status and perceived level of risk. For example, the presence of a calf was associated with more time spent searching by female caribou under the risk of predation (Table 2). Furthermore, parturient female caribou were more vigilant where predators were present than they were where predators were absent (Table 2). Such relationships have also been observed with female red deer (*Cervus elaphus*) (Clutton-Brock & Guinness, 1975), mountain goats (*Oreamnos americanus*) (Chadwick, 1977), pronghorn antelope (Lipetz & Beckoff, 1982), and bighorn sheep (Berger, 1978). In contrast to the above observations, however, rates of vigilance did not differ between parturient and nonparturient females in Alaska (Table 2). We sug-

gest that this is due to small sample size, but it is worth noting that female white-tailed deer (*Odocoileus virginianus*) were observed to display a consistent level of anti-predator behaviour regardless of whether or not they were accompanied by fawns (Caro *et al.*, 1995).

Contrary to our predictions, the presence or absence of predation risk did not influence whether time spent searching by female caribou would decrease with group size, as searching time was inversely related to group size in both Alaska and West Greenland (Fig. 2). Caribou in West Greenland were vigilant and, like those in Alaska, apparently perceived less risk in larger groups despite the lack of natural predators in the area. Because searching time decreased more gradually with group size in Alaska than in West Greenland, however, we suggest that the «predator-safe threshold» (Skogland, 1989) is higher in Alaska than in West Greenland. Support for this suggestion is lent by our observation that mean group size was greater in Alaska than in West Greenland. It must be noted, however, that although there is ample evidence that predation risk influences group size in ungulates (Estes, 1974; Jarman, 1974; Heard, 1992), habitat structure and forage distribution certainly do as well (Jarman, 1974; Focardi & Paveri-Fontana, 1992; Post & Klein, 1996).

Finally, that neither time spent foraging nor frequency of vigilance was related to group size in caribou sets this species apart from other ungulates for which these relationships have been documented, such as pronghorn antelope (Lipetz & Beckoff, 1982), bighorn sheep (Berger, 1978), and mountain goats (Chadwick, 1977). For caribou, distribution and quality of forage influence both group size (Post & Klein, 1996) and time spent foraging (Roby, 1980; Roby & Thing, 1985); the combined influences of these environmental variables may override the influence of sociality on feeding time. Similarly, variation in forage density has a confounding influence on the relationship between vigilance and group size in other species of herbivores (Clutton-Brock & Guinness, 1975; Elgar, 1989). It is apparent, therefore, that while risk of predation affects foraging behaviour of female caribou, its influence acts in combination with environmental variables.

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