Warble infestations in some Canadian caribou and their significance

Donald C. Thomas[1] and **Hendrick P. L. Kiliaan**[1]

[1]Canadian Wildlife Service, 4999-98 Avenue, Room 210, Edmonton, Alberta, Canada T6B 2X3.

Abstract: Warble fly larvae *(Oedemagena tarandi)* occurred in 97-100% of barren-ground caribou *(R.t. groenlandicus)* sampled in March from the Beverly herd. In December, they occurred in 98% of males and 75% of females. Larvae numbers increased up to several-fold from December to March. Within age classes, males generally were more heavily infected than females. Annual differences were small. Larvae occurred in 14 and 26% ofitwo populations of Peary caribou *(Rangifer tarandus pearyi)* on the Canadian Arctic Islands. In them, incidences of larvae were unrelated to sex or age. Greater than average numbers ofi larvae in barren-ground caribou sometimes were associated with females in relatively poor condition and therefore less fecund. These results are discussed in relation to current hypotheses of the factors that affect warble infections.

Key words: condition, fecundity, *Oedemagena*, *Rangifer*

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Introduction

Data are scarce on the infestation levels of warble parasites in caribou in northern Canada. Kelsall (1975) reported frequencies and numbers of scars and holes in 312 museum hides of caribou obtained throughout Canada. The only other data for barren-ground caribou in north-central Canada were for 132 specimens from various seasons and herds (Kelsall, 1968), including Banfield's (1954) data.

Even less is known about the possible influences of the adult fly and its larvae (Dieterich and Haas, 1981) on the ecology of caribou. Tashnikov (1971) apparently found a positive relationship between numbers of larvae and fat reserves; Huot and Beaulieu (1985) the same for yearlings.

Several reasons were advanced to explain differences in infection levels among caribou herds and age classes and between the sexes. Climatic differences and migratory habits are most frequently implicated (e.g., Kelsall, 1975). Immunological factors are now believed to be important (e.g., Helle, 1980; Solomakha, 1990).

The purpose of this paper is to: (1) examine the effects of latitude, year, season, age, and sex on larval frequencies and numbers in a sample of 1 377 caribou; (2) explore relationships between infestation levels and fat reserves and fecundity; and (3) discuss the factors influencing the infestation levels.

