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Effect of Insect Harassment on the Behaviour of the Rivière George Caribou

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ABSTRACT. Recent studies on the body condition of females of the Rivière George caribou herd (RGH) in northern Québec have shown that fat reserves declined markedly during the first month of lactation. For many populations of reindeer and caribou, it is widely accepted that insect harassment can affect food intake, energy expenditure, and consequently the accumulation of body reserves. To assess the role of biting and parasitic insects on caribou body condition, we monitored the behaviour and habitat use of RGH females from late June to early August in summers 1992 and 1993. In 1992, biting insect activity started on 27 July, while in 1993, insects were active from 14 July. Oestrids were present on the post-calving range in 1993 only. In both summers, we observed caribou harassed by flies on only four days. When insects were present, harassment reduced the time spent feeding from 53% to 30%, increased the time spent standing from 1% to 39%, and modified habitat use towards snow patches. Insect harassment had a significant impact on caribou behaviour, but its contribution to the negative energy balance during the first month of lactation seems negligible.

Key words: caribou, *Rangifer tarandus*, George River, Québec, behaviour, insect harassment, mosquito, oestrid, summer range, habitat selection

RÉSUMÉ. Des études récentes sur la condition physique des caribous femelles du troupeau de la Rivière George (TRG) au Québec nordique ont mis en évidence que, durant le premier mois de la lactation, les réserves de lipides diminuent de façon marquée. Il a été démontré, pour plusieurs populations de rennes et de caribous, que le harcèlement par les insectes peut affecter la prise de nourriture, les dépenses énergétiques et par conséquent l'accumulation de réserves corporelles. Afin d'évaluer l'influence des insectes piqueurs et parasites sur la condition physique des femelles du TRG, nous avons quantifié le comportement des animaux et leur utilisation des habitats de la fin juin jusqu'au début du mois d'août 1992 et 1993. En 1992, les insectes piqueurs ont débuté leur activité le 27 juillet et en 1993, le 14 juillet. La présence des oestres sur les pâturages d'été ne fut détectée qu'en 1993. Au cours des deux étés, nous avons observé les caribous harcelés par les insectes quatre journées seulement. La présence des insectes a réduit le temps consacré à l'alimentation de 53 à 30 p. cent, augmenté de 1 à 39 p. cent le temps passé en station debout, et augmenté l'utilisation des plaques de neige. Le harcèlement par les insectes a eu un impact significatif sur le comportement des caribous. Toutefois, sa contribution au bilan énergétique négatif durant le premier mois de la lactation semble négligeable.

Mots clés: caribou, *Rangifer tarandus*, Rivière George, Québec, comportement, harcèlement par les insectes, moustique, oestre, habitat d'été, sélection de l'habitat

INTRODUCTION

After a steady increase at an annual rate exceeding 10% for several decades (Messier et al., 1988; Crête and Huot, 1993), the Rivière George caribou herd (RGH) peaked at over 600 000 individuals in the mid-1980s. The last census, conducted in summer 1993, suggested that the population size had stabilized, at least within estimation confidence limits, at around 680 000 (Couturier et al., 1996). Recent studies on RGH have reported a decrease in fecundity and survival that has affected the herd since 1984 (Messier et al., 1988; Crête and Huot, 1993) and may even have initiated a decline of the herd (Crête et al., 1996). Also, the fat reserves of the dams are completely exhausted during the first month of lactation, and calf growth is low (Huot, 1989; Crête and Huot, 1993; Manseau, 1996). Inadequate summer nutrition resulting from range overgrazing has been suggested to be the regulating factor for the herd (Huot, 1989; Crête and Huot, 1993). However, insect harassment has been proposed as an alternative cause of the poor condition of the RGH females in fall.

Many researchers have documented the influence of insect harassment on the behaviour of domestic and wild ungulates (Darling, 1937; Pruitt, 1960; Espmark and Langvatn, 1979; Helle, 1981; Hugues et al., 1981; Woollard and Bullock, 1987; Renecker and Hudson, 1990; Ralley et al., 1993). Insects interfere with feeding activity and habitat utilization (Duncan and Cowtan, 1980; Harvey and Launchbaugh, 1982; Keiper and Berger, 1982; Sleeman and Gray, 1982; Downes et al., 1986). For caribou and reindeer, three major effects of insect harassment are recognized. Insect harassment can force animals into nonproductive activities instead of feeding, induce costly annoyance responses, and concentrate animals in low-quality habitats such as ridge tops, coastal regions, snow patches, and unvegetated areas (Kelsall, 1968;

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Downes, 1984; Helle and Aspi, 1984; Dau, 1986; Camps and Linders, 1989; Helle et al., 1992; Walsh et al., 1992). It is widely accepted that severe insect harassment could result in a negative energy balance and eventually in the poor physical condition of animals in autumn of some years (Roby, 1978; Russell et al., 1993; Helle and Kojola, 1994). However, few studies have attempted to quantify insect activity and harassment in relation to the caribou activity budget over a continuous period covering the seven weeks after calving.

