Caribou reactions to provocation by snowmachines in Newfoundland

Mahoney, S. P.¹, K. Mawhinney², C. McCarthy³, Doug Anions³ & S. Taylor³

¹ Government of Newfoundland and Labrador, Inland Fish and Wildlife Division, P.O. Box 8700, St. John's, NF A1B 4J6, Canada (shanemahoney@mail.gov.nf.ca).

² Parks Canada, 1869 Upper Water Street, Halifax, NS B3J 189, Canada.

³ Gros Morne National Park, P.O. Box 130, Rocky Harbour, NF A1B 4J6, Canada.

Abstract: Caribou in Gros Morne National Park reacted to provocation by snowmachine with significant differences in their response between years. Upon exposure to snowmachines, caribou were displaced 60 to 237 m from their initial locations. Groups with calves allowed the snowmachines to approach more closely before responding (5 to 600 m) than adult-only groups (30 to 1300 m), and their overall flight distances were less. Time spent in locomotion and overall reaction time were greater for animals engaged in the most sedentary activities (eg. standing; $\bar{x} = 239$ s and $\bar{x} = 262$ s, and lying; $\bar{x} = 166$ s and $\bar{x} = 273$ s) than for animals already engaged in more dynamic activities such as walking ($\bar{x} = 118$ s and $\bar{x} = 133$ s), running ($\bar{x} = 74$ s and $\bar{x} = 63$ s) and feeding ($\bar{x} = 118$ s and $\bar{x} = 133$ s). Annual differences in the response of adult-only groups were not due to differences in the sex ratio of these groups, but may be related to annual variation in winter weather conditions.

Key words: behaviour, disturbance, Rangifer tarandus, snowmachine, weather conditions.

Rangifer, 21 (1): 35-43

Introduction

Since their introduction in 1959, snowmachines have become popular recreational and work vehicles, with over 2.3 million in use, and the focus of a multi-billion dollar industry in North America (Felcher & Liberman, 2000). More than any other technology, these vehicles have enabled increasing numbers of people to access formerly remote areas in winter, and their combination of high speed, rapid manouverability and loud noise makes them a conspicuous and potentially alarming stimulus. This increased human access, and the high potential for inadvertant disturbance or deliberate harassment of winter stressed animals, has led to concern over the effects snowmachines might have on wildlife. While the recreational use of snowmachines is largely prohibited within the Canadian National Park system (Deichmann, 1990), the 1973 Federal/Provincial agreement establishing Gros Morne National Park included a provision for the use of snowmachines by Newfoundland residents living in the park. Snowmachine use has increased considerably since then (Deichmann, 1990), and its effect on wildlife, especially caribou (*Rangifer tarandus terranovae*), has been raised as a concern, both within the National Park and throughout Newfoundland in general, where more than fifty thousand snowmachines are currrently in use.

While considerable information exists regarding white-tailed deer (*Odocoileus virgineanus*) and mule deer (O. hemionus) response to snowmachine activity (Moen, 1978; Richens & Lavigne, 1978; Freddy et al, 1986), little is available for caribou. Although Simpson (1988) reported that caribou avoided areas where large numbers of snowmachines operated in British Columbia, Tyler's (1991) work on reactions of the highly specialised Svalbard reindeer (R. t. platyrbyncbus) remains the only experimental study involving Rangifer yet published. Furthermore, while the specific effects of snowmachine activity on caribou populations are poorly known, the significance of human disturbance generally on caribou also remains much debated and in need of clarification (Klein, 1980; Bergerud et al., 1984; Tyler, 1991). It might be that exposure to snowmachine noise and pursuit could result in changes in caribou movement rates and behaviour, and to changes in habitat use and distribution (Cameron & Whitten, 1979; Dorrace et al., 1975; Klein, 1980; Curatolo & Murphy, 1986; Murphy & Curatolo, 1987; Cameron et al., 1992). Depending upon the magnitude of such responses, animal condition might be negatively affected, which in turn could lead to changes in herd productivity and survival (Klein, 1999). We report here on the behavioural responses of woodland caribou (R. t. terranovae) to snowmachines during controlled disturbance trials in Gros Morne National Park, Newfoundland.