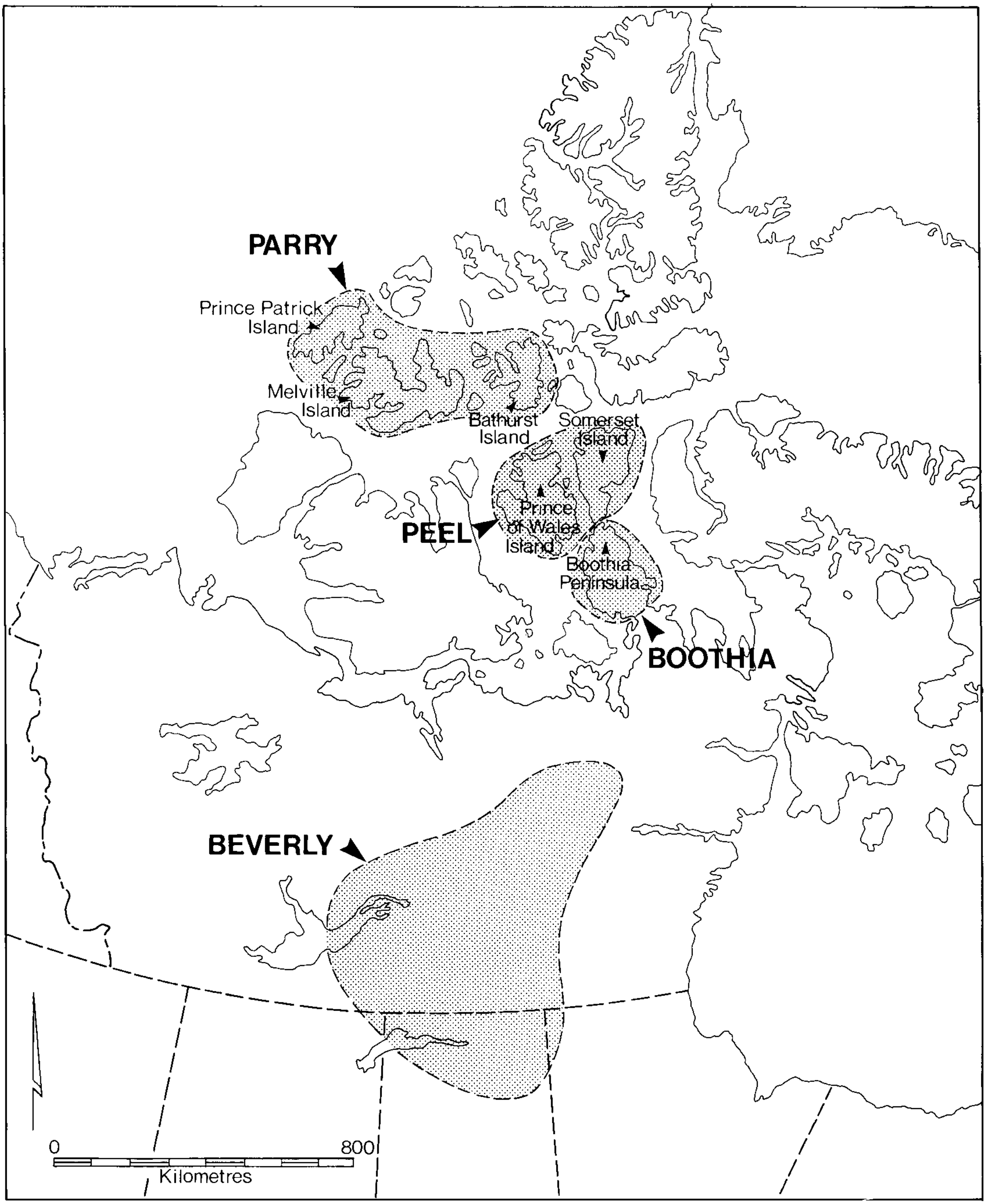

Fig. 1. Geographic locations of caribou populations mentioned in this report.

Methods

The barren-ground caribou were obtained from the Beverly herd in north-central Canada. The insular sample consisted of 203 caribou from the following locations: Boothia Peninsula (n=22); and Somerset (47); Prince of Wales (48); Bathurst (6); Melville (35); Eglinton (7); and Prince Patrick (38) islands. Data analysis revealed that three major groupings of locations could be made to increase sample sizes: Boothia Peninsula, Peel Islands (Somerset and Prince of Wales) and Parry Islands (all the others).

Hides of shot caribou were removed and the larvae or the larval holes were counted. Where numbers were >100, the larvae were counted only on one lateral half of the hide. Numbers of larval holes in hides were bilaterally similar (Kelsall, 1975).

Ages of caribou < 2 years old were obtained by teeth eruption criteria. The ages of older caribou were estimated from counts of lines in the stained cementum of the first incisor and first molar. Age is expressed to the next birthday, i.e., caribou 1 1/2 and 1 3/4 years old in December and March samples, respectively, are presented as 2 years old. Mean numbers of larvae included all caribou in the Beverly herd and only infected animals on the arctic islands. Data for warble larvae are highly variable, which precludes statistical differences between data sets unless the means are markedly different and large samples are available.

The grouping ofi age classes was based on homogeneity of means: generally >2 years for numbers of warble larvae, back fat depths, and weight of kidney fat; > 3 years for body weight of females; and > 4 years for body weight of males and fecunndity of females. We used Kruskal-Wallis ANOVA and t statistics for comparisons among and between means and regression analysis to explore relationships among variables.

