

Do reindeer aggregate on snow patches to reduce harassment by parasitic flies or to thermoregulate?

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Abstract: During warm, sunny days (Max. temp. 22 °C - 25 °C) CO₂-baited traps operated at sites on and off snow patches (SP's) in subarctic Norway caught significantly fewer culicids, simuliids and tabanids on snow in both 1985 and 1987. However, for overnight catches (18.30 - 07.30 h) there was no significant difference in the number of culicids caught on versus off SP's. Analysis of videotapes taken in 1987 showed that defensive anti-fly behaviors of reindeer on and off SP's remained low (< 1/4 min) throughout the day. Based on reindeer anti-fly behaviors, harassment was greatest from 10.30 to 12.30 h (Norwegian Standard Time), but reindeer continued to aggregate on SP's while anti-fly behaviors were lowest (13.30 - 20.00 h). Groups of >150 animals often occupied the entire surface of a snow patch.

At the fly densities and climatic conditions encountered it seemed apparent that reindeer intermittently used SP's primarily to thermoregulate following periods of foraging. Almost all reindeer remained on SP's from 11.00 to 12.30 h, but at other times between 08.00 and 19.00 h about half the herd (ca. 800 animals) foraged for about an hour while the other half aggregated on SP's. However, by 20.00 h, during the cooler period when trap catches of mosquitoes were increasing, almost all reindeer had moved off SP's.

The small decreases in anti-fly defensive behaviors observed for reindeer on SP's versus animals foraging in snow-free areas indicated that their presence on SP's may have resulted in a minor, coincidental reduction in harassment. Significantly more tabanids were caught during the morning trapping period than at other times, and significantly more mosquitoes were caught during the evening/overnight trapping period than at other times.

Key words: *Rangifer tarandus*, thermoregulation, parasitic fly harassment, anti-fly behavior, videotape analyses, CO₂-baited trap catches.

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Introduction

Reports of massive swarms of host-seeking mosquitoes and other parasitic flies attacking herds of caribou/reindeer (*Rangifer tarandus*) in arctic and subarctic biomes are legendary (e.g. Bergman, 1917; Murie, 1935; Kelsall, 1968; Zhigunov, 1968; Baskin, 1970; Thomson, 1971; White *et al.*, 1975,

1981; Wright, 1980; Thing, 1984). However, these (and other) largely anecdotal accounts are almost always based only on mosquitoes attacking humans, and they rarely are supported by quantitative data on insect abundance. In response to inferred harassment by mosquitoes and other fly parasites, caribou/reindeer have been reported to seek refuge at

such microhabitats as wind-swept mountain tops, barren coastal areas, snow fields and isolated patches of snow (e.g. Pruitt, 1960; Kelsall, 1968; Skjenneberg & Slagsvold, 1968; Bergerud, 1971; Thomson, 1971; Gaare *et al.*, 1975; Low, 1976; Boertje, 1985; Sokolov, 1984; Vodop'yanov, 1984; Ion & Kershaw, 1989). However, in the absence of quantitative insect data and identification of species, such a presumptive cause: effect relationship remains mostly conjectural.

Most studies of refuge-seeking behavior by caribou/reindeer have been hindered by the inherent difficulties of trapping or collecting associated flies and by the inability to closely observe animals in expansive, rugged arctic/subarctic terrain. Moreover, during most days, arctic/subarctic climatic conditions are unfavorable for fly activity (Thomson, 1971; Skogland, 1984; Anderson & Nilssen, 1996), thus limiting opportunities to assess interactions between caribou/reindeer and their associated dipteran parasites. Because quantitative sampling of parasitic flies attacking animals under these field conditions has not been possible, inferred assessments of "insect" abundance have been based on: 1) descriptive observations of animal behavior associated with the use of a temperature/wind velocity index to estimate the severity of insect harassment (e.g. Thomson, 1971; White *et al.*, 1975; Helle & Tervainen, 1984; Skogland, 1984), 2) use of habitat by caribou associated with predicted days of harassment by insects (Walsh *et al.*, 1992), or 3) collections of mosquitoes around humans (e.g. Downes *et al.*, 1986; Russell *et al.*, 1993; Toupin *et al.*, 1996). Only in studies by Breev (1950, 1951) did workers tally reindeer attack rates for *Hypoderma tarandi* L. and *Cephenemyia trompe* (Modeer) (Oestridae) and for culicids, simuliids and tabanids. Breev (1950) also collected and identified samples of the parasitic fly fauna that attacked tethered reindeer in USSR. Recent trapping studies (Helle *et al.*, 1992; Anderson & Nilssen, 1996) found that the fly species caught in CO₂-baited traps, as well as their relative abundance (Helle *et al.*, 1992), was the same as those caught attacking tame reindeer.

Although many authors have suggested that reindeer and caribou use snow patches (SP's) to obtain relief from insect attack, only Downes *et al.* (1986) and Ion & Kershaw (1989) have investigated this hypothesis. During insect trapping studies in 1984 (Anderson & Nilssen, 1996), we observed reindeer aggregations on SP's in distant mountains on warm,

sunny days, and in subsequent years we operated insect traps in an accessible area having temporary summer SP's.

To investigate whether reindeer might be using SP's to obtain relief from attacks by parasitic flies, our primary objective in 1985 and 1987 was to compare the number of flies caught in host-mimicking CO₂-baited insect flight traps placed on SP's with the number caught in similar traps concurrently operated at nearby adjacent sites on snowfree terrain. The second objective was to determine the number of flies caught at different times of the day. Other objectives in 1987 were to determine the effect of experimental host silhouettes on CO₂-baited trap catches on and off SP's, and to determine the behavior of reindeer observed on and off SP's while traps were operating.

Materials and methods

Studies were conducted on a treeless mountain *vidda* (tundra-like biome) at Kvængsfjellet (460 - 620 m above sea level) in northern Norway (69°53'N, 21°30'E). All trapping was conducted on warm, sunny days having low wind velocities. We used insect flight traps (2.2 m h X 1.6 m w), in which most insects are trapped in a clear apically-mounted collecting container (Anderson & Nilssen, 1996). Each trap was baited with 4 - 6 kg of dry ice per trapping period. The dry ice was placed in a styrofoam box (32 cm³), with sublimated CO₂ being released from four 2.5 cm holes located 5.0 cm from the bottom of each side. Dry ice boxes were set at the base of a traps' center support pole. CO₂ emission rates of 1.5 - 2.5 l/min were determined by periodically weighing boxes (Anderson & Nilssen, 1996).