This study assessed the effect of insect harassment on the behaviour of RGH female caribou during early lactation. Specially, we quantified insect abundance in different habitats, measured insect activity according to different times of the day and weather parameters, and examined the influence of insects on the activity budget, display of annoyance responses, and habitat use of caribou.

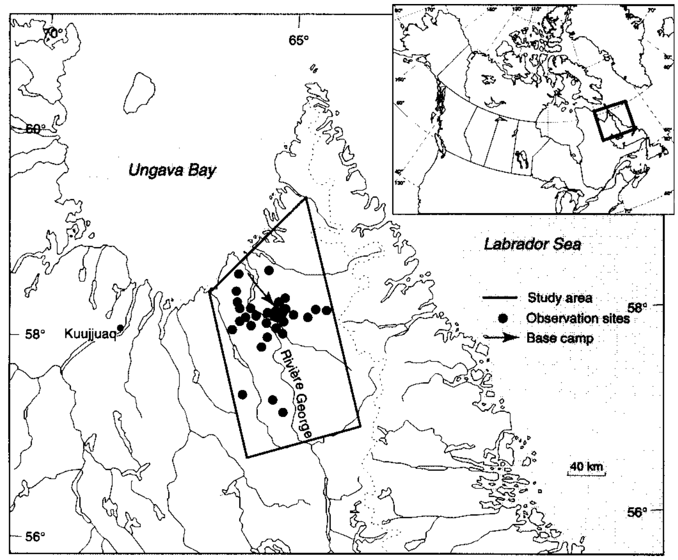

FIG. 1. Map of the study area showing the observation sites.

STUDY AREA

The study was conducted on the calving and summer range of the Rivière George caribou herd in northern Québec and Labrador (Fig. 1) (Manseau et al., 1996). For at least two decades, females of the RGH have used the plateaus of the Rivière George for calving, which usually occurs during the second week of June. The area used for post-calving aggregations in late June and July extends eastward from about 70˚W longitude to the Torngat Mountains (elevations up to about 1500 m) and the coast of Labrador and northward from about 55˚30′N latitude to the coast of Ungava Bay (Russell et al., 1994). The main plant communities of this range are the shrub tundra, sedge meadows, and stands of spruce (*Picea mariana* and *Picea glauca*), krummholz spruce (*Picea mariana*) and dwarf birch (*Betula glandulosa*). We restricted our study area to the northern-central part of the summer range. This area covers approximately 20 000 km^2. The dominant biting insects are mosquitoes (*Aedes* spp., Diptera, Culicidae) and blackflies (Diptera, Simuliidae). Two parasitic insects (*Hypoderma tarandi* and *Cephenemyia trompe,* Diptera, Oestridae) could also represent a serious nuisance in July and August during egg (*H. tarandi*) or larva (*C. trompe*) deposition. Even in small numbers, these parasitic flies induce vigorous reactions from reindeer and caribou (Karter and Folstad, 1989; Folstad et al., 1991).

METHODS

Mosquito and Blackfly Sampling

Mosquito and blackfly sampling was carried out from 25 June to 8 August 1992 and 1993 in an area of approximately 1.5 km^2 close to the base camp (Lake de Caen, 58˚19′N and 65˚41′W). We sampled three habitats (one site per habitat) used extensively by caribou: shrub tundra, sedge meadow, and stands of dwarf birch and krummholz spruce. The shrub tundra site was composed of low shrubs (*Vaccinium uliginosum, V. vitis-idaea, Ledum decumbens, Empetrum nigrum*), graminoids, and lichens (*Stereocaulon paschale, Cetraria nivalis*) (Manseau et al., 1996). Vegetation height was about 15 cm. The sedge meadow site was located at the bottom of a broad valley on poorly drained terrain and was composed of *Carex rariflora, Eriophorum angustifolium* and *Scirpus caespitosus*. The third site was composed of stands of dwarf birch (*Betula glandulosa*) and krummholz spruce (*Picea mariana*) reaching 1.5 m in height. It was located on a well-drained sloping terrain. Sampling was done four times a day in 1992 and three times a day in 1993 in each habitat. Sampling sequences were randomly determined. In 1993, we sampled once a day until mosquitoes and blackflies became active, and three times a day subsequently. In 1992, sampling of mosquitoes and blackflies consisted of catching individuals lying or flying at 15 cm or less over a black cloth surface of 40 × 40 cm with a modified handheld vacuum cleaner, operated for two minutes. During a sampling period, we collected five "two-minute" samples in each habitat. In 1993, on the basis of the previous year's experience, we decided to use a sweep net. The canvas net was 50 cm in diameter with a handle 1 m long. While standing, a single observer made sweeps in a figure-eight motion at approximately one sweep per second (the observer was the same person during the whole field season). Sweeps spanned 0.5 – 2.0 m above ground. Five samples of 20 sweeps each were taken successively in the three habitats.