Observations of the behavior of barren-ground and Peary caribou were obtained over several summers. Included were general opportunistic observations and interval scanning of focal individuals.

Results

Occurrence and numbers of warble larvae in barren-ground caribou

Warble larvae were present in all but 1 of 238 males examined in March and 2 of 123 inspected in December. Larvae were present in 97-100% of females in March samples, 1980-87, and in 61-92% of females > 1 year old in December samples, 1982-86. In females > 2 years old, average numbers of larvae were 21, 12, 3, 6, and 8 in December, 1982 through 1986, and 33, 35, 39, 56, 37, 33, 33, and 37 in March, 1980 through 1987. Standard deviations were almost double the means in December and about equal to the March means, e.g., overall means 9.1 (SD 18.8) and 38.3 (SD 42.9). Lack of a statistical difference does not preclude a biological difference in the 1982-83 sample.

In pooled samples for each season (Table 1), the largest numbers of larvae were in males > 5 years old, followed by males 5, 2 and 1 year old, and finally by males 3 and 4 years old. In females, those 1 and 2 years old were most-heavily infected with marginal differences in older classes. There was an overall downward trend ($P<0.05$) with age of females in December and March. Comparable changes were found within winters.

Average numbers of larvae present in March were in some cases orders of magnitude larger than in December (Table 1). A correction for those with no warbles in December would reduce the difference marginally. Larvae were slower to develop in females than in males and slower in females > 3 years than in younger ones.

Occurrence and numbers of warble larvae in Peary caribou

Frequency of occurrence was unrelated to age or sex. E.g., Peel Islands (largest sample): females 1-4 years, 29% (n=34), females > 4 years, 28% (n=29); Boothia 79% for 14 females vs 63% for 8 males, Peel 29% for 63 females vs 26% for 27 males; and Parry 14% for 51 females vs 15% for 20 males. The overall incidences of warble larvae in all ages and both sexes were: Boothia 73% (n=22); Peel 28% (90); and Parry 14% (71). Warble larvae occurred in only 11 and 16% of 35 and 38 caribou sampled on Melville and Prince Patrick islands, respectively. There was a general increase in warble numbers in infected caribou aged 1-4 years on Boothia Peninsula but sample sizes

Table 1. Frequency of occurrence (percent) and mean numbers of warble larvae under the skin of caribou sampled from the Beverly herds in December (1982-86) and March (1980-87).

Sex/age (yr)	Numbers of warble larvae							
	December				March			
	Freq. %	Mean	SE	n	Freq. %	Mean	SE	n
F 1	100	18.8	4.1	5	100	124.7	14.1	29
M 1	100	65.3	14.0	15	100	118.7	18.3	20
F 2	92	23.7	4.1	26	100	114.2	11.6	59
M 2	100	47.6	6.4	26	100	171.1	16.1	57
F 3	87	14.1	3.0	30	98	45.7	5.1	82
M 3	95	18.4	2.8	42	99	93.1	9.4	90
F 4	61	5.8	1.5	38	97	46.2	5.0	61
M 4	100	25.9	5.2	24	100	80.8	10.3	28
F 5	84	12.2	7.2	25	98	28.3	3.8	56
M 5	100	77.0	22.0	10	100	145.5	43.7	20
F 6-8	76	10.5	2.5	58	97	36.1	3.8	153
F 9-11	59	4.2	1.3	22	99	37.1	4.9	91
M>5	100	147.7	49.1	6	100	222.6	36.4	23
F>11	61	5.4	2.4	18	97	35.9	5.5	36
F>3	70	8.2	1.5	161	98	36.8	2.1	397
M>3	100	56.9	11.6	40	100	144.9	18.6	71
F>4	72	9.0	1.9	123	98	35.1	2.3	336
M>4	100	103.5	23.7	16	100	186.7	28.4	43

were small (Table 2). No such trend was present in Peary caribou on the Peel Islands except perhaps in males.