At the end of each collecting period, a modified battery-powered aspirator (Meyer *et al.*, 1983) was used to collect all insects resting on the inside surfaces of a nylon mesh trap, after which the apical collecting container on the trap was removed, sealed and replaced with an empty container. The aspirator collection and apical container were placed in sealed polyethylene bags, and frozen in dry ice boxes. Collections were examined, sorted and identified to order/family level at our temporary field laboratory, and representative specimens for specific identification were pinned or preserved in 70% ethanol.

From 9 through 11 July 1985, we operated one trap near the center of each of three discrete SP's (Fig. 1). These SP's were located 470 m a.s.l. and

500 to 800 m from several other SP's that were concurrently occupied by groups of 50 to 200 reindeer, either standing or reclining on the snow (Fig. 1). The latter SP's varied in size from about 140 to 300 m², and they were located at 500 to 600 m a.s.l. Each SP trap was paired with a trap located at an adjacent snow-free vidda site; the latter traps were set 1 - 3 m from the edge of different SP's (Figs. 1, 2). The axis between each pair of traps was located perpendicular to the prevailing wind direction to reduce possible differences in position effects. The first trapping period was from 08.00 to 14.00 h (Norwegian Standard Time) and the second from 14.00 to 20.00 h (N.S.T.). A thermohygrograph was used to record ambient air temperature continually during trapping periods, and wind velocities were intermittently measured with a hand held Elvometer AB Ventimeter.

On 18 and 19 July 1987, we operated two traps set on each of two SP's matched with an adjacent pair of traps set at two snow-free vidda sites. Fig. 3

shows traps on and off SP-I sited perpendicular to the prevailing wind direction. There was about 30 m between each trap. Each SP trap was 9 to 10 m from either edge of the SP, and each snow-free trap was 10 m from the edge of the SP. At a second elliptical SP (25 X 290 m) traps on and off snow were positioned similarly. At each SP and vidda site 10 - 12 cardboard boxes (varying in size from about 35 cm³ to 50 cm³) were grouped around one of the paired traps to simulate silhouettes of reclining reindeer (Fig. 3). The boxes were rotated to the other trap on the second day.

The two SP's with traps were 460 and 470 m a.s.l. and located 400 m apart. The nearest SP with traps was located 400 to 700 m from the nearest 10 - 12 SP's on which groups of 14 to about 250 reindeer intermittently aggregated. The most distant SP with traps was located about 800 m from the nearest SP's on which reindeer aggregated. The SP's used by reindeer were 500 to 600 m a.s.l., and they ranged from about 50 to 10 000 m².

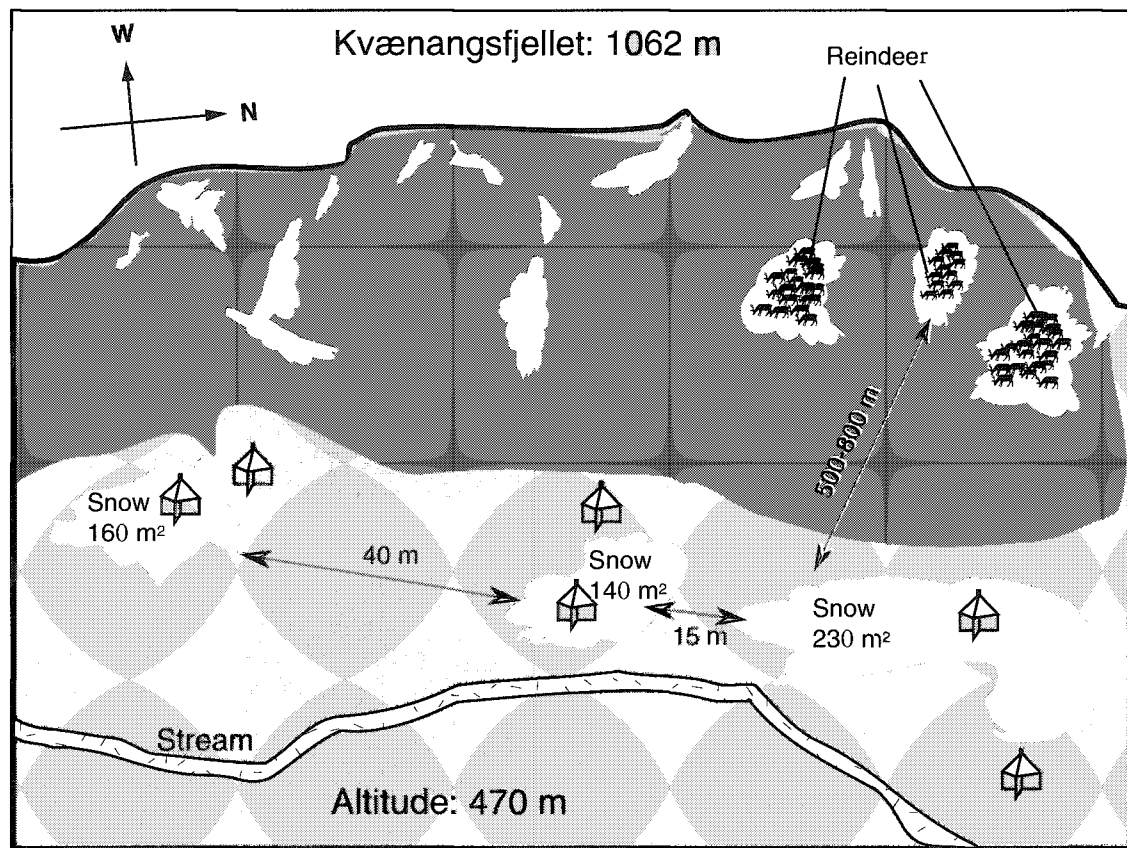


Fig. 1. Diagrammatic position of CO₂-baited insect flight traps with respect to snow patches on which reindeer aggregated, 1985.