Study area

Gros Morne National Park lies on the western flank of the Great Northern Peninsula of Newfoundland. It is a complex 1805 km² landscape dominated by two contrasting land forms; the broad coastal lowlands on the seaward side and the Long Range Mountains which run northsouth through the region's interior and rise to a maximum elevation of 800 m (Fig. 1). Productive coniferous forest comprised primarily of balsam fir (Abies balsamea), black spruce (Picea mariana) and white spruce (Picea glauca), and small stands of white birch (Betula papyrifera) and trembling aspen (Populous tremuloides), is restricted to lower elevations including mountain slopes. Upland vegetation is dominated by forested heath and shrub barrens. Deep fjord lakes, serpentine barrens and numerous small ponds and rivers add to the region's ecological diversity, which is characterized by a high endemism of

36

arctic plants and animals, the latter including arctic hare (*Lepus arcticus*) and rock ptarmigan (*Lagopus mutus*). Winters in the region are long and snow cover is usually continuous from December through April. Snow depths range from 2.5-3 m on the coastal lowlands to 11 m on the mountain plateau. The caribou population is currently estimated at 2700 animals (Mawhinney *et al.*, 1998).

Methods

Caribou reaction to snowmachine disturbance was assessed by the method of Tyler (1991). Two observers searched for animals using two snowmachines between November and April, 1994-1997. Groups were defined as having no two individuals >30 m apart and forming an apparently discrete social unit. When a caribou group was first observed, both snowmachines were stopped and the following information recorded using 7 x 40 m binoculars and/or 15 - 60x spotting scopes: (i) number, age (adult, calf), and sex of animals; (ii) principal activity of the group (> 50%; feeding, standing, lying, walking); (iii) time of day and date; (iv) location; (v) weather conditions (wind speed, wind direction, temperature and cloud cover); (iv) terrain features (flat, hilly); and (v) tree cover (open, broken).

Groups were provoked by driving one snowmachine slowly (20 km/h) until it reached the spot where the animals had been when first observed. Each approach was characterized as direct (straight at the group) or oblique (45° angle to group). Caribou were watched continuously during the approach and a stick was dropped to mark the position on the first occasion that any member of a group showed any visible reaction to the snowmachine. A second stick was dropped on the first occasion that any member of the group showed signs of unease or alarm. A third stick was dropped when the group fled. The 'attacker' drove from the third stick to where the animals had been and from there to where they first settled. He then drove back to the starting point and measured four distances (in m) with a tape or snowmachine odometer: (i) distance at minimum reaction: distance between a group of caribou and the 'attacker' at the first occasion that any member of the group reacted visibly to his presence; (ii) disturbance distance: distance between a group of caribou and 'attack-



Fig. 1. Boundaries of Gros Morne National Park on the Great Northern Peninsula, Newfoundland.

er' at the first occasion any member of the group showed any sign of unease or alarm; (iii) distance at initial flight: distance between a group of caribou and the 'attacker' at the instant the animals first fled; and (iv) net distance of flight: distance from the 'attacker' at the start of provocation to distance where the animals settled. The observer watched each group continuously during the trial to corroborate the marking of each distance, and recorded (in s) each phase of the animals' flight with a stopwatch , including (v) total running time, (vi) total locomotion (running

Rangifer, 21 (1), 2001

and walking) time, and (vii) maximum duration of disturbance (time from the instant a group bolted until all members of the group had subsequently settled).

These seven measured responses were compared with respect to group sex and age composition, group majority activity at time of approach (feeding *vs.* lying, etc), terrain (open *vs.* broken) and the animals' view of the 'attack' approach (direct *vs.* oblique) using a multivariate analysis of variance (MANOVA). Two types of groups were recognized in the analysis: adult-only groups and groups with calves. Skew was tested using the *t* statistic (Sokal & Rohlf, 1969). Time or distance parameters were compared between years and groups using two-way analysis of variance (ANOVA) (Segal, 1956).

Results

One hundred and sixty-two caribou groups were tested between March 3 - April 26, 1994 (n = 51), January 17 - April 18, 1995 (n = 50), December 16, 1995 - April 16, 1996 (n = 13) and February 28 - May 7, 1997 (n = 48) (Table 1). Overall mean group size was 7 (range 1 - 51) and included 114 adult-only and 46 groups with calves. Group median response values were as follows: distance at minimum reaction, 205 m; disturbance distance, 172 m; distance at initial flight, 100 m; net distance of flight, 65 m; total running time, 11 s; total locomotion time, 52 s; and maximum duration of disturbance, 70 s.

