

Are warbles and bots related to reproductive status in West Greenland caribou?

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Abstract: In March–April 2008–09, using CARMA protocols, 81 cows and 16 calves were collected in West Greenland from two caribou populations; Akia-Maniitsoq (AM) and Kangerlussuaq-Sisimiut (KS). In both populations, warble larvae numbers were highest in calves and higher in non-pregnant than pregnant cows. Nose bots showed no relationship with pregnancy or lactation; KS calves had higher nose bot loads than cows, a pattern not observed in AM. Pregnant cows had more rump fat than non-pregnant cows. KS cows lacking rump fat entirely had the highest warble burdens. We observed lactating pregnant cows with moderate larval burdens. Projected energy cost of the heaviest observed combined larvae burdens was equivalent to 2–5 days basal metabolic rate (BMR) for a cow, and 7–12 days BMR for a calf. Foregone fattening in adult cows with average burdens was 0.2 to 0.5 kg, but almost doubled with the heaviest infestations to 0.4 and 0.8 kg. Average burdens in calves resulted in forgone fattening of about 0.5 kg, with peak costs equivalent to 0.7 and 1.1 kg fat for AM and KS calves respectively. Although modest, these projected energy costs of hosting larvae for cows support the negative relationship between rump fat and larvae burden. For calves, hosting high burdens of warble larvae could affect winter survival, specifically those weaned normally in October or in early winter. Harmful effects of oestrid larvae burdens may remain subtle but clearly cumulative in relation to seasonal forage availability and incidence of other parasites.

Key words: energetics; nose bot larvae; oestridae; *Rangifer*; reproduction; survival; warble larvae.

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Introduction

Parasites are increasingly considered to play an important role in cycles of host abundance and population dynamics (Hudson *et al.*, 2001; Gunn & Irvine, 2003). In totally or relatively predator-free environments, gastro-intestinal parasites with direct life-cycles, have been shown to have population level

consequences in hares (*Lepus timidus*), feral Soay sheep (*Ovis aries*) and Svalbard reindeer (*Rangifer tarandus platyrhynchus*), reducing fecundity and contributing to population instability (Dobson & Hudson, 1992; Gulland *et al.*, 1993; Iver *et al.*, 2002; Albon *et al.*, 2004; Newery & Thirgood, 2004). The parasite-mediated reduction in calf production in Svalbard

reindeer was dependent on parasite density in the host, which in turn was a delayed density dependent response to host densities (Albon *et al.*, 2004). The effects of other direct life-cycle parasites in predator-free environments are not well understood.

Whereas intestinal parasites exert influence through metabolic effects within the host (Hudson *et al.*, 2001; Gunn & Irvine 2003), macro-parasites such as larvae of warble (*Hypoderma tarandi*) and nose bot flies (*Cephenemyia trompe*) of the Oestridae family, that are host-specific endoparasites in reindeer and caribou (*Rangifer tarandus*), as well as having metabolic costs, also cause energetically costly behavioural responses. In summer, the presence of adult oestrid flies can provoke intense behavioural responses in *Rangifer*, disturbing foraging and increasing movement (Kellsall, 1968; White *et al.*, 1975; Reimers, 1980; Helle & Tarvainen, 1984; Kojola, 1991; Walsh *et al.*, 1992; Russell, *et al.*, 1993; Iver *et al.*, 2002; Bergerud *et al.*, 2008; Witter *et al.*, 2011). Adult flies are strong fast fliers (Nilssen & Anderson 1995), which make it easy to locate, track and follow their hosts (Iver, *et al.*, 2002). Hot summers increase adult fly activity and thus harassment of caribou (Thomas & Kiliaan, 1990; Folstad *et al.*, 1991; Nilssen & Haugerud, 1994; Mörschell, 1999; Witter *et al.*, 2011). An extreme example of the influence of oestrid flies was the summer of 1977 in north-west Alaska. High temperatures and exceptionally low precipitation (Haugen & Brown, 1980) resulted in warble fly harassment and overwinter loss of a portion of the 1977 calf cohort. Warble larvae numbered between 1900 and 2000 in one dead calf (Davis *et al.*, 1980), in excess of 1000 in others (White, unpubl. data), and upon palpation, hides of these dead calves resembled bubble-wrap in appearance and texture (White, unpubl. observations). In semi-domestic reindeer extreme cases of parasitic larvae infection, which weaken body condition, can cause death (Helle, 1980; Folstad, *et al.*, 1989). Scandinavian reindeer husbandry considers warbles the parasite causing the most losses (Josefsen *et al.*, 2006). Thus combined effects of adult warble fly disturbance and the energetic cost of harbouring larval stages internally can impact demography. In addition to mortality, a negative relationship between the number of warble larvae and the probability of pregnancy, or of fat reserves in cows in late winter, could also drive demographic outcomes (Thomas & Kiliaan, 1990; Hughes *et al.*, 2009).