Oestrid Sampling

During both summers, special attention was paid in detecting the presence of parasitic flies anytime we were in the field. In 1992, we used sticky traps to catch oestrid flies. Each trap consisted of a cylinder 30 cm in diameter and 60 cm in height, placed 20 cm above ground. The sides were coated with a viscous non-attractant insect-trapping adhesive (Stick'em, Seabright Enterprises, Berkeley, California). One trap was placed in each habitat type (shrub tundra, sedge meadow, birch/krummholz stands). Traps were visited during each mosquito/blackfly sampling period. The sticky coating was replaced every 7–10 days. Trapping was unsuccessful during summer 1992. We suspected that the method was not an effective means of estimating oestrid activity when the population is low. Therefore, in 1993, oestrid flies were identified or captured (by hand or net) whenever they were observed. On each occasion, weather and habitat type were recorded.

Weather

Weather parameters were monitored at the base camp, which was approximately 0.5 km from the sampling sites. Air temperature was continuously recorded using a thermograph placed in a meteorological Stevenson shelter. Precipitation was collected in a pluviometer. Wind velocity was measured at the base camp with a handheld anemometer (Simerl, model K/K, Nurnberg, Germany) at 1.5 m above ground. Wind measurements were taken at 0800 and 2000 during each mosquito/blackfly sampling period and at one-hour intervals during caribou observations.

Caribou Behaviour and Habitat Use

Caribou were observed on 27 days from 24 June to 30 July 1992 and on 17 days from 23 June to 19 July 1993. Caribou were located by boat when they were close to camp or by helicopter. Observations were made on aggregations of various sizes (1–75 000 caribou (Manseau, 1996) and at different sites in the study area (Fig. 1). We covered an area of approximately 20 000 km^2. Periods of observation lasted four to six hours during daylight hours (from 0500 to 2100). Instantaneous scan sampling (ISS) and focal individual sampling (FIS) (Altmann, 1974) were used to record caribou behaviour. Depending on group size, one or two observers performed ISS while the other(s) (1–3) performed FIS. ISS was conducted every 60 minutes to estimate the activity budget and habitat use of the animals. Activity budget was recorded as the proportion of animals observed feeding (which included foraging behaviour, walking with nose near the ground below knee height), lying, walking (head up), running, or standing. Habitat use was recorded as the proportion of animals observed in the five habitat types: dwarf birch/krummholz stands, shrub tundra (vegetation typically less than 20 cm height including some unvegetated areas and rock outcrops), open spruce stands, sedge meadows, or snow patches. Availability of each habitat in the study area was estimated by aerial transects (Manseau et al., 1996). For FIS, an individual in the observed group was chosen at random and sampled for up to 30 minutes. As most groups were composed of lactating animals, the majority of observations concerned these animals. FIS was used to estimate the frequency of occurrence of specified responses to insect harassment. The responses recorded were head shake, body shake, ear flicking, foot stamping, tail wagging, and biting.

Statistical Analysis

Since it was not possible to assume a direct correlation between the results obtained with the vacuum cleaner and the sweep net techniques, 1992 and 1993 mosquito and blackfly data were analyzed separately. Nonparametric Kruskal-Wallis and Tukey tests were used to detect differences in insect abundance between sites or time of the day.