Group responses did not vary with snowma-

chine approach angle and there were no measurable effects of terrain or forest cover on animal response (P>0.05 in all cases). There were, however, significant differences in all measured group responses between years (P<0.05, Table 2). Groups tested in 1995 showed minimum reaction scores for all but two variables, distance at initial flight and total running time, which were both marginally lower in 1997; while those tested in 1994 showed maximum scores for all but one, maximum duration of disturbance, which was marginally higher in 1997. In general, caribou groups in 1994 reacted earlier to snowmachines and moved greater distances, while in 1995 animals allowed machines a closer approach and moved shorter distances when disturbed. Group responses in 1996 and 1997 were intermediate and generally similar to one another (Table 1). The range of between year differences in response was substantial. Total locomotion times and maximum duration of disturbance, for example, varied by six and four times respectively between their minimum and maximum values.

While all measured responses differed between years, only disturbance distance and distance at initial flight (P=0.006 and P=0.007) also varied with group composition (Table 2). These differences were not related to the adult sex ratio of the groups (i.e. male *vs.* female biased groups, P>0.05 in all cases), but rather depended on the presence/absence of calves. In all years groups with calves allowed snowmachines to approach closer before responding than did adult-only groups and their maximum

Table 1.	Measured mean responses	(standard deviation	in parentheses)	by caribou	in Gros	Morne	National P	'ark to
	provocation by snowmach	ines, 1994-1997 (san	ple size in paren	theses after	year).			

			Year		
-	1994 (51)	1995 (50)	1996 (13)	1997 (48)	1994-1997 (162)
Mean group size	5	7	13	7	7
Female:male in adult only groups	1:0.1	1:0.5	1:2	1:1	1:1
Response					
Minimum reaction distance (m)	386 (314)	210 (176)	268 (152)	248 (187)	282 (240)
Disturbance distance (m)	313 (253)	170 (138)	231 (160)	184 (155)	225 (197)
Distance at initial flight (m)	225 (223)	135 (133)	203 (159)	129 (164)	167 (180)
Net distance of flight (m)	237 (272)	60 (141)	93 (67)	210 (406)	161 (288)
Total running time (s)	83 (213)	23 (63)	22 (16)	19 (26)	39 (124)
Total locomotion time (s)	216 (249)	39 (176)	130 (119)	124 (158)	127 (205)
Maximum duration of disturbance (s)	215 (260)	55 (193)	159 (137)	219 (287)	160 (248)

Table 2.	Results of 2-way ANOVA's evaluating the responses of adult only groups of
	caribou and groups with calves to provocation by snowmachines in Gros
	Morne National Park, 1994-1997.

Source of Variation	Independent Variable	F	P^{i}
Minimum reaction distance (m)	Group composition	2.292	0.132
	Year	5.255	0.002
Disturbance distance (m)	Group composition	7.855	0.006
	Year	6.594	0.001
Distance at initial flight (m)	Group composition	7.455	0.007
	Year	4.549	0.004
Net distance of flight (m)	Group composition	0.234	0.629
-	Year	4.179	0.007
Total running time (s)	Group composition	0.171	0.68
	Year	2.658	0.051
Total locomotion time (s)	Group composition	1.136	0.288
	Year	6.622	0.001
Maximum duration of disturbance	(s) Group composition	1.19	0.277
	Year	4.73	0.004

disturbance times were less. Furthermore, in all but one year in each case, net flight distances, total running times and total locomotion times were less for groups with calves (Table 3). Furthermore, despite significant annual variations, adult-only and groups with calves showed

consistent relative patterns of response between years (Fig. 2). The only responses that varied significantly with caribou behaviour prior to snowmachine provocation were maximum duration of disturbance and total locomotion times (Table 4). Minimum reaction distance (F=2.2, P=0.08), disturbance distance (F=2.2, P=0.08), distance at initial flight (F=1.9, P=0.1), net distance of flight (F=0.8, P=0.5) and total running time (F=0.9, P=0.4) did not.