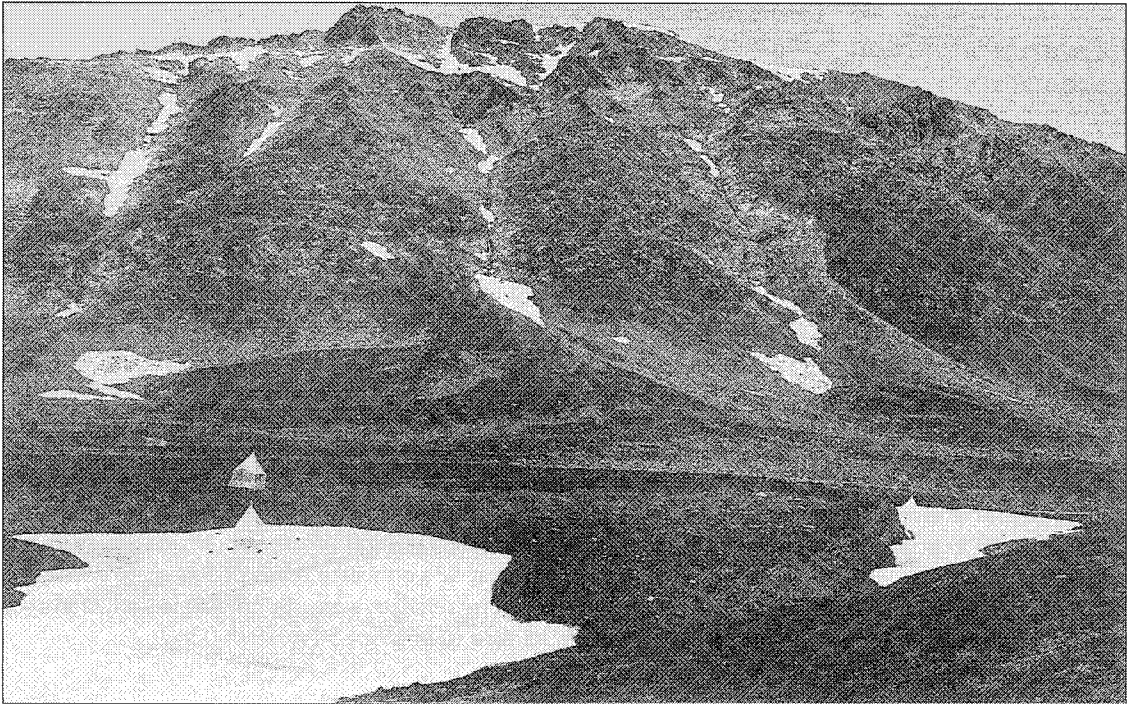


Fig. 2. Position of center and right pair of traps with respect to large groups of reindeer on three different snow patches, 1985.

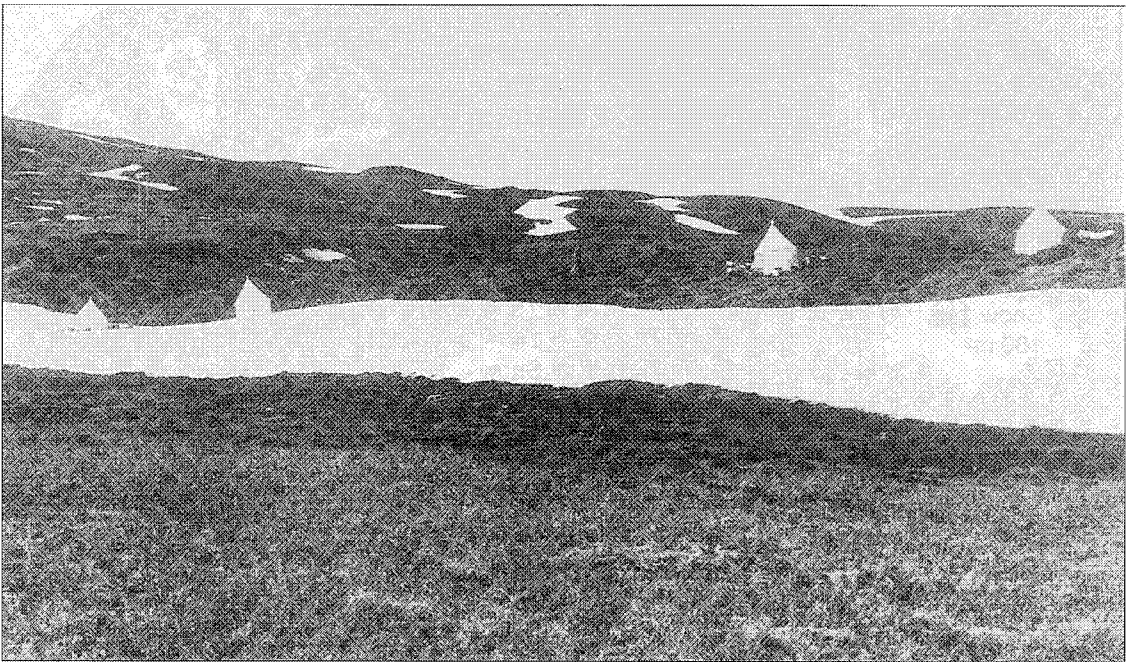


Fig. 3. Position of two CO₂-baited traps sited on a 25 X 330 m elliptical snow patch with respect to paired CO₂-baited traps at snow-free vidda sites, 1987.

Table 1. Species of Nematocera caught in CO₂-baited traps set on and off snow patches in 1985 and 1987.

Culicidae ¹	Simuliidae ²
<i>Aedes communis</i> (DeG.)	<i>Metacnephia saileri</i> (Stone)
<i>A. nigripes</i> (Zellerstedt)	<i>Prosimulium hirtipes</i> (Fries)
<i>A. pionips</i> Dyar	<i>Simulium corbis</i> Twinn
<i>A. punctor</i> (Kirby)	<i>S. ornatum</i> Meigen
	<i>S. rostratum</i> (Lundstrom)
	<i>S. vernalis</i> (Macquart)

¹ In other studies (unpubl. data) in July/August we collected all species except *A. nigripes* from a CO₂-baited reindeer model and from humans, and we collected *A. pionips* from a reindeer calf. Other Culicidae previously recorded from northern Norway include: *A. cataphylla* Dyar, *A. cinereus* Meig., *A. excrucians* (Walk.), *A. hexodontus* Dyar, *A. nearcticus* Dyar and *A. pullatus* (Coq) (Ardo, 1958; Mehl *et al.*, 1983). Some of these species may occur earlier or later in the year than when our studies were done.

² Larvae of other species collected from the study area included: *P. macropygum* (Lundstrom), *P. ferrugineum* (Wahlberg) and *S. cryophilum* (Rubtsov).

On 18 July the first trapping period was from 08.30 to 13.30 h (N.S.T.), the second from 13.30 to 18.30 h and the third "overnight" period from 18.30 to 07.30 h on 19 July. On 19 July traps were operated for only the first two periods (07.30 to 13.00 h and 13.00 to 18.30 h). Ambient temperature, light intensity and wind velocities were recorded periodically on both days. A Sontek BAT-12 with a microprobe constant of 0.25 s was used to measure shaded air temperature at different heights adjacent to traps set on and off SP's, and a Gossen Panlux Luxmeter (0 - 120 000 lux) was used to measure light intensities 1 m above ground. Wind velocities were measured as in 1985.

During trap operation on 18 July 1987, the behavior of groups of reindeer foraging within 200 to 300 m of the nearest trapping area was observed with binoculars and videotaped from distances of 15 to 100 m. Reindeer aggregated on the nearest SP's while traps were operated were observed and videotaped from distances of about 150 to 300 m. Videotapes were analyzed for individual and group foraging behaviors and for defensive, anti-fly behavioral responses of yearlings and adults (playful jumping/kicking movements of calves might have conflicted with defensive responses to flies).