Contingency tables (χ^2 test) were used to compare the activity budget of caribou in the pre-insect and insect seasons. According to insect abundance estimated by sampling, the seasons when caribou were in the study area were divided into pre-insect and insect periods. The pre-insect period began after calving and extended to the moment when mosquitoes and blackflies became abundant. It lasted from 24 June to 26 July in 1992 and from 23 June to 13 July in 1993. The pre-insect period was further divided into two periods according to the plant phenology: before and after emergence of shrub leaves. Shrub leaf emergence began on 6 July in 1992 and on 25 June in 1993. The insect periods, which followed accordingly, corresponded to one day (30 July) in 1992 and three days (16 to 19 July) in 1993 (No observations were made on 18 July 1993). Observations ceased when all caribou groups had moved southwest into the boreal forest and were no longer accessible from the research area. The insect season was divided into two categories (mild and severe) according to the degree of harassment suffered by caribou. The harassment was mild on 30 July 1992 and 17 July 1993 and severe on 16 and 19 July 1993. Habitat use was compared to availability in both pre-insect and insect periods, following the method of Neu et al. (1974). The scans (ISS) were done hourly. Within an hour, a given animal might have stayed in the scanned area. However, the probability of recording a given animal in the same behaviour in two consecutive scans was low, as a behaviour bout rarely lasted an hour. To test for autocorrelation between scans, we estimated the component of the variance of all dependent variables associated to a "caribou observation site" and a "scan" effect (PROC VARCOMP, SAS Inc.). The analysis did not detect a "caribou observation site" effect for any of the dependent variables, and therefore we considered successive scans as independent.

A chi-square test was used to determine whether caribou exhibited more frequent annoyance responses under severe harassment than under mild harassment.

RESULTS

Insect Abundance and Activity

Mosquitoes and Blackflies: The seasonal variation in mean daily abundance of mosquitoes and blackflies is shown in Figure 2. In 1992, mosquitoes were first caught on 4 July, but abundance remained low until 27 July. Then, mosquitoes were abundant until 6 August. Blackflies were caught regularly starting on 27 July. In 1993, mosquitoes and blackflies were first caught on 14 July and were present until the end of

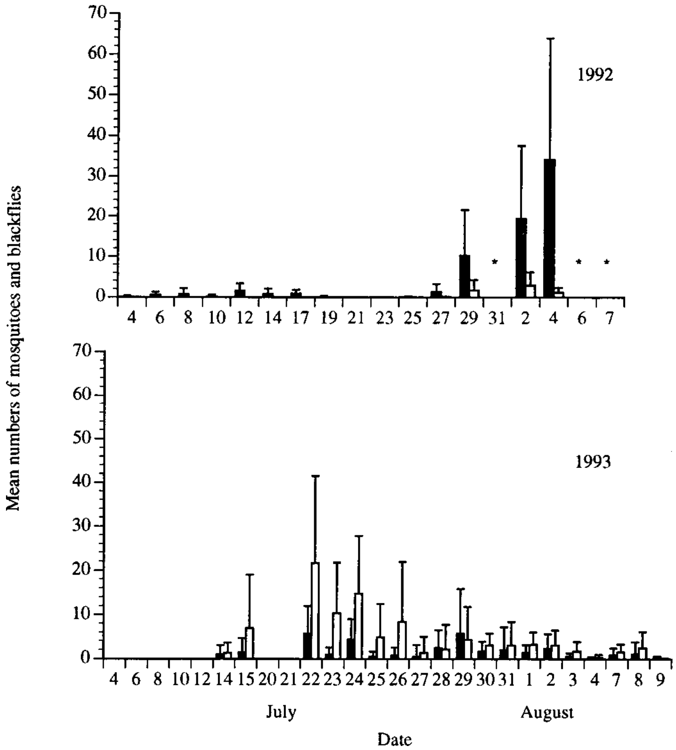

FIG. 2. Seasonal variation in daily abundance (mean ± SD) of mosquitoes and blackflies on the RGH summer range in 1992 and 1993. Solid histogram bars refer to mosquitoes, and open bars to blackflies. Because of technical problems, sampling was not performed on days marked with an asterisk.

TABLE 1. Diurnal variation in mosquito and blackfly abundance (number of insects·min^{-1} or number of insects; median (min; max)) on the Rivière George caribou herd summer range in 1992 and 1993.

	0830	1230	1630	2030	n[1]	χ^2	*p*
1992							
Mosquitoes	0.3 (0;33)	0.9 (0;36)	1.8 (0;54)	0.4 (0;68)	134	5.59	0.13
Blackflies	2.0 (0;5)	0.6 (0;13)	1.4 (0;8)	0.0 (0;3)	50	1.41	0.70
	0930	1330	1730		n[1]	χ^2	*p*
1993							
Mosquitoes	0.2 (0;7)a[2]	0.2 (0;5)a	1.2 (0;21)b		138	16.32	0.00
Blackflies	2.2 (0;24)a	1.0 (0;32)a	4.8 (0;37)b		138	19.07	0.00

[1] n = number of sampling periods
[2] a and b values followed by the same letter are not significantly different at $p = 0.05$ (Tukey test)

TABLE 2. Variation among sites in mosquito and blackfly abundance (number of insects·min^{-1} or number of insects; median (min; max)) on the Rivière George caribou herd summer range in 1992 and 1993.