Oestrid flies have a one year direct life cycle, with no intermediate hosts (Savel'ev, 1961; Anderson & Nilssen, 1990; Nilssen & Haugerud, 1994, 1995; Nilssen, 1997). Adult flies develop and mate in summer, while larvae over-winter inside reindeer/caribou.

Over-wintering warble larvae live under the skin, typically on either side of the host's spine, and nose bot larvae live in nasal cavities and pharynx. Warble numbers in caribou vary widely both among populations and years (Kellsall, 1975; Bergerud *et al.*, 2008). Mean larvae numbers in North American caribou cows of 38 ± 43 (Thomas & Kiliaan, 1990) and 51 ± 4 have been observed (Bergerud *et al.*, 2008), and means of under a 100 larvae are common (Kellsall, 1975). Semi-domestic reindeer cows in Finland had mean warble numbers < 50 larvae (Helle, 1980). However, exceptional maximums of from 300 to 600 warble larvae also were observed in female caribou (Kellsall, 1975).

Caribou are not defenceless against their oestrid parasite predators. In addition to initial avoidance reactions to the presence of adult flies, a caribou's immune system mounts biochemical and inflammatory responses to larvae (Helle, 1980; Solomakha, 1990) and larval mortality has been observed (Kellsall, 1975). There is high mortality among warble larvae in the first larval stage, specifically in hosts of good body condition (Savel'ev, 1961). Although oestrid larvae occur in 97-100% of caribou, calves or juveniles generally have greater warble infections than adults, and bulls more than cows (Helle, 1980; Folstad, *et al.*, 1989; Thomas & Kiliaan, 1990; Syroechkovskii 1995; Bergerud *et al.*, 2008). Beyond weather and caribou density, individual variation in defence response, e.g., migratory behaviour, avoidance behaviour, immune response and timing of hair moult, may account for observed differences in larvae number by late winter (Thomas & Kiliaan 1990).

We explored the number and weight of warble and nose bot fly larvae parasites in Greenland caribou cows and their calves-at-heel. We also investigated late-winter body condition and reproductive status, which was categorized by whether the cow was pregnant, lactating, recently weaned, had a calf at heel or any combination thereof. Specifically we tested whether: 1) 10-month old calves-at-heel had greater number / weight of larvae than adults, 2) non-pregnant cows had greater number / weight of larvae than pregnant cows, and 3) non-lactating cows had greater number / weight of larvae than lactating cows. Since the energetic cost of larvae loads may not be trivial, we also calculated the approximate energetic cost to the host associated with the cumulative oestrid parasite burden and discuss this cost in relation to the basal metabolic rates of cows and calves, the amount of foregone fattening based on the energy costs, and possible consequences for winter survival.



Fig. 1. Regions for the Kangerlussuaq-Sisimiut and Akia-Maniitsoq caribou herds in West Greenland, elevations are not shown.