Numbers of larvae relative to condition in barren-ground caribou

Regressions of warble numbers and condition variables for each caribou produced no significant correlation coefficients. The test was unduly influenced by some extreme numbers of larvae. Kruskal-Wallis tests indicated nine significant relationships between warble number frequencies, in 25- and 50-unit intervals, and condition variables: in males and females 2 years old in December (back fat); in males 3 years old in March (weight); in males > 3 years old in March (weight and back fat); and in females > 4 years old in December (weight and back fat) and in March (back fat and kidney fat). Correlations were positive in females and negative in males.

Analysis of data for females 3-5 and >2 years old in the March 1986 sample (Thomas unpubl.) revealed significant ($P<0.05$) differences in back fat depths and kidney fat indices between those with greater than, and less than, the median numbers of warble larvae for those age classes. We pooled the data for all years and made similar comparisons using the mean

Table 2. Mean numbers of warble larvae in infected caribou, mostly *R.t. pearyi*, sampled from three areas of the Canadian Arctic north of 70°, 1974-79.

Age Class (yr)	Mean number of larvae (n)					
	Boothia Pen.		Peel Isl.[a]		Parry Isl.[b]	
	Females	Males	Females	Males	Females	Males
1	13(2)	4(1)	33(1)	5(1)	(0)	(0)
2	28(1)	42(2)	37(5)	18(2)	(0)	(0)
3	(0)	278(1)	29(2)	5(2)	(0)	(0)
4	53(2)	91(1)	36(2)	35(1)	(0)	(0)
>4	10(6)	(0)	42(8)	153(1)	54(7)	47(3)
1-4	32(5)	91(5)	35(10)	12(6)	(0)	(0)
All	21(11)	91(5)	38(18)	34(7)	54(7)	47(3)

[a] Somerset and Prince of Wales islands.
[b] Bathurst, Melville, Eglinton and Prince Patrick islands.

Table 3. Physical condition variables in females having fewer than, and more than, the mean number of warble larvae in pooled samples in December, 1982-86, and March, 1980-87.

Age (yr)	Condition variable	December			March		
		<mean		>mean	<mean		>mean
2	Weight (kg)	61.1		62.9	60.3		64.0
3	Weight (kg)	74.0		75.8	77.3		76.1
>3	Weight (kg)	84.8	**	79.0	85.2	**	82.2
2	Back fat (mm)	8.1		4.5	3.9		4.3
>2	Back fat (mm)	14.9	**	7.6	15.5	**	11.9
2	Kidney fat (g)	56.6		43.5	55.8		57.6
>2	Kidney fat (g)	83.7	**	67.8	109.5	**	87.9

**$P<0.01$

numbers of larvae. The results indicated higher condition indices in females > 2 and > 3 years old with fewer than the mean number of warble larvae (Table 3). Sample sizes varied from 41 to 147 in December; from 133 to 349 in March. In males 1, 2, 3, 4, and >4 years old, the same condition variables were larger in those with more than the average numbers of larvae in 22 cases (2 significantly so), lower in 7 cases and equal in 1.

In samples from individual years, condition variables differed ($P< 0.05$) between those with more than, and fewer than, the mean number of warble larvae for the sample period in 20 of 36 cases (Table 4). The March 1981 sample was inadequate. The anomalous March 1984 sample was from a different component comprised of fatter and more fecund individuals compared with the December 1983 sample. A pooling of females > 3 years old produced significant back fat differences in all five December samples and in four of the eight March samp-

Table 4. Mean wights (kg) in < 3 year old and back fat depths (mm) and kidney fat (g) in 2 year old female barren-ground caribou with more than, and less than, the mean number of warble larvae in the sample period.