Time spent in locomotion and overall disturbance times were greater for animals engaged in sedentary activities (eg. standing; \bar{x} =239 s and \bar{x} =262 s, and lying; \bar{x} =166 s and \bar{x} =273 s) than for those engaged in dynamic activities (e.g. walking \bar{x} =118 s and \bar{x} =133 s, running \bar{x} =4 s and \bar{x} =63 s and feeding \bar{x} =118 s



Discussion Although the implica-

and \bar{x} =133 s).

tions of caribou reactions to human disturbance have been much debated (Klein, 1980; Bergerud et al., 1984), there is general agreement that the most significant potential effects relate to range loss and increased energy expenditure. In principle, caribou avoidance of snowmachines could reduce available winter range and depress reproduction and survival through harassment of pregnant fe-

Fig. 2.

Rangifer, 21 (1), 2001

Table 3.	Summary of measur	red mean respo	nses (st	andard deviation	in parentheses) by	caribou in Gros I	Morne National Par	k to provocatic	on by snowmac	hines, 1994-1997.
Year	Group Composition	Group Size (Range)	u	Minimum reaction distance (m)	Disturbance distance (m)	Distance at initial flight (m)	Net distance of flight (m)	Total running time (s)	Total locomotion time (s)	Maximum duration of disturbance (s)
1994	Adult only Adult + calves	5 (1-25) 6 (2-27)	32 16	382 (328) 357 (259)	337 (283) 233 (113)	259 (254) 160 (125)	213 (272) 293 (281)	88 (248) 77 (103)	235 (283) 175 (172)	228 (298) 189 (174)
1995	Adult only Adult + calves	8 (1-32) 3 (1-5)	6 3 5	229 (176) 41 (25)	185 (138) 41 (25)	147 (137) 43 (33)	64 (150) 28 (39)	26 (67) 5 (0)	43 (189) 13 (18)	61 (207) 13 (18)
1996	Adult only Adult + calves	2 (1-4) 18 (3-51)	4 0	339 (105) 236 (134)	317 (130) 193 (163)	262 (135) 177 (169)	141 (86) 72 (48)	16(9) 25(18)	236 (151) 83 (67)	228 (205) 129 (95)
1997	Adult only Adult + calves	6 (1-50) 10 (3-32)	32 15	261 (218) 220 (103)	202 (182) 144 (82)	150 (190) 82 (81)	253 (495) 126 (105)	22 (32) 13 (7)	120 (104) 132 (232)	239 (278) 187 (309)
Overall	Adult only Adult + calves	6 (1-50) 10 (1-51)	114 45	288 (247) 252 (201)	240 (212) 174 (123)	186 (198) 123 (122)	161 (316) 116 (203)	42 (143) 42 (143)	129 (220) 129 (220)	163 (266) 163 (266)
	AMULT CALVES			(107) 7(7	1/1 /1/2/	C71		((07) 011 (771		(077) (71 ((LT) 71 ((07) 011 (771

males and/or through effects on energy assimilation mediated by losses in grazing and resting periods, altered habitat selection and increases in energy consuming activities such as running and standing (Klein, 1971; Shank, 1979; Skogland & Grovan, 1988). All such effects would be contingent on induced changes to normal schedules of behaviour.

Simpson (1988) reported that caribou in British Columbia did avoid otherwise attractive areas when snowmachine activity was extensive and indicated that human scent and large numbers of machines operating in the area were the most important stimuli. He did not, however, experimentally test caribou responses. Meanwhile, Tyler (1991) reported the behavioural responses of 101 groups of Svalbard reindeer provoked by snowmachines and concluded, given their level of response and the low frequency of disturbance, that snowmachines would not cause substantial increases in energy expenditure or losses of grazing time for animals there.

When median reaction scores for the Svalbard and present studies are compared, Gros Morne National Park caribou reacted more slowly to snowmachines (had shorter reaction and disturbance distances: 640 m vs. 205 m; 410 m vs. 172 m) and showed less reaction overall (had lower flight distances, 160 m vs. 65 m; lower total running time, 22 s vs. 11s; and lower maximum duration of disturbance, 193 s vs. 70 s). While these differences may derive generally from subspecific behavioural variation, they may also be a reflection of each population's disturbance experience. Thus while Svalbard animals are «notable for their docile, sedentary behaviour», they were nevertheless more responsive to snowmachines than Gros Morne caribou. This is surprising given that Svalbard animals have no history of large mammal predation, and have experienced little hunting (Tyler, 1991). Gros Morne caribou on the other hand have experienced wolf (Canis lupus) predation in the past, and are currently preved upon by black bears (Ursus americanus), lynx (Lynx canadensis) and coyotes (Canis latrans); they are also exposed to legal hunting when outside the park and to some illegal hunting within it (Mawhinney et al., 1998). Dorrance et al. (1975) had demonstrated that white-tailed deer responses to snowmachine activity were more pronounced in a hunted than in an unhunted population, suggesting such populations were more sensitized to disturbance generally. These factors suggest that Gros Morne animals should be more, not less, reactive than Svalbard animals.