Study area and populations

We studied the largest, Kangerlussuaq-Sisimiut (KS), and second largest, Akia-Maniitsoq (AM), caribou populations in West Greenland (Fig. 1), as both are commercially important and significant to Greenland culture and traditions (Cuyler *et al.*, 2005). KS caribou were from the North region in close proximity to the Greenland Ice Cap, 67°03'N, 50°59'W, in an area characterised by dry continental desert steppe climate and lacking the macro-lichens favoured by caribou. The winter diet of KS caribou is dependent on dwarf shrubs, grasses and sedges, which regenerate each year (Lund *et al.*, 2000). Winter snow cover often arrives late, is incomplete (patchy), light (< 15 cm deep), often absent, and can disappear early. The terrain is rugged and largely under 500 m elevation. AM caribou were from the Central region's Akia-Nordland area north of the Godthåbfjord system, 64°34'N, 51°44'W, where although rugged, elevations are largely < 100 metres. The area is characterised by a wet maritime climate and presence of macro-lichens that are showing signs of overgrazing. The AM winter diet is dependent on lichens (Lund *et al.*, 2000), which may take decades to regenerate and about a century to achieve climax status (Kumpula *et al.*, 2000). Similar to KS, AM winter snow cover is incomplete; however it can be ca. 70 cm deep, arrive early and remain late. In summer many AM cows migrate to the inland near the Greenland Ice Cap where elevations are generally 500-800 m. Throughout their range, AM caribou have access to

elevations >500 m. Local knowledge, which is neither confirmed or refuted, states that warbles and bots arrived in Greenland with the introduction of semi-domesticated reindeer from Norway to the inner fjord system east of Nuuk in 1952.

In March 2010 the KS and AM populations numbered approximately 98 000 and 32 000 respectively (Cuyler, *et al.*, 2011). The KS and AM herds have been at high abundance for at least the last decade, with current densities on preferred winter range of about seven and two caribou per square kilometre respectively (Cuyler *et al.*, 2005, 2011). While the KS herd has remained stable in number, the AM herd abundance has declined slowly (Cuyler *et al.*, 2011). Both herds are predator free. Spring migration distances are short and on a generally east-west gradient for both the KS and AM caribou, with maximums of about 60 and 170 km respectively (Cuyler & Linnell, 2004).

Methods

From 29 March to 13 April 2008, we shot 41 cows and 6 calves-at-heel (age ca. 10-months) from the AM caribou population. Similarly, 40 cows and 10 calves-at-heel (age ca. 10-months) were collected from the KS caribou population from 3 to 17 March 2009. Animals were shot in the neck. We conducted thorough post-mortem examinations as detailed in CARMA (CircumArctic Rangifer Monitoring & Assessment) protocols (<http://www.carmanetwork.com>). For each caribou these included measuring total and dressed carcass weight (i.e., carcass minus hide, head, all thoracic and abdominal organs, and the metacarpals / metatarsals with hooves), rump fat depth, the presence or absence of pregnancy, lactation status (white/milky-lactating, or clear liquid-recently weaned (R.G. White & W.E. Hauer, unpubl. observations; White *et al.*, 2000)), and presence of calf-at-heel. We counted the number of warble larvae manually, and weighed 10. This weight with the total number was used to calculate total warble larvae weight. Bot larvae were measured similarly.

We used weather data from the CARMA MERRA files (Russell *et al.*, in press), for the period 15 June to 15 August for the preceding summers to the AM and KS collections, i.e., 2007 and 2008 respectively, to calculate an oestrid fly activity index (OFI). The index employed daily mean temperature (T , °C) and wind (W , m/s). Thus $OFI = T_1 \times W_1$, where, $T_1=1$ if (daily mean temperature >18 °C) else if (daily mean temperature <13 °C) = 0 else = $1 - ((18 - \text{daily mean temperature})/10)$, and $W_1=0$ if (wind at 10 m/s > 9) else = $(9 - \text{wind } 10 \text{ m/s})/9$ (Russell *et al.*, 1993).