Month	Year	Mean no. larvae	Group vs. $\bar{x}$	Weight		Back fat		Kid. fat	
				n	mean	n	mean	n	mean
Dec	1982	21.6	<	27	81.4	28	9.3	31	74.4
			>	7	79.6	7	5.6	7	73.6
Dec	1983	8.8	<	16	82.6	18	16.0	18	95.5
			>	11	79.3	15	9.7	15	76.9
Dec	1984	2.3	<	30	86.1	32	20.1	32	88.1
			>	7	85.7	12	15.2	12	63.0
Dec	1985	4.3	<	29	86.9	32	14.9	30	83.4
				12	80.3**	15	8.7	15	56.8
Dec	1986	6.8	<	19	83.8	22	12.5	22	86.1
			>	8	78.9**	13	7.2	13	79.4
Mar	1980	31.7	<	7	79.7	13	4.9	11	68.7
			>	7	80.3	11	3.3	11	64.2
Mar	1982	36.3	<	30	84.9	32	16.7	31	107.4
			>	22	84.5	26	16.5	24	88.3
Mar	1983	53.3	<	45	81.3	52	11.5	49	94.8
			>	24	76.5**	30	6.1	30	72.3
Mar	1984	30.7	<	60	85.4	66	18.3	66	118.5
			>	17	86.5	24	20.5	24	119.9
Mar	1985	34.2	<	57	88.7	74	19.8	72	126.2
				32	87.1	37	16.2	37	103.4
Mar	1986	32.8	<	50	86.6	58	13.0	58	104.3
			>	25	81.4**	31	8.8	31	79.1
Mar	1987	35.0	<	23	81.2	26	10.7	27	100.7
			>	11	77.0**	14	8.1	14	75.4

**P <0.01

les; equivalent differences for kidney fat occurred in three of the December samples and in five of the March samples.

Warble larvae and fecundity of barren-ground caribou

There was no relationship between fecundity and average numbers of warble larvae in December and in March using the sample means for females 3, 4, and > 4 years old in individual collections. In five of six samples obtained in March, the mean numbers of larvae in females > 4 years varied from only 31 to 34; the pregnancy rate varied from 76 to 98%.

We selected age groupings where the means were similar and compared numbers of warble larvae in pregnant and nonpregnant females (Table 5). Two differences were significant and the trend towards fewer larvae in pregnant fe-

Table 5. Numbers of warble larvae under the skin of pregnant and non-pregnant, female, barren-ground caribou sampled in December (1982-86) and March (1980-87).

Age class (yr)	Month	Numbers of warble larvae: Pregnant $\bar{x}$	SE	n	Not pregnant $\bar{x}$	SE	n
2	Dec	20.0	16.0	2	24.0	4.4	24
3	Dec	11.3	2.5	17	17.7	6.0	13
4	Dec	4.8	1.6	29	8.0	4.3	8
<4	Dec	8.4	2.2	102	12.8	4.0	18
2	Mar	109.9	18.4	8	114.8	13.1	51
3	Mar	40.5	5.0	61	60.6	13.3	21
4	Mar	40.1	4.3	49	71.1	16.7	12
<4	Mar	31.9	2.3	297	59.3	9.3	38

*$P<0.05$
**$P<0.01$

males was consistent.

Warble fly avoidance behavior in barren-ground caribou

One observed strategy was to find escape habitat such as sand dunes, to disassociate from other caribou, and to lie still, preferably in a depression, until discovered. Then the caribou runs at full speed in an attempt to lose the fly. Occasionally the caribou stops and quickly lies down. One cow that "flopped" 10 m from an observer was breathing at 110 cycles/min. Cows will temporarily disassociate themselves from their calves in an attempt to avoid flies.

A second strategy common with adult bulls is to stand in about 0.5 m of water, ripple the skin and shake the body whenever a large fly comes near, stompe the legs if a fly attempts to land on them and swing the head back in an attempt to pin the fly against the legs or body. It may then run at full speed for up to 1-2 km and sometimes circle back to the same pond. A third strategy is to stand with the head lowered almost to the surface, usually over sand or in a meadow.