	Birch/krummholz stands	Low shrub tundra	Sedge meadows	n[1]	χ^2	*p*
1992						
Mosquitoes	1.3 (0;68)	0.7 (0;68)	0.6 (0;36)	134	0.14	0.93
Black flies	1.4 (0;8)	0.6 (0;13)	0.6 (0;5)	50	3.21	0.20
1993						
Mosquitoes	0.2 (0;5)a[2]	0.7 (0;21)ab	0.6 (0;16)b	138	7.19	0.03
Black flies	1.6 (0;37)	2.8 (0;20)	2.4 (0;36)	138	0.85	0.65

[1] n = number of sampling periods
[2] a and b values followed by the same letter are not significantly different at $p = 0.05$ (Tukey test)

field season (9 August). In 1992, mosquito and blackfly abundance did not vary with time of the day (Table 1) or among sites (Table 2). In 1993, differences were found between times of the day (Table 1) and among sites (Table 2) for mosquitoes and between times of the day (Table 1) for blackflies. More mosquitoes and blackflies were caught at 1730 than at 0930 or at 1330, and mosquitoes were more abundant in meadows and less so in birch/krummholz stands.

Temperature and wind speed thresholds were estimated. No mosquito or blackfly was caught when temperature was under 6˚C and their activity remained low up to 10˚C (Fig. 3). Activity ceased when wind velocity reached 20 km·h^{-1} or more (Fig. 4).

Oestrids: No oestrids were caught or seen during summer 1992. In 1993, between 19 and 30 July, 14 flies were seen, and seven of them were caught. Two specimens, one female of *Hypoderma tarandi* and one female of *Cephenemyia trompe*, were captured near a caribou group under severe harassment on 19 July. Other oestrids were caught or seen during mosquito and blackfly sampling in the vicinity of our camp location. Oestrids were active throughout the day, i.e., between 0900 and 2000. They were seen or caught at temperatures varying from 16˚C to 24.5˚C, wind velocity between 0 and 17 km·h^{-1}, and cloud cover between 0% and 100%. Habitat type did not seem to affect oestrid activity. Four specimens were found in low shrub tundra, three in birch/krummholz stands, and three in sedge meadows. The four other specimens were found in unidentified habitats.

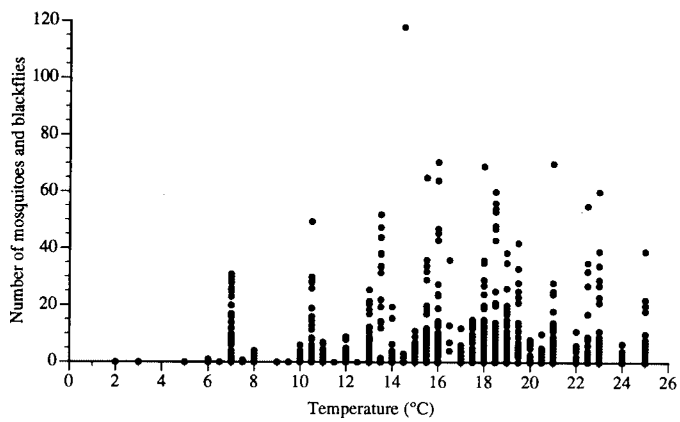

FIG. 3. Variation in the number of mosquitoes and blackflies caught as a function of ambient temperature on the RGH summer range in 1992 and 1993.

Weather

We divided the summers into four periods to compare temperature, wind velocity, and precipitation. Summer 1992 was cooler than summer 1993, especially at the end of June and in the second part of July; mean temperature—and in particular mean maximum and minimum temperatures—

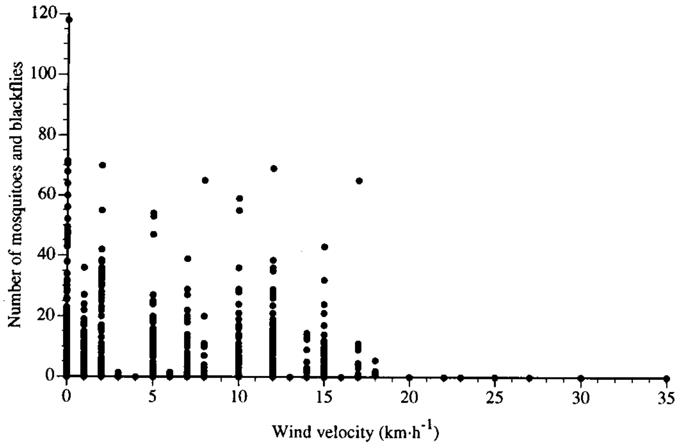

FIG. 4. Variation in the number of mosquitoes and blackflies caught as a function of wind velocity on the RGH summer range in 1992 and 1993.