The differences in response by Svalbard and Gros Morne animals may arise because Gros Morne caribou

Table 4.	Mean measured responses (standard deviations in parentheses) by caribou involved in different beh	naviors
	prior to provocation by snowmachines in Gros Morne National Park, 1994-1997.	

Activity	п	Minimum reaction distance (m)	Disturbance distance (m)	Distance at initial flight (m)	Net distance of flight (m)	Total running time (s)	Total locomotion time (s)	Maximum duration of disturbance (s)
Standing	34	350 (326)	284 (280)	192 (233)	116 (143)	68 (229)	239 (289)	262 (330)
Lying	12	237 (121)	162 (86)	67 (43)	106 (73)	9 (5)	166 (331)	273 (375)
Walking	34	305 (273)	233 (194)	185 (189)	202 (437)	43 (72)	118 (173)	133 (189)
Running	21	215 (208)	215 (208)	213 (210)	146 (246)	47 (98)	74 (122)	63 (121)
Feeding	15	252 (155)	192 (126)	135 (123)	193 (280)	18 (20)	64 (67)	126 (187)
MANOVA								
F		1.6	1.5	2.1	0.7	0.9	3.9	3
		0.19	0.21	0.1	0.63	0.94	0.006	0.022

are more frequently exposed to snowmachine activity, and with greater habituation are waiting longer before engaging in energetically expensive avoidance reactions (Mahoney et al., in prep.). In Svalbard, the frequency of non-experimental snowmachine disturbance was apparently quite low, due to the fact that in winter animals there primarily inhabit mountain sides and high plateaus while snowmachine routes follow river valleys (Tyler, 1991). In Gros Morne National Park on the other hand, the frequency of snowmachine encounter can be high, particularly in the lower elevations where caribou winter distribution is coincident with areas of high snowmachine travel and where all of our observations were made (Mahoney et al., in prep.).

Significantly, the Svalbard study did report some extreme but localised examples of reindeer habituation to snowmachines and other vehicular traffic there, and also recorded lower levels of response to snowmachine provocation across all measured variables for reindeer in areas of higher snowmachine use. A generally lower habituation level of animals there, however, may explain why Svalbard reindeer that were lying down when provoked by snowmachines had the greatest distances at initial flight (Tyler, 1991), whereas the opposite was true for Newfoundland caribou, and why in our study terrain and angle of approach had no effect on animal response. Greater habituation by Newfoundland animals is also suggested by their shorter disturbance duration and running times.

In contrast to reports that caribou groups containing cows with calves are more easily alarmed by and more likely to flee from a potential threat

Rangifer, 21 (1), 2001

than are adult only groups (De Vos, 1960; Lent, 1966; Bergerud, 1974), groups with calves in this study took longer to respond to snowmachine disturbance and their overall flight distances were less. Although this might in part be explained by the differences in group size (groups containing calves were slightly larger), Tyler (1991) also reported shorter maximum duration of disturbance times for reindeer groups including calves on Svalbard in the absence of any apparent group size relationship. Caribou calves are especially susceptible to winter depletion of nutrient reserves (Reimers et al., 1982) and their reduced response to disturbance at this time of year would have clear survival advantages, as would the heightened reactions to disturbance reported for cows and calves during the early post-natal period (de Vos, 1960), when calves are highly susceptible to predation (Mahoney et al., 1990).

In Gros Morne, annual variation in response to snowmachine disturbance by adult-only caribou groups was not related to sex ratio, but may have been related to differences in winter conditions (Mawhinney et al., 1998). Caribou responded more slowly and fled for a shorter period of time in 1995 when winter snowfall was highest (Mawhinney et al., 1998) and this may reflect an attempt by animals to reduce their energy expenditures when the cost of locomotion is higher and the availability of forage is reduced. During winters of high snow accumulation and incidences of surface crusting, the cost of behavioural displacement due to disturbance may triple (Fancy & White, 1987). Presumably, the cost of locomotion was lower in 1994, 1996 and 1997,

when there was less snow, and caribou responded more quickly and for greater lengths of time and distance to approaching snowmachines. Bradshaw *et al.* (1997) reported similar results in their experimental study of the effects of noise on wintering caribou in Alberta, where caribou showed lower movement rates and linear displacement distances when snow was deepest.