We used caribou body weights from adult cows, to estimate basal metabolic rate ($BMR_{kcal} = 70 \times \text{weight}^{0.75}$, weight given in kg) in kcal (Kleiber, 1975), and converted to kJ by multiplying by the factor 4.187. Metabolic rate of individual larvae was estimated from its weight assuming a BMR of 5% of interspecies coefficient (Glazier, 2005). Thus oestrid daily $BMR = (0.05 \times 70 \times 4.187 \times (\text{individual larvae weight, kg})^{0.75})$. Larvae weights during the growing period were estimated from observed mean weights in March-April, and an emergent weight of 2.25 g. The metabolic cost of BMR, i.e., maintenance cost of an individual larva, was determined as the integral of daily BMR of an individual larva assuming an efficiency of use of the host's metabolizable energy of 0.85. To estimate net energy deposited in the larvae (NE, kJ) we assumed a larva was composed of 60% water and 40% dry matter that was composed of 50% fat at 39.54 kJ/g, 40% protein at 23.7 kJ/g, and 10% carbohydrate at 17.5 kJ/g (Standard energy contents - White, *et al.*, 2010). We assumed metabolizable energy absorbed from the host was deposited as NE in larvae fat, protein and carbohydrate with 98% efficiency. Cost to the host for NE was the individual larval NE/0.98 multiplied by the number of larvae. Costs of BMR to the host were assessed as the accumulated daily BMR/0.85 to a shedding weight of 2.25 g for warbles and 0.5 g for bots on or about 1 June. Total energy cost to the host was $(NE/0.98) + (\text{cumulative BMR}/0.85)$. Average and maximum cumulative energy costs of the oestrid larvae burden were calculated for calves-at-heel and for adult cows stratified by pregnancy status. In calculating the energy cost of larvae burden we ignored the energy costs of mounting an immune response and that due to increased heat loss that would result from a disrupted fur surface. Specific cow age was obtained from incisor cementum rings (McEwan, 1963; Reimers & Nordby, 1968). Alternately we used two age categories in analyses, 10-month old calves or adults (age > 3 years). Adult cows were classified by reproductive status into four categories; pregnant and non-lactating (P+NL), pregnant and lactating (P+L), non-pregnant and non-lactating (NP+NL) and non-pregnant and lactating (NP+L).

We used the Student's *t*-test to compare dressed carcass weights and rump fat depths of pregnant and non-pregnant adult cows. We used ANOVA's to describe differences in parasite burden with the four reproductive categories and age. Herds were analysed separately because collections were made in separate years. In all cases assumptions of the model were met or violation of an assumption was insubstantial to the result of the test. If the original ANOVA was

significant, we conducted three planned comparisons (i.e. 1-tailed contrasts) to further test our hypotheses that larval numbers and weights vary by age and reproductive status (Crawley 2007). All analyses were conducted in R (R Development Core Team, 2009). We used regressions to examine cow age against their rump fat depth or pregnancy.

Results

Pregnancy and age of sampled caribou

The 41 cows shot in March/April 2008 from the AM herd included 34 adults of age > 3-years (Fig. 2) and seven sub-adults. The latter were 2.83 years old, not pregnant and had no calf-at-heel. Similarly, among the 40 cows shot in March 2009 from the KS herd, 36 were adults of age > 3-years (Fig. 3) and four sub-adults aged 2.83 years. One of the latter was pregnant, and none had a calf-at-heel. The pregnancy rates among sampled adult cows were 82% for the AM herd and 53% for the KS. Six female calves-at-heel were sampled from the AM herd and six females and four male calves from the KS herd. There was no relationship between cow age and pregnancy ($P > 0.05$) in KS and AM caribou.