were lower in 1992 (Table 3). The mean number of hours when T ≥ 6˚C was lower in summer 1992 at the end of June, in late July, and in early August while it was the same for both years in early July. The mean number of hours when T ≥ 10˚C was lower in summer 1992 from the end of June up to the end of July, and was greater in early August (Table 3). Wind velocities measured at the base camp at 0800 and 2000 were mostly suitable for insect activity in both years (Table 3). Except for the beginning of August, precipitation was more abundant in 1992 than in 1993 (Table 3).

Caribou Behaviour

During the field seasons 1992 and 1993, 257 scans were conducted on the Rivière George plateaus: 239 in the pre-insect period and 18 in the insect period.

Change in Activity Pattern: During the total pre-insect period, feeding (52%) and lying (25%) were the dominant activities (Table 4). Before shrub leaf emergence more animals were observed feeding (61%), and fewer walking (10%), than after shrub leaf emergence (48% feeding; 27% walking). Under insect harassment, caribou strongly modified their activity pattern (Table 4, $\chi^2 = 55.76$, $p < 0.0001$). Feeding decreased to 30% and lying to 8.5%. Standing and running increased to 39% and 5%. The effects of insect disturbance on caribou behaviour varied with the intensity of harassment (Table 4). Under mild harassment, the proportion of caribou feeding was 60% and the proportion standing was 20%, while the proportion lying was 16% and the proportion walking was 3%. Under severe insect harassment, the proportion of caribou feeding and lying decreased drastically to 6% and 3%, respectively, while the proportion walking and standing increased to 29% and 53% respectively.

Even under mild harassment, annoyance responses were visible during field observations (Table 5). The most frequent responses were head and body shakes and foot stamping. When harassment became more severe, caribou also used ear flicking, tail wagging, and biting to chase insects. No significant difference was detected in the frequencies of annoyance responses between mild and severe harassment periods ($\chi^2 = 0.05$, $p > 0.05$).

Habitat Use: In the pre-insect period, birch/krummholz stands (27%) and sedge meadows (21%) were used more than expected, while the shrub tundra (47%) and open spruce stands (4%) were used less than expected from their availability (Table 6). During the insect period, shrub tundra (36%) was used less than expected, while use of snow patches increased (Table 6). Because of the small sample size during the insect period, we could not compare use of meadow and open spruce stands with their availability. Sedge meadow use was 10%, and open spruce stand use was not observed.

DISCUSSION

During the first month of lactation, RGH caribou were observed under insect harassment on only four days. In both years, the insect period began only a few days before animals moved away to the boreal forest: on 30 July in 1992 and on 16 July in 1993. Reports of mosquito emergence in subarctic and arctic locations in Canada indicate that adult mosquitoes emerge from late June to mid-July (Curtis, 1953; Haufe and Burgess, 1956; Corbet, 1966; Maire and Bussières, 1983). The accumulation of degree-days in a given season is normally used to predict insect development and emergence (Haufe and Burgess, 1956), as temperature determines the time and duration of development (Maire and Aubin, 1976). Data provided by Environnement Québec in Kuujjuaq indicate that the number of degree-days of development above 5˚C in June 1992 was 61% lower than the 1961–90 average (Fig. 5). This cooling could explain the delayed emergence of

TABLE 3. Comparison of weather parameters on the Rivière George caribou herd summer range in 1992 and 1993.

	From 18 to 30 June		From 1 to 15 July		From 16 to 31 July		From 1 to 8 August	
	1992	1993	1992	1993	1992	1993	1992	1993
Mean temperature (˚C)*	7.4	8.5	10.9	11.6	10.1	15.0	12.6	12.1
Mean maximum temperature (˚C)	6.8	11.8	16.4	16.8	15.2	20.6	18.3	15.4
Mean minimum temperature (˚C)	2.2	3.0	4.8	7.2	5.7	10.4	7.4	8.9
Mean number of hours when T˚ ≥ 6˚C*	13	18	18	18	18	23	22	24
Mean number of hours when T˚ ≥ 10˚C*	0	11	12	14	12	21	16	15
Total precipitation (mm)	42	26	37	27	34	15	3	36
% of sampling when wind < 20 km·h^{-1}	58	100	100	87	88	90	100	100

* Exceptionally, the first period began on 25 June

TABLE 4. Activity budgets (percentage of animals per scan (SE)) of Rivière George caribou in relation to the presence of insects in summers 1992 and 1993.