Videotaping was conducted at about hourly intervals from 10.30 to 15.30 h, and at 19.00 and

20.00 h (after 15.30 h we left the area to recharge batteries). For 4 min each, we videotaped focal groups of 14 to 165 reindeer on a SP immediately followed by focal groups of 10 to 65 reindeer foraging on the vidda. By replaying videos numerous times each of the 274 reindeer in focal groups of 10-44 animals (Fig. 4) was observed for 2 - 4 min (some foraging animals moved out of view during a 4 min period). In the more closely clumped focal groups of 58-165 reindeer (Fig. 5) videotaped animals were observed in subgroups of 5-20 animals. As few animals on SP's exhibited anti-fly behavioral reactions during a 4 min period, videotape replays made it possible to quantify such reactions within subgroups. Most of the 824 reindeer in the eight videotaped periods were therefore observed for 4 mins each.

A three-way analysis of variance (ANOVA) (Systat, 1992) was performed to evaluate the effects of date, period of day, snow, and significant interactions for the 1985 data, and to evaluate the effects



Fig. 4. View of typical position of a small group of reindeer along the edge of a snow patch when occupying only about 15% of the total area, 1987.

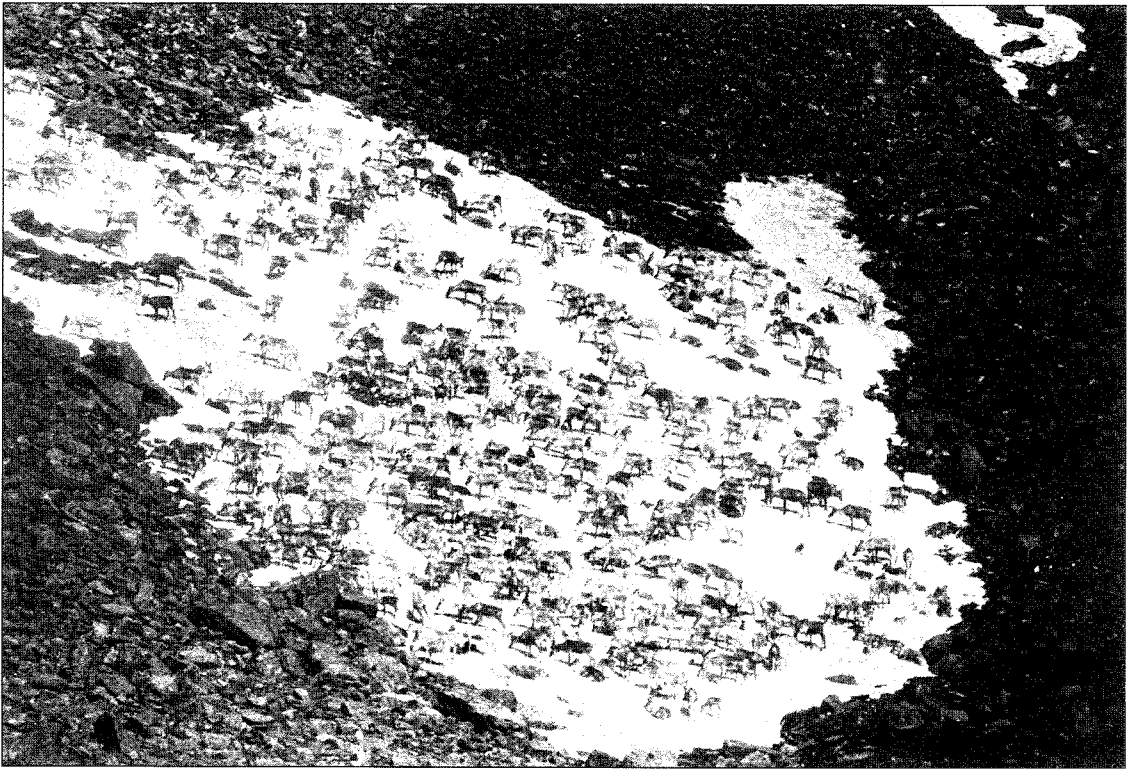


Fig. 5. View of typical aggregation of *a large group* of reindeer occupying an entire snow patch, 1985.



Fig. 6. Reindeer completely occupying a tiny remnant snow patch.

Table 2. Effects of snow (A) and of period of day (B) on insects trapped, 9 - 11 July 1985 and 18 - 19 July 1987¹.

(A) Effect of snow:

Year	Insect group	F	df	P	Adjusted least square means	
					On snow	Off snow
1985	Tabanidae	49.11	1	<0.00001	7.2	30.9
	Culicidae	13.10	1	0.014	32.1	78.0
	Simuliidae	31.56	1	<0.00001	0.6	3.9
	Misc. insects	155.71	1	<0.00001	8.0	110.6
1987	Tabanidae	96.18	1	<0.00001	0.6	11.4
	Culicidae	16.22	1	0.0004	14.5	54.7
	Simuliidae	112.95	1	<0.00001	0.06	4.6

(B) Effect of period of day:

Year	Insect group	F	df	P	Adjusted least square means		
					0800-1400 h	1400-2000 h	
1985	Tabanidae	11.23	1	0.003	21.4	10.7	
	Culicidae	20.19	1	0.00015	29.0	86.4	
	Simuliidae	24.61	1	0.00005	0.7	3.6	
	Misc. insects	6.72	1	0.016	23.3	40.2	
1987	Tabanidae	3.88	1	0.032	5.2	3.9	1.9
	Culicidae	58.38	1	0.000001	5.3	8.0	440.4
	Simuliidae	18.25	1	0.00001	0.3	1.5	3.3

¹ Results of test of effect of snow patches (A) and period of day (B) on insect catches in threeway ANOVAs (snow, period of day, and date as factors in 1985; snow, period of day, and boxes as factors in 1987). In 1985, date (the third cofactor not shown here) was significant for Tabanidae and Simuliidae. In 1987, boxes (the third cofactor not shown here) were significant only for Tabanidae (negative effect, $P=0.008$). Catch data were $\log_{10}(x+1)$ -transformed before analyses. Back transformed adjusted least square mean catches are also given to observe the magnitude of the effects.

of snow, period of day, boxes and significant interactions for the 1987 data. One-way ANOVA was used to test for differences between individual traps on and off snow. For all analyses trap catches of flies were transformed using $\log_{10}(n + 1)$ to eliminate dependence of the variance upon the mean and to aid additivity.