Rump fat and lactation

Four mature AM cows (Fig. 2), aged ca. 7.85 to 9.85 years, possessed rump fat while being pregnant and with a ca. 10-month old calf-at-heel. Their rump fat depths were a mean 0.7 cm with a range of 0.5 to 1.0 cm. Based on expressible mammary fluid two of these cows were producing white milk and still nursing their calf. Two of the four cows had recently weaned, based on clear expressible liquid, and a further cow had recently weaned and had no visible calf-at-heel. All non-pregnant adult cows with a calf-at-heel were producing white milk. There was no relationship between cow age and rump fat depth or lactation ($P > 0.05$) in KS and AM caribou.

Of the 19 pregnant adult KS cows (Fig. 3), three aged ca. 4.83, 7.83 and 8.83 years, were pregnant, had their 10-month old calf-at-heel, which they were nursing, and still possessed some remaining rump fat. The youngest had a fat depth of 1.5 cm remaining, while the two older cows had 0.8 and 0.1 respectively ($n=3$, mean 0.8 cm). For the pregnant cows, three that had a calf-at heel had recently weaned. A further five pregnant cows had probably weaned as they showed a clear mammary fluid, but had no visible calf-at-heel. Of the 17 non-pregnant adult KS cows, 15 had their calf-at-heel and 14 of these were producing white milk.

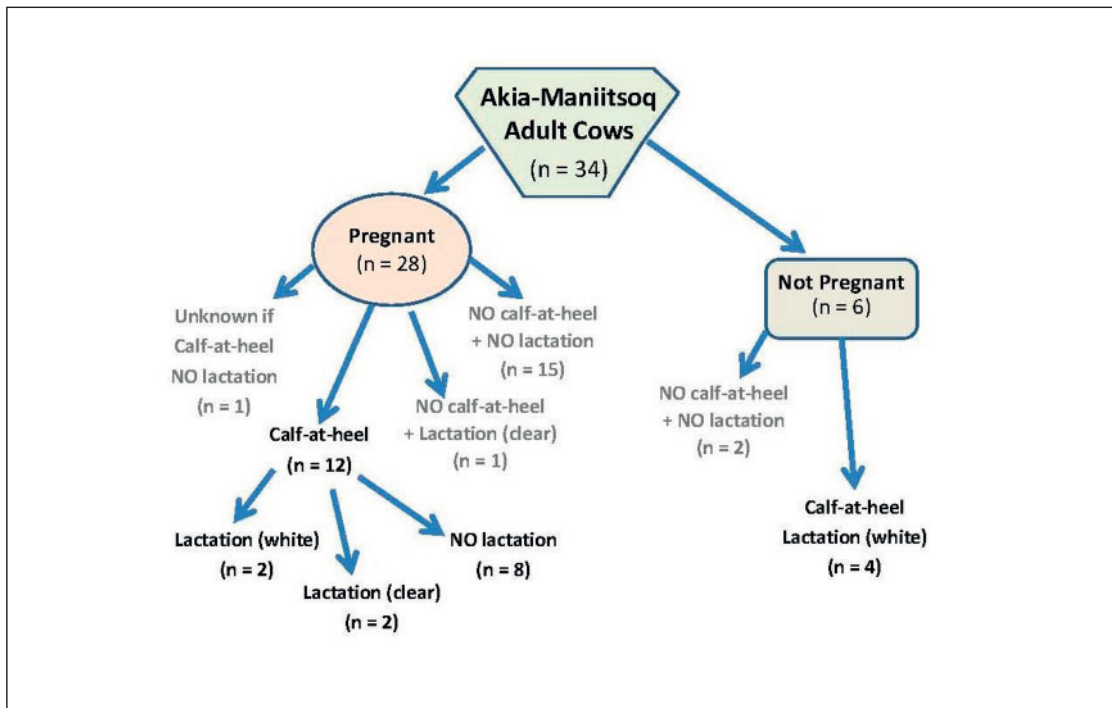


Fig. 2. Reproductive status among the adult cows from the Akia-Maniitsoq caribou herd of West Greenland collected from 29 March to 13 April 2008.