Early in August, when harassment by mosquitoes and warble files overlaps, several caribou may stand together. The warble fly is highly active only on certain days and especially on warm, sunny afternoons. By about 1800 hours (in late July-early August) the attacks cease and the caribou regroup and move away from the escape terrain to feed.

Discussion

A definite relationship was demonstrated between numbers of warble larvae and condition variables in adult (>2 years), female barren-ground caribou. The degree of fatness in turn affected fecundity. Why a trend in the opposite direction exists in males is unknown. Males that expose themselves to more flies in their summer movement patterns may be selecting better feeding conditions, e.g., more optimally following gradients of plant phenology. Parturient females have evolved movement patterns that enhance the survival of their calves.

Our data suggest that harassment by the fly is more important than reactions caused by the larvae. This conclusion is based on similar physical condition differences in December and March between those with more and less than the mean number of larvae. Larvae were small and not numerous in December. Further, the average number of larvae in March is only moderately high and large numbers (200-400) occur in a small proportion of the young (<2 years) of both sexes and in adult males (>3 years). Cause and effect remain unresolved. The likely explanation is that both factors are involved, i.e., that severe fly harassment reduces fat gain in the summer and leaner caribou are more susceptible to having eggs laid on them by the fly.

Infestation levels of warble larvae in caribou appear to be related to at least five factors: (1) climate; (2) caribou density; (3) migratory behavior; and (4) avoidance behavior in caribou; and (5) intrinsic immunological factors. Caribou morphological differences (Kelsall,1975) and the timing of pelage replacement are other possible factors.

The progressively lower incidence of larvae in the Beverly, Boothia, Peel Islands and Parry Islands populations (Tables 1 & 2) implicates climatic and density factors. Summer temperatures and caribou densities also decrease progressively in the series. Mean number per infected female caribou did not vary as much as the percent infected. Climate appears to be the more important of the two because some low density southern populations of woodland caribou *(R.t. caribou)* have large numbers of larvae (Kelsall, 1975). The warble fly appears to be near its distributional limit on the Parry Islands where the maximum temperature seldom attains 13-15°C, the quoted threshold for activity (Brejew, 1956), and sunny days are few.

The later migration of adult males in spring and early summer may explain why they have the largest numbers of larvae (Table 1). They may encounter flies emerging from larvae dropped from earlier migrants. These temporal relationships are consistent with the earlier development of larvae in males versus females (Table 1) and the slower development of larvae in older females versus younger ones (old females are believed to migrate the earliest). This factor explains the large numbers of larvae in relatively sedentary caribou such as those in the Rocky Mountains (Kelsall, 1975). Movement distance from larval shedding areas influenced infection incidences in reindeer in Norway (Folstad and Nilssen, 1990).

The avoidance behavior of caribou to warble flies includes pronounced changes in group size and tactics by individuals. There is a sharp decrease in group size from mid-July to early August. Avoidance strategies for mosquitoes and warble flies are opposite in terms of caribou group size (Roby, 1978). The individual is the optimum unit in avoiding warble flies as indicated by observations of behavior. Some of this behavior obviously has a genetic basis. A learned component might explain some of the variation in larval numbers and the relatively high numbers in caribou up to 2 years old.

A gradual acquisition of immunity to warble larvae also is consistent with the higher numbers of larvae in young caribou of the Beverly herd (Table 1). Solomakha (1990) revealed that antibodies to warble larvae were transferred from the dam to the fetus and via the milk to the calf, The absence of any age-related relationship with warble numbers i Peary caribou is consistent with lower intrinsic resistance in the less frequently infected subspecies.

This review points to the complex nature of the subject. Phenomena can be explained by more than one factor in most cases. For example, the decline in warble numbers with age in females (Parker, 1981; this study) can be explained by differences inmovement patterns (time of infection), avoidance behavior, and acquired immunological resistance. We suggesst that all of the discussed factors are implicated and their relative contributions may vary regionally.

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