	Pre-insect period			Insect period		
	Shrub leaf emergence			Harassment		
	Before n[1] = 81	After n = 158	Total n = 239	Mild n = 8	Severe n = 10	Total n = 18
Feeding	61.1 (3.0)	48.0 (1.9)	52.5 (1.7)	60.3 (8.8)	6.3 (3.0)	30.3 (7.7)
Lying	27.8 (2.8)	24.2 (1.6)	25.5 (1.4)	16.0 (4.0)	2.5 (2.3)	8.5 (2.7)
Running	0.5 (0.4)	0.1 (0.0)	0.2 (0.1)	0.0 (0.0)	8.8 (5.8)	4.9 (3.3)
Standing	0.4 (0.4)	0.9 (0.4)	0.7 (0.3)	20.2 (7.2)	53.2 (12.7)	38.5 (8.5)
Walking	9.6 (1.9)	26.7 (2.2)	20.9 (1.7)	3.2 (1.0)	29.2 (12.4)	17.6 (7.4)

[1]n = number of scans

TABLE 5. Frequency (mean number of responses·min^{-1}) of annoyance responses displayed by caribou of the Rivière George herd under insect harassment, in summer 1992 and 1993.

	Mild harassment n[1] = 32	Severe harassment n = 109
Head shake	0.24	1.90
Body shake	0.38	2.24
Ear flicking	0.15	0.64
Foot stamping	0.22	0.99
Tail wagging	0.07	0.43
Biting	0.01	0.12

[1] n = number of caribou observed

TABLE 6. Comparison between habitat availability and habitat use (percentage of animals and confidence intervals (p = 0.10)) by Rivière George caribou in summers 1992 and 1993.

	Availability	Habitat use			
		Total pre-insect period n = 239		Total insect period n = 18	
Birch/krummholz stands	15.8	26.6	(6.6) *	28.0	(24.6)
Shrub tundra	68.6	47.3	(7.5) *	36.4	(26.4) *
Open spruce stands	8.1	4.2	(3.0) *	0	
Sedge meadows	7.1	20.6	(6.1) *	9.6	
Snow patches	0.4	1.3	(1.7)	26.0	(24.1) *

* significant difference between habitat use and availability

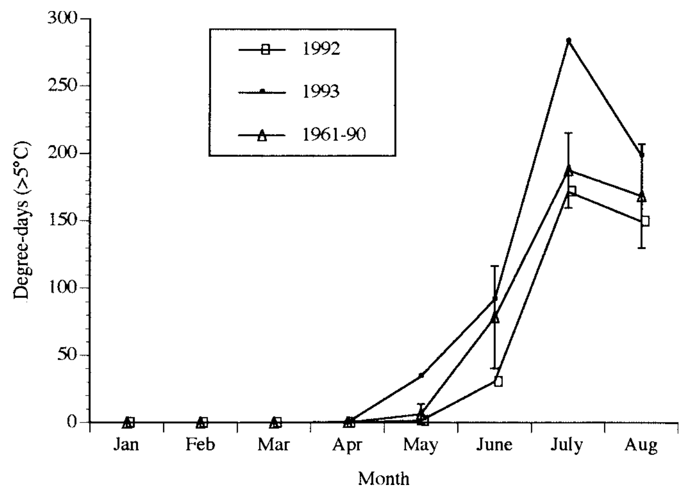

FIG. 5. Monthly heat accumulation (degree-days > 5˚C) in Kuujjuaq, Québec (1992, 1993 and 1961–90 period, mean ± SD).

mosquitoes and blackflies. Catches of blackflies and most mosquito species remained low until the last week of July. In 1993, spring conditions were quite different from those of 1992. Accumulation of degree-days above 5˚C in May 1993 was greater than the 1961–90 average in Kuujjuaq (Fig. 5). Spring 1993 was particularly early, and insect activity became noticeable on 14 July. We had the chance to study RGH caribou during two years when spring conditions differed greatly. Spring 1992 was later than the long-term average, while spring 1993 was earlier (Fig. 5). Even though spring conditions in the two years we studied were widely different, insect harassment on caribou was sporadic during both years.