Results

Insect fauna trapped

Insects selected for species identification revealed that the CO₂-baited traps caught the species of Culicidae and Simuliidae listed in Table 1, plus *Hybomitra auripila* (Meigen) (Tabanidae) and *Hypoderma tarandi* (L.) (Oestridae). Because only a small portion of the insects trapped were specifically identified, it is likely that other species of Culicidae, Simuliidae and Tabanidae were included in the total

numbers trapped. The miscellaneous non-hematophagous insects trapped consisted mostly of midges and crane flies (Diptera) and caddisflies (Trichoptera). Other Diptera, Hymenoptera, Plecoptera, Ephemeroptera and Lepidoptera were trapped in far fewer numbers. Hematophagous species of Ceratopogonidae were included with tallies of other midges.

Analysis of trapping data

Analysis of 1985 data (Table 2) revealed that CO₂-baited traps placed on SP's caught significantly fewer tabanids, culicids, simuliids and miscellaneous insects than paired traps on snow-free vidda terrain. All hematophagous flies caught were females, and for the Tabanidae, 98% were *H. auripila*. Significantly more tabanids were caught during the first period, whereas significantly more culicids and simuliids were caught during the second period

Table 3. Total numbers of parasitic flies caught in CO₂-baited insect flight traps, 18 and 19 July 1987¹.

Taxon	Traps on snow patches		Traps on snow-free sites	
	Boxes ²	No Boxes	Boxes ²	No Boxes
Culicidae	709	1144	1376	1352
Simuliidae	1	0	64	65
Tabanidae	5	18	127	292

¹ A pair of traps set 15 m and 30 m apart on each of two snow patches was matched with a pair of traps set at 20 and 25 m apart at two snow-free vidda sites (see methods for other details of the experimental design).

² Ten to 12 cardboard boxes were arranged around the peripheral margin of a trap to simulate silhouettes of reindeer resting on a snow patch.

(Table 2). The total numbers of insects caught on:off SP's were: Tabanidae, 172:746; Culicidae, 934:1834; Simuliidae, 22:124; miscellaneous insects, 219:2124. In addition, traps located off SP's caught four female *H. tarandi* compared to none on SP's.

We found no position effects between sets of traps as there were no significant differences ($P>0.07$) among trap catches on SP's or off SP's for any of the insect taxa in both years.

The total number of parasitic flies caught in 1987 is shown in Table 3. In 1987 oestrid flies were neither seen nor trapped in the SP study area; at a warmer, inland study area 130 km SE we first trapped female *H. tarandi* on 20 July and *Cephenemyia trompe* (Modeer) on 21 July (Anderson & Nilssen, 1996). Analysis of the 1987 trapping data (Table 2) revealed that paired CO₂-baited traps operated on SP's caught significantly fewer tabanids, culicids and simuliids than similar pairs of traps operated at snow-free vidda sites 10 m from the edge of SP's. In 1987, significantly more culicids and simuliids

Table 4. Temperatures (°C) recorded at different hours during operation of CO₂-baited traps.

Date	0900	Max	1500	2100
9 VII '85	18	22	18	15
10 VII '85	17	22	17	15
11 VII '85	17	23	21	16
18 VII '87	18	25	23	18
19 VII '87	23	25	23	—

were caught in the overnight trapping period (18.30 - 07.30 h), but during this peak period of mosquito host-seeking activity there was no significant difference in the number of mosquitoes caught on versus off SP's ($F=0.85$, $P=0.41$, $df=1$). Significantly fewer tabanids were caught in the overnight trapping period and in traps operated with boxes deployed as reindeer silhouettes (Table 2). However, boxes resulted in no significant difference in catches of either mosquitoes or simuliids (Table 2). As we periodically monitored trap catches we saw that many tabanids attracted to traps with boxes kept flying from box to box and crawling over box surfaces. This behavior resulted in many of the tabanids seen on boxes not entering the interior of the flight trap, and not, therefore, being captured.

Table 5. Mean temperatures (°C) at four traps set on snow patches and four traps set at snow-free vidda sites.¹

Height above substratum	Snow patch traps	Vidda traps
0.5 m	20.5 ± 1.49	22.8 ± 0.44
1.0 m	22.3 ± 0.60	23.2 ± 0.22
2.0 m	22.9 ± 0.29	23.3 ± 0.09

¹ Temperatures recorded between 17.30 and 18.00 on 19 July 1987. At 13.30 h temperatures at SP-I were 23.3 at 0.5 m, 24.5 at 1.0 m and 24.0 at 2.0 m; at the paired vidda trap it was 25.0 at 1.0 m. On 18 July at 20.00 h the temperature at SP-II was 15.6 at 1.0 m and 19.0 at 1.0 m above the vidda.

Weather conditions on trapping days

The weather remained sunny and unusually warm during the three 1985 trapping days (Table 4), and the wind velocity never exceeded 4 m/s. A long period of cold (5 - 8 °C), rainy weather prevented further SP trapping before accessible SP's melted. Both 18 and 19 July 1987, were exceptionally warm, sunny days (Table 4). Wind velocities varied from 0 - 3 m/s, and light intensity varied from 90 000 to 100 000 lux. Throughout the day there was little difference in shaded air temperature taken at traps operated on and off SP's (Table 5).

General foraging/resting cycles of observed reindeer

On 18 July 1987, an observed herd of about 800 reindeer composed of cow-calf pairs, yearlings and young bulls remained separated into two approxi-

Table 6. Reindeer defensive anti-fly behavioral reactions to observed and inferred insect harassment.

Reactions observed from 0900 to 1600 h (tabanids predominant)	Reactions observed after 1600 h (mosquitoes predominant)
– Head shake only	– Head shake only
– Head and neck shake	– Head and neck shake
– Head, neck and shoulder shaking in rapid succession	– Head, neck and shoulder shaking in rapid succession
– Body shaking ¹	
– Rump shaking only	– Rump shaking only
– Biting at shoulder, rump or hind leg	– Ear flapping (twitching)
– Kicking front or hind leg	– Brief scratching of face with hind leg (as distinct from a rapid brushing motion)
– Brushing face or ear (or both) with a hind leg	
– Slow elliptical rotation of head from side to side, as when trying to prevent a large fly from landing, rather than shaking it off (as distinct from rapidly shaking the head from side to side) ²	

¹ Simultaneous shaking of shoulders, abdomen and rump.