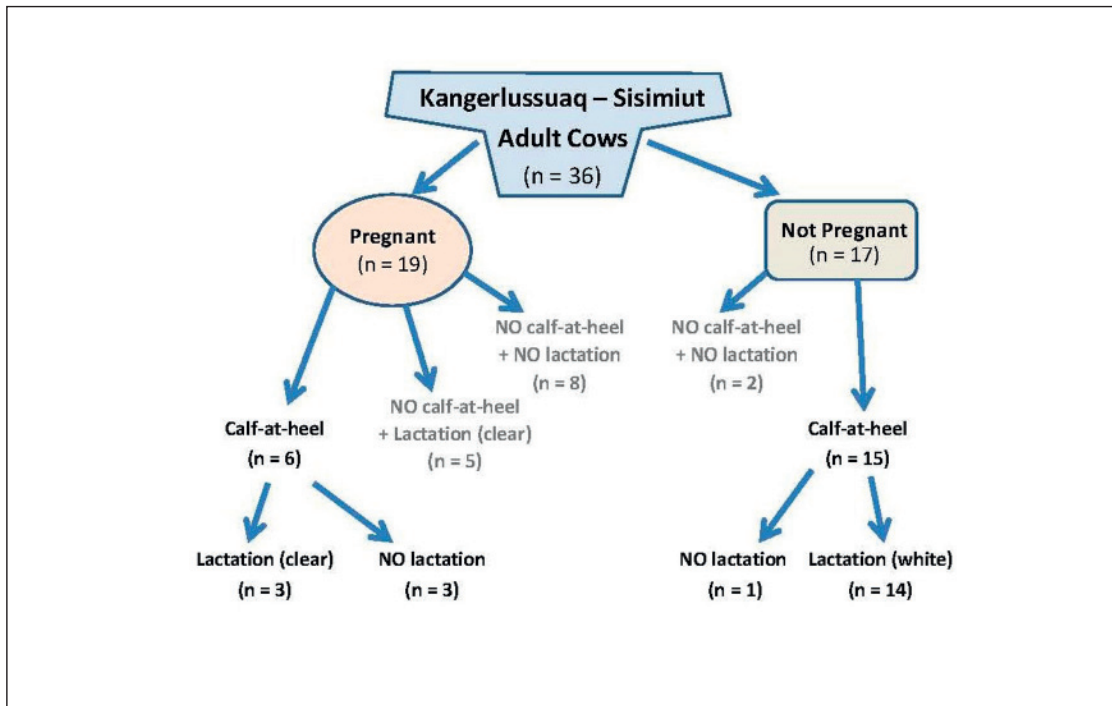


Fig. 3. Reproductive status among the adult cows from the Kangerlussuaq-Sisimiut caribou herd of West Greenland collected from 3 to 17 March 2009.

Table 1. Akia-Maniitsoq caribou of West Greenland: data from adult cows (age > 3-years) and calves-at-heel (age 10-months) collected 29 March – 13 April 2008, mean \pm SD or maximum.