We could also hypothesize that ambient air temperatures and wind velocity prevailing during behavioral observations precluded insect activity and biased our estimate of when this period really started. In order to test this hypothesis, we calculated the number of scans conducted under three different conditions (Table 7). The first one (T˚ ≥ 6˚C and wind < 20 km·h^{-1}) represents the lower and upper threshold of temperature and wind velocity measured for mosquito and blackfly activity; the second (T˚ ≥ 10˚C and wind < 20 km·h^{-1}) is the minimum temperature at which mosquito and blackfly activity became more important; and the third is the insect period. Our thresholds of temperature and wind velocity for insect activity are representative of what is widely accepted in the literature. The mosquito and blackfly temperature threshold is usually reported as 7˚C (Wolfe and Peterson, 1960; Bennett and Fallis, 1971; Downes, 1984; Nixon, 1991), whereas, the wind threshold is 6 m·s^{-1} (21.6 km·h^{-1}) (Dau, 1986; Nixon, 1991). Ambient air temperatures and wind velocities during our scans were suitable for insect activity for 93% of the time in 1992, and 72% in 1993 (T˚≥ 6˚C); and for 78% of the time in 1992, and 69% in 1993 (T˚≥ 10˚C). In comparison, insects were present in 3% and 20% of all scans in 1992 and 1993 respectively. Thus, we conclude that temperature and wind during our scans were not the cause of low numbers of insects observed.

When insects were present, RGH caribou exhibited responses similar to those previously documented (Pruitt, 1960; Helle, 1981; Dau; 1986; Downes et al., 1986). During the insect period, insect harassment resulted in a sharp decline in the time spent feeding and lying, which was associated with a marked increase in the time spent standing and running. The increase in the rate of characteristic annoyance responses under harassment also imposed a constraint on animals. These movements distracted caribou from their feeding activity. We observed that animals reacting to insects often interrupted feeding and displayed annoyance reactions (Anderson, 1975; Camps and Linders, 1989). Insect harassment seems to be costly in terms of energy, as observed in other herds, and to reduce the quantity of food ingested

TABLE 7. Number of scans under various conditions from date of shrub-leaf emergence to the end of the behavioral observations.

	Summer	
	1992	1993
Temperature ≥ 6°C and Wind < 20 km·h^{-1}	94	54
Temperature ≥ 10°C and Wind < 20 km·h^{-1}	79	52
Insect period	3	15
Total	101	75

(Gaare et al., 1975). However, we observed that under mild insect harassment, caribou appeared to maintain an activity budget that did not negatively influence their feeding regime and energy expenditures. Russell et al. (1993), in a computer-assisted simulation model, showed that the energy balance, from post-calving (11 June) to mid-July, was positive when measured in a "good" year (mild insect harassment), whereas it was negative in a "bad" year (severe insect harassment).

Previous research on distribution of caribou on their summer range has shown that animals use rivers, seashores, and elevations to avoid insect harassment (Helle and Aspi, 1984; Dau, 1986; Downes et al., 1986). For the RGH, satellite telemetry data (Ministère Environnement et Faune, 1993) indicated that at the end of July, the herd moved west into the boreal forest instead of north to the Ungava Bay riparian areas or east to the Torngat Mountains.

Snow patches were used intensively by RGH caribou when insects were present, although snow covered less than 1% of the ground. Two main reasons are usually proposed for such utilization: reduction of insect harassment and thermoregulation. Ion and Kershaw (1989), in a similar study in the Northwest Territories, noted that 0.5 m above a snowpatch temperatures are consistently 3˚C cooler than above adjacent areas. They also observed caribou ingesting snow and lying down on snow patches in order to cool off (Ion and Kershaw, 1989). Even though caribou receive a thermoregulatory benefit from using snow patches, they can tolerate ambient temperatures well above those recorded on that study site (10–20˚C). Ion and Kershaw concluded that snowpatch selection is a means of reducing insect harassment. Because ambient air temperatures were of the same magnitude and RGH caribou used snow patches mainly during the insect period, we agree that selection of snow was probably a means of reducing insect harassment. However, we cannot deny the thermoregulatory benefit that caribou get from it.

Insect disturbance on RGH caribou behaviour was not of major concern during the first month of lactation in the two years we studied the herd. The exhaustion of body fat reserves in lactating females (Crête and Huot, 1993; Manseau, 1996) during this period could not be explained by insect harassment. It is true that the presence of insects altered the activity budget by reducing the time spent feeding and lying while increasing the time spent standing and running in late July. However, insect harassment was only sporadic. It lasted only four days: two of mild and two of severe harassment.

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