² Observed only for animals on snow patches.

mately equal groups from 07.30 to 11.00 h and 12.30 to 15.30 h. While one group foraged for about an hour, animals in the other group remained standing or lying on SP's. As foraging animals approached and moved onto SP's, animals on SP's moved off the snow onto the vidda where they began foraging. These two groups of animals continued to exchange positions and activities throughout most of the day. From 11.00 to 12.30 h, 85 - 90% of all reindeer were aggregated on SP's, whereas at 19.00 and 20.00 h, only 15 and 10% of the reindeer were on SP's. By 20.30 h only a few reindeer were on SP's. From 06.40 to 07.00 h on 19 July, all reindeer were seen lying down either on (90%), or next to, two of the highest SP's in the area. By 07.00 h on this warm (23 °C), sunny morning all reindeer had dispersed over the mountains and out of the area. In 1984 and 1985 few reindeer were seen on SP's after 20.00 - 21.00 h.

The SP resting reindeer intermittently used any of 10 - 12 different SP's, with most animals aggregated on just three or four SP's. All SP's used by reindeer were 100 - 150 m higher and within about 400 - 700 m of the SP's with insect flight traps.

Activity and grouping of reindeer on snow patches

As animals first moved onto a SP many ingested snow, and some occasionally did this well into the 4 min observation period. The majority of reindeer in all focal groups on SP's were spaced from < 1.0 to 2.0 m apart; groups over 100 were primarily group-

ped along one edge, occupying only 15 - 25% of the total available SP. Smaller groups (also bunched near an edge) occupied less than 10% of a SP (Fig. 4). Many animals in the larger groups remained standing or lying within less than a meter from the edge. Reindeer on large SP's were never seen aggregated in the center of a patch, but on some SP's the combined bulk of 100, or more, reindeer would nearly obscure the entire SP (Fig. 5).

Animals on SP's mostly remained immobile (either standing or lying). At 10.30 h 50% were lying on the snow. From 11.30 through 15.30 h 5 - 10% were lying, and at 19.00 and 20.00 h 90% and 95% were lying down. Many standing animals had their legs slightly extended outward, and their neck extended forward and down so the head and muzzle were positioned close to the snow (Figs. 4, 5, 6). Once positioned on a SP 10 - 25% of the animals occasionally walked a few steps to change position (often after exhibiting an anti-fly defensive behavior) and then again remained immobile.

Activity of foraging reindeer

Reindeer mostly foraged peacefully while slowly moving over the vidda. In contrast to SP reindeer, most foraging animals were spaced several meters apart. Their typical foraging behavior was much like that reported by Thomson (1971), with trotting being rare. The general foraging behavior of different focal groups observed throughout the day is described in Fig. 7.

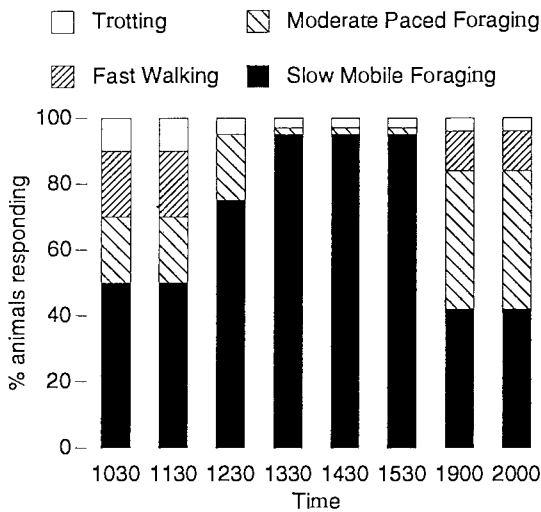


Fig. 7. Foraging activity of observed focal groups of reindeer at different times, 1987 (SMF, animals taking a bite of forage every few steps; FW, bites only at every several meters).

Anti-fly behavior of reindeer

Reindeer on and off SP's exhibited the same behavioral responses to observed and inferred harassment by flies (Table 6). Although reindeer exhibited several similar anti-fly behaviors when either mosquitoes or tabanids were most abundant (Table 6), notable differences included: leg kicks; biting at the shoulder, rump or hind leg; and face rubbing with the hind leg. These were common reactions seen between 09.00 and 16.00 h, and rarely seen after that. Tabanids were seen landing on the face, back and legs, and mosquitoes were seen flying around the head, and landing on the face and around the eyes, but species of both taxa may have fed elsewhere, as well. At the time of our observations most adult reindeer appeared to have shed less than half of their winter hair.

Focal groups of foraging reindeer were most harassed by flies from 10.30 to 13.30 h (Fig. 8). Concurrent trap catches (and anti-fly defensive behaviors) indicated that they were responding to maximum tabanid host seeking activity in the morning. During periods of peak tabanid activity, the pace of the foraging group increased two- to threefold compared to that at other times of the day (Fig. 7). Individual animals walked faster as they foraged, and few stopped longer than to take a few bites. The most reactive animals periodically shook their heads from side to side or shook head, neck and shoulders

in rapid succession; some occasionally stopped and lightly shook their body or only their rump. Because harassment by the total number of concurrently active parasitic flies was no more than moderate at any time, it was common to see some animals calmly lying on the vidda while others were mildly reacting to flies. Reindeer exhibited much lower levels of anti-fly reactions to increasing numbers of mosquitoes than to tabanids (Fig. 8). Overall, the proportional harassment level never reached more than one anti-fly defensive reaction per animal during a 4 min period (Fig. 8). Even then only 30 - 40% of the reindeer videotaped exhibited one, or more, anti-fly defensive behavioral response during a 4 min period.

Compared to foraging animals the anti-fly behavioral responses among reindeer on SP's occurred at much reduced levels at 10.30 and 12.30 h, but at only somewhat reduced levels at other times (Fig. 8). As for foraging reindeer, only a few animals in each SP group exhibited anti-fly behaviors during a 4 min period (Fig. 7). At 14.30 h, for example, only 33 of 165 SP resting reindeer exhibited 55 defensive anti-fly behaviors (0.33/animal/4 min), whereas 5 of 24 foraging reindeer exhibited nine such reac-

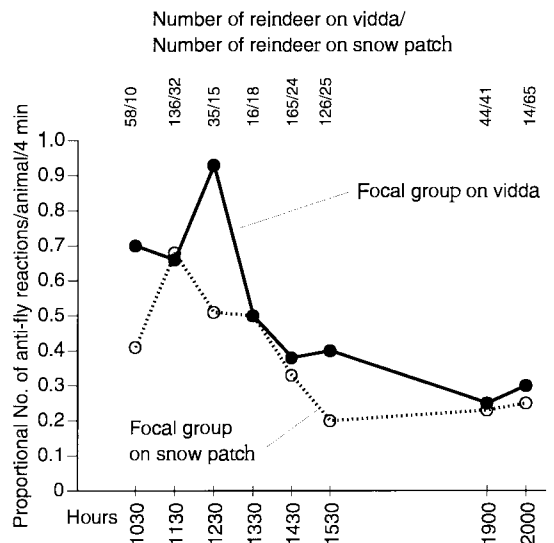


Fig. 8. Proportional number of defensive anti-fly reactions per reindeer during 4-min observation periods of focal groups resting on snow patches and foraging over snow-free vidda areas, 18 July 1987. At 12.30 h, 6 of 15 vidda animals exhibited 14 anti-fly behaviors, and at 20.00 h, only 9 of 65 vidda animals exhibited 21 anti-fly behaviors.

tions (0.38/animal/4 min). Some animals exhibited several anti-fly behaviors in succession.