While the energetic implications of our findings are presented elsewhere (Mahoney *et al.*, in prep), results presented here indicate that approaching snowmachines displaced Gros Morne caribou from resting activities, and initiated avoidance reactions that interrupted feeding bouts and increased locomotion rates, and therefore altered the animals' normal feeding and resting schedules. The question is, however, under what conditions are such effects likely to have serious implications?

Of particular interest here are our findings of wide variation in response, not only for individual groups, but also between years for the same population and between the caribou subspecies of Svalbard and Newfoundland. This variability cautions resource managers against quick environmental assessment decisions that are based upon a single year's research or findings that are limited to a single population. Caution is further advised by the implications of this and other disturbance studies (Bradshaw *et al.*, 1997) that suggest stochastic environmental variation, in this case snow depth, can alter behavioural responses.

At the same time, however, managers should not, out of hand, assume that animals will be continuously or significantly affected by novel stimuli. Only when such stimuli are rare, or threaten or pursue, or otherwise cause discomfort to the animal should this be so. Ungulates show considerable capacity to habituate to predictable, non-threatening stimuli, including vehicular traffic of many kinds, as evidenced by numerous species in both our National Parks and in urban areas where hunting is prohibited (Geist, 1978). We suggest that to some extent caribou in Gros Morne, which have readily habituated to vehicular traffic along the highway, are doing so with snowmachines, at least in comparison with animals on Svalbard. The extent to which they can do this will ultimately depend upon how often they are confronted by these machines and whether or not they are pursued

or otherwise harassed by them, both within the park and elsewhere.

Acknowledgments

We thank the numerous staff from the Park Warden Service of Gros Morne National Park for assistance with field work and data base management. This work received financial support from Gros Morne National Park and the Newfoundland and Labrador Wildlife Division. B. McLaren, N. Tyler and an anonymous reviewer provided comments which helped to improve earlier versions of this manuscript.

References

- Bergerud, A. T. 1974. The role of the environment in the aggregation, movement and disturbance behaviour of caribou. – *In:* V. Geist & F. Walther (eds.). *The behaviour of ungulates and its relation to management*. Vol. 2. International Union for Conservation of Nature and Natural Resources Publications. New Series Number 24.
- Bergerud, A. T., R. D. Jakimchuck & D. R. Carruthers. 1984. The buffalo of the north: caribou (*Rangifer tarandus*) and human developments. *Arctic* 37: 7–22.
- Bradshaw, C. J. A., S. Boutin & D. M. Hebert. 1997. Effects of petroleum exploration on woodland caribou in northeastern Alberta. – *J. Wildl. Manage*. 61: 1127–1133.
- Cameron, R. D., D. J. Reed, J. R. Dau & W. T. Smith. 1992. Redistribution of calving caribou in response to oil field development on the Arctic slope of Alaska. – *Arctic* 45: 338–342.
- Cameron, R. D. & K. R. Whitten. 1979. Caribou distribution and group composition associated with construction of the trans-Alaska pipeline. *Can. Field-Nat.* 93: 155–162.
- Curatolo, J. A. & S. M. Murphy. 1986. The effects of pipelines, roads and traffic on movements of caribou, *Rangifer tarandus. Can Field-Nat.* 100: 218–224.
- Deichmann, K. H. 1990. An assessment of environmental impacts relating to past and present use of over-snow vehicles within the boundaries of Gros Morne National Park. Parks Canada. Unpubl. report.
- **De Vos, A.** 1960. Behaviour of barren-grounds caribou on their calving grounds. – *J. Wildl. Manage*. 24: 250–258.
- **Dorrance, M. J., Savage, P. J. & Huff, D. E.** 1975. Effects of snowmobiles on white-tailed deer. – *J. Wildl. Manage.* 39: 563–569.
- Eckstein, R. G., O'Brien, T. F., Rongstad, O. J., & Bollinger, J. G. 1979. Snowmobile effects on

movements of white-tailed deer: a case study. – *Environ. Con.:* 45–51.