	Akia-Maniitsoq 2008		
	Pregnant	Non-pregnant	Calf-at-heel
Number collected (n)	28	6	6
Mean age (yr)	6.2 \pm 2.3	8.3 \pm 1.4	10-months
Mean total body weight (kg)	60.5 \pm 3.2	52.8 \pm 7.1	30.8 \pm 4.2
Mean dressed carcass weight (kg)	29.0 \pm 2.1	27.1 \pm 4.0	15.3 \pm 3.1
Mean BMR ¹ caribou (kJ/day)	6361 \pm 251	5735 \pm 579	3821 \pm 385
Mean rump fat depth (cm)	0.8 \pm 0.7	0.05 \pm 0.08	0
Mean warble number	119 \pm 77	205 \pm 186	318 \pm 160
Max warble number	294	537	517
Mean weight ONE warble larva (g)	1.35 \pm 0.18	1.28 \pm 0.16	1.54 \pm 0.13
Mean warbles total weight (g)	160 \pm 107	260 \pm 246	478 \pm 218
Mean energy cost warbles (kJ)	6240	10 749	16 674
Mean fat equivalent warbles (g)	158	271	421
Maximum ¹ energy cost warbles (kJ)	15 416	28 158	27 109
Maximum fat equivalent warbles (g)	389	711	685
Mean nose bot number	70 \pm 63	67 \pm 63	53 \pm 50
Max nose bot number	180	178	125
Mean weight ONE nose bot larva (g)	0.22 \pm 0.13	0.18 \pm 0.14	0.18 \pm 0.06
Mean nose bot total weight (g)	21 \pm 25	19 \pm 28	10 \pm 11
Mean energy cost nose bots (kJ)	667	639	505
Mean fat equivalent nose bots (g)	17	16	13
Maximum energy cost nose bots (kJ)	1716	1697	1192
Maximum fat equivalent nose bots (g)	43	43	30
Warbles & bots combined			
Mean energy cost (kJ)	6907	11 388	17 180
Mean fat equivalent (g)	174	288	434
Maximum energy cost (kJ)	17 132	29 855	28 301
Maximum fat equivalent (g)	433	754	715
Mean equivalent days of caribou BMR	1.1	2	4.5
Maximum equivalent days of caribou BMR	2.7	5.2	7.4

¹ Maximums were the heaviest infestations observed.

Within herds, pregnant adult cows (age > 3-years) possessed significantly greater rump fat than non-pregnant (AM $P < 0.0001$, $df = 32$, $t = 5.929$; KS $P = 0.0005$, $df = 34$, $t = 3.849$) (Table 1, 2). Fat depth did not differ between herds for either pregnant or non-pregnant adult cows. All 10-month old calves-at-heel had zero rump fat regardless of herd. Zero rump fat on adult cows was observed on 22 KS and 9 AM cows. All seven AM sub-adult cows and two of the four KS sub-adults had zero rump fat and were not pregnant. The remaining two KS sub-adult cows had rump fat depths of 0.1 and 0.4 cm, and the latter sub-

adult was pregnant. Although mean rump fat depths were 1.2 \pm 0.7 cm for the 14 KS adult cows possessing rump fat and 0.9 \pm 0.6 for the 25 AM adult cows, the difference was not significant ($P = 0.12$, $df = 37$, $t = 1.570$). Within the KS herd adult cows with zero rump fat had significantly higher larvae burdens than cows possessing rump fat ($P = 0.0005$, $df = 34$, $t = 3.857$). In contrast, no significant difference was found among AM adult cows ($P = 0.17$, $df = 32$, $t = 1.401$).

Table 2. Kangerlussuaq-Sisimiut caribou of West Greenland: data from adult cows (age > 3-years) and calves-at-heel (age 10-months) collected 3 – 17 March 2009, mean ± SD or maximum.

	Kangerlussuaq-Sisimiut 2009		
	Pregnant	Non-pregnant	Calf-at-heel
Number collected (n)	19	17	10
Mean age (yr)	8.0 ± 2.5	8.1 ± 2.9	10-months
Mean total body weight (kg)	68.3 ± 3.7	61.8 ± 3.6	32.8 ± 4.4
Mean dressed carcass weight (kg)	32.8 ± 2.3	29.5 ± 2.0	15.5 ± 2.7
Mean BMR1 caribou (kJ/day)	6961 ± 279	6458 ± 282	4006 ± 401
Mean rump fat depth (cm)	0.8 ± 0.8	0.1 ± 0.2	0
Mean warble number	138 ± 64	311 ± 189	457 ± 284
Max warble number	287	722	1008
Mean weight ONE warble larva (g)	0.87 ± 0.23	0.99 ± 0.13	1.12 ± 0.11
Mean warbles total weight (g)	127 ± 82	298 ± 165	498 ± 299
Mean energy cost warbles (kJ)	6