Discussion

Hematophagous flies known to be attracted by CO₂ and host odors were caught in proportionately much greater numbers in CO₂-baited traps sited on SP's than were the various non-hematophagous insects (Table 2). Nearly 10 times as many of the latter, non-host-related insects were caught in traps set at snow-free sites. Nevertheless, except for mosquito catches during the overnight trapping period (18.00 - 07.30 h) in both 1985 and 1987, traps on SP's caught significantly fewer tabanids, culicids and simuliids than traps at snow-free sites.

Our trap catch data indicate that during warm diel periods reindeer might obtain relief from attacking flies while resting on SP's because of lower fly densities than on snow-free vidda areas. However, analysis of videotapes for reindeer anti-fly activities on and off SP's indicated that such relief usually was minimal (Fig. 8). Instead, at the fly densities and climatic conditions encountered, reindeer appeared to use SP's primarily as a means of thermoregulation. The fact that most reindeer had moved off SP's by the time mosquito host-seeking activity was beginning to peak during cooler evening hours supports this conclusion.

The contradiction between trap catches on and off SP's and the observed fly harassment index of reindeer on and off SP's can be elucidated by noting: (i) that host odors and CO₂ emitted by 50 - 150 reindeer occupying an entire SP (Fig. 5), or grouped along the edge of a large SP (Fig. 4), would constitute a much greater source of attraction for parasitic flies than just one or two CO₂-baited traps confined to the center of a SP, and (ii) that the various anti-fly defensive reactions of reindeer on SP's indirectly indicated that flies in the following swarm continued to pursue and attack animals as they moved onto a SP. Attacks by tabanids and mosquitoes that pursued and attempted to bite humans as we walked onto SP's to service traps confirmed such behavior. After 5-min waiting periods, Downes *et al.* (1986) also reported mosquitoes landing on people positioned on SP's.

We inferred fly attraction to reindeer on SP's from the fact that, throughout different 4-min observation/videotaping periods, reindeer in SP focal groups exhibited the same anti-fly behaviors seen when flies were observed attacking foraging

animals. Reindeer that had been on a SP for an undetermined period of time before videotaping began also exhibited these same anti-fly behaviors. The data in Table 6 show that reindeer, like many other animals, respond in many similar ways to attacks by different species of flies. They may flick/twitch their ears or tail in response to any landing/feeding fly and, in response to *H. tarandi*, tabanids, and larger numbers of culicids than encountered in this study, reindeer usually react with the same type of overall body shaking used to shake off water. Thus, when animals are observed from afar there often is no way to determine whether they are responding to tabanids, culicids or some other kinds of flies. In such circumstances concurrent catches of flies in host-mimicking traps provide important data.

Although their unbaited sticky traps on SP's caught no mosquitoes (and no other parasitic Diptera) Ion & Kershaw (1989) reported that insect harassment of reindeer "... was generally higher on snow ... than off snow ...". We did not see or trap oestrid parasites in 1987, but Downes *et al.* (1986) reported that, "Frequent observations of oestrid-avoidance behavior were made while the animals were on the snow patches". Eight of the 25 *H. tarandi* females caught by these workers were captured on SP's (Downes *et al.*, 1986). Bergman (1917) and Natvig (1916, 1918) also reported seeing reindeer on SP's attacked by oestrids.

The small decreases in anti-fly defensive behaviors observed for animals on SP's (Fig. 8) indicate that the use of SP's for thermoregulation also may have secondarily resulted in a coincidental, non-causal related, minor reduction in numbers of parasitic flies attacking reindeer. When exposed to larger densities of tabanids and mosquitoes than we encountered, reindeer may aggregate on large SP's and windy mountain tops to obtain relief from attacking flies, but we found no quantitative fly data associated with such behavior, and few accounts of climatic conditions when such behavior was observed.

For horses, Hughes *et al.* (1981) reported that animals moving to a Chamadon relief area (usually exposed to high wind velocities) did not experience a reduction in the number of tabanids harassing them. Thus, horses and reindeer may be more tolerant of attacking flies (and respond with fewer anti-fly behaviors) when heat stress is reduced. In close range observations of tame reindeer, Bergman (1917) and Espmark (1961) reported that resting

reindeer that had been ruminating for awhile had a much higher level of tolerance to parasitic flies than other reindeer. Our results (Fig. 8) agree with these observations, as can be seen from the reduced anti-fly reactions among SP focal groups videotaped at 10.30, 12.30, 15.30, 19.00 and 20.00 h (already present on a SP for an undetermined period of time before the 4 min period started), compared to SP focal groups videotaped at 11.30, 13.30 and 14.30 h (videotaped immediately after moving onto a SP). However, for reindeer standing or lying on SP's, reductions in anti-fly behaviors may result from both an increased level of tolerance and a reduction in the number of fly attacks with increasing time spent on a SP.

Our observations of reindeer behavior indicate that the numbers of parasitic flies attacking foraging animals were not large enough to cause the tight grouping of individuals (for protection) into a single large herd as reported by several others (e.g. Breev, 1951; Pruitt, 1960; Kelsall, 1968; Baskin, 1970; Thomson, 1971; Calef & Heard, 1980). The close bunching of reindeer in herds or groups, or bunched grouping of traps, results in reduced harassment by flies (Breev, 1951) and reduced trap catches (Helle & Aspi, 1983; Helle *et al.*, 1992), although the benefit derived by individual animals (or reduced trap catches) depends on the position within the group.

The 1987 CO₂-baited trap catches (and reactions of foraging animals) revealed that fly harassment levels were low throughout most of the day. Baited traps caught about 105 tabanids/trap/day (most caught from 08.00 to 16.00 h) and about 700 mosquitoes/trap/day (most caught during the crepuscular period). Because, on the basis of animal weight, the CO₂ output of a trap equalled that of 3-4 reindeer, one animal would have been attacked by an estimated 170-230 mosquitoes/day and 25-35 tabanids/day. The estimated attack rate during the couple of peak morning hours of tabanid activity was 4-6 flies/h, and at other times only 1-3 flies/h. As CO₂-baited traps catch the same species that attack reindeer (Helle *et al.*, 1992, Anderson & Nilssen, 1996), and in the same relative abundance (Helle *et al.*, 1992), trap catches can be used to estimate the numbers of flies attacking animals. Because isolated reindeer and traps attract many more flies per animal or trap than when animals or traps are clumped (Breev, 1950, 1951; Helle & Aspi, 1983; Helle *et al.*, 1992), we believe our estimates represent maximum attack rates.

Because reindeer continued to exhibit the same intermittent SP resting behavior from 13.30 to 18.30 h (when trap catches were lowest), it seems evident that reindeer moved onto SP's to cool down after a period of foraging during a warm, sunny day. The fact that 90% of the reindeer were aggregated on SP's between 11.00 and 12.00 h (Fig. 8) suggests that this might have been related to increasing numbers of tabanids (Table 2). However, in view of the rapid increase in temperature on 18 July (15 °C at 07.30, 18 °C at 09.00, 21 °C at 10.00 and 24 °C at 12.00 h), animals foraging prior to these times also may have been moving onto SP's to cool down, as they did at other times of the day. The interplay between fly harassment (mostly by tabanids) and high temperatures on sunny days probably accelerated a reindeer's need to cool down (energy expended in anti-fly defensive behaviors and in increased rates of locomotion would contribute to a faster rise in body temperature).

Segal (1980) noted that high summer body temperature (heat stress) in reindeer was associated with solar radiation at high ambient temperature, and that body surface evaporative cooling was minimal because reindeer lack thermoregulatory sweat glands and a perspiratory system. However, on hot, sunny days reindeer may enhance heat dissipation by panting (Segal, 1980; Blix & Johnson, 1983; Folkow & Mercer, 1986), and by behavioral actions (e.g. standing on SP's, in shady or windy areas, or in cool water (Segal, 1980). Much heat loss occurs by way of the legs (Scholander *et al.*, 1950; Segal, 1980; Folkow & Mercer, 1986) and hoofs (N.A. Øritsland, Norsk Polarinstitut, Oslo, pers. comm.) of caribou/reindeer. Movement to cooler environmental habitats (like SP's) would enable reindeer to accelerate heat loss rates (through conductive heat loss to snow and convective heat loss to cool air), without having to engage as heavily in panting, which is an energy-demanding activity (Folkow & Mercer, 1986).

Other evidence that the use of SP's represented thermoregulatory behavior of observed reindeer in our study was: (i) biting and ingesting snow (usually after first walking onto the SP), (ii) lying down on the snow, (iii) standing body posture with neck extended forward and down and the muzzle held just above the snow surface (presumably to inhale cool air; *C. trompe* females were neither seen nor trapped during these studies), (iv) minimal movement while on the SP, whether lying or standing and (v) non-use of SP's during cooler nighttime

hours. In other studies (Anderson & Nilssen, 1996; unpubl. data) we noted that reindeer did not aggregate on SP's on cooler, mostly cloudy days, although CO₂-baited traps caught even larger numbers of mosquitoes and black flies throughout some such days, and large swarms also attacked humans. In subarctic USSR, Breev (1950) also reported that attacks of mosquitoes and simuliids increased during overcast periods. Although we did not see reindeer aggregated on SP's during nighttime hours, or on cool, cloudy days when mosquitoes and simuliids were active, or trap tabanids or oestrids on such days, near Tromsø, Norway, on warm, sunny days we saw reindeer on SP's as early as late May 1984, prior to seasonal parasitic fly activity. Downes *et al.* (1986) also saw caribou using SP's prior to the appearance of parasitic flies. Although their mosquito counts at humans suggested that caribou could reduce harassment by mosquitoes by moving to SP's and to higher elevations, Downes *et al.* (1986) also concluded that, for the Burwash herd in British Columbia, Canada, SP habitat likely served a thermoregulatory function. Ion & Kershaw (1989) on the other hand, surprisingly concluded that relief from insects was a more likely explanation for caribou occupation of SP's than was thermoregulation, although they reported more insect avoidance activity of caribou on SP's than off.

During the warm, sunny days of our study mosquito and simuliid catches increased from morning through the evening and nighttime hours, whereas the activity of tabanids declined throughout the day (Table 2). Such diel activities are similar to those of many other trapping studies. For example, it is commonly known that mosquito biting activity is suppressed during warm, sunny periods of a day, and our trapping results (even for an area far north of the arctic circle) confirmed this fact. Therefore, because 50 - 90% of the reindeer we observed were intermittently occupying SP's when mosquito densities were lowest (Table 2) and only about 10% of the animals were on SP's at the time mosquito numbers were greatest, it may be erroneous to relate mosquito landing/biting counts on humans to the choice of microhabitats used by caribou/reindeer between 09.00 and 19.00 h on warm, sunny days, although several previous studies have done so. Compared to daytime hours, it was interesting to learn that during the evening/overnight periods, SP's had the opposite effect on the behavior of reindeer and mosquitoes (*i.e.*, few reindeer occupied SP's then, whereas during the peak period of host-see-

king activity of mosquitoes there was no significant difference in the numbers caught on versus off SP's).

Overall, the bulk of our data support the conclusion that reindeer observed in this study used SP's to assist in thermoregulation on warm, sunny days, much like *Alces alces* in Canada seek out wetland areas and lay in water to reduce heat stress (Renecker & Hudson, 1990). Videotapes proved invaluable for observing and quantifying the anti-fly behaviors of reindeer engaged in various activities at different times of the day. Repeated viewings of each group of reindeer videotaped while on and off SP's resulted in some 800 animals being observed for 4 mins each.

The fact that significantly fewer hematophagous flies were caught when just one or two baited traps were centered on a SP (versus paired traps set at snow-free vidda sites) suggests that if only 5 - 10 reindeer occupied the center or the upwind edge of a large SP on a windy day, the number of parasitic flies attacking them might be greatly reduced (the CO₂ output of one trap approximated that of 3 - 4 reindeer). However, because of the gregarious nature of reindeer, it is rare to see so few animals on a SP. Most reindeer we observed aggregated and remained in large groups on just two or three SP's at the same time as 10 - 20 neighboring SP's had no reindeer. Considering the odoriferous and other attractive factors associated with a biomass of 50 to several hundred reindeer, it seems doubtful that aggregation of such numbers on a SP would result in much of a reduction in the numbers of attacking flies, particularly for the many animals standing/lying a meter or less from the edge of a SP (Figs. 4, 5). There would be even less possibility of obtaining relief from attacking flies when most animals crowded together on tiny remnant SP's are only a step away from snow-free terrain (Fig. 8). To investigate the motivation and benefits of caribou/reindeer SP aggregation behavior in more depth, workers would need to operate many more baited traps set on and off SP's, and to observe and collect flies from tame animals.

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