- Fancy, S. & R. White. 1987. Energy expenditure for locomotion by barren-ground caribou. – *Can. J. Zool.* 65: 122–128.
- Felcher, E. M.& E. C. Liberman. 2000. Intruders in the snow: will snowmobiles ruin our national parks? – *Wildlife Conservation*. Jan./Feb. 2000: 24–29.
- Freddy, D. J., W. M. Bronaugh & M. C. Fowler. 1986. Responses of mule deer to disturbance by persons affoot and snowmobiles. – *Wildl. Soc. Bull.* 14: 63–68.
- Geist, V. 1978. Behavior. In: Schmidt, J. L. & Gilbert, D.C. (eds.). Big Game of North America: Ecology and Management. Stackpole Books. Harrisburg, Penn., pp. 283–296.
- Klein, D. R. 1980. Reactions of caribou and reindeer to obstructions - a reassessment. – *In:* Reimers, E. Gaare, E. & Skjenneberg, S. (eds.). *Proc.* 2nd *Int. Reindeer/Caribou Symp., Røros, Norway,* 1979, pp. 519–527.
- Klein, D. R., M. Meldgaard & S. G. Fancy. 1987. Factors determining leg length in *Rangifer* tarandus. - J. Mammal. 68: 642–655.
- Klein, D. R. & E. Post 1999. Caribou calf production and seasonal range quality during a population decline. – J. Wildl. Manage. 63: 335–345.
- Lent, P. C. 1966. Calving and related social behaviour in the barren-ground caribou. – Zeitschrift für Tierpsychologie 6: 701–756.
- Mahoney, S. P., H. Abbott, L. H. Russell & R. B. Porter. 1990. Woodland caribou calf mortality in insular Newfoundland. – *In: Trans. 19^b IUGB Congress, Trondheim, 1989*, pp. 592–599.
- Mahoney, S. P., K. Mawhinney, C. McCarthy & S. Taylor. Energetic implications of snowmachine disturbance on woodland caribou in Gros Morne National Park. – J. Appl. Ecol. In prep.
- Mawhinney, K., S. P. Mahoney, C. McCarthy, S. Taylor & D. Anions. 1998. Caribou ecology in Gros Morne National Park, 1992-1998. Summary Report. Canadian Heritage Parks Canada Unpubl. report. 99pp.

- Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism and forage intake of white-tailed deer. *J. Wildl. Manage*. 42: 715–738.
- Moen, A. N., S. Whittemore & B. Buxton. 1982. Effects of disturbance by snowmobiles on heart rate of captive white-tailed deer. – *N.Y. Fish and Game Journal* 29: 177–183.
- **Murphy, S. M. & J. A. Curatolo.** 1987. Activity budgets and movement rates of caribou encountering pipelines, roads and traffic in northern Alaska. *Can. J. Zool.* 65: 2483–2490.
- Reimers, E., T. Ringberg & R. Sørumgård. 1982. Body composition of Svalbard reindeer. – *Can. J. Zool.* 60: 1812–1821.
- Richens, V. B. & G. R. Lavigne 1978. Response of White-tailed Deer to snowmobiles and snowmobile trails in Maine. – *Can. Field-Nat.* 92: 334–344.
- Segal, S. 1956. Nonparametric statistics for the behavioural sciences. McGraw-Hill Kogakshua, Tokyo.
- Shank, C. C. 1979. Human-related behavioural disturbances to northern large mammals: a bibliography and review. Report prepared for Foothills Pipe Lines (South Yukon) Ltd. Calgary.
- **Skogland, T. & B. Grovan.** 1988. The effects of food and maternal conditions on fetal growth and size in wild reindeer. *Rangifer* 4 (2): 39–46.
- Sokal, R. R. & F. J. Rohlf. 1969. Biometry: The principles and practice of statistics in biological research. W.H. Freeman, San Francisco.
- Simpson, K. 1988. The effects of snowmobiling on winter range use of Mountain Caribou. – In: R. Page (ed.). Caribou Research and Management in British Columbia: Proceedings of a Workshop. B.C. Ministry of Forests, Research Branch, WHR-27. B.C. Ministry of Environment, Wildlife Branch, WR-41. Victoria, B.C.
- **Tyler, N. J. C.** 1991. Short-term behavioural responses of Svalbard reindeer *Rangifer tarandus platyrbynchus* to direct provocation by a snowmobile. – *Biol. Cons.* 56: 179–194.

Manuscript received 5 February, 2000 accepted 27 May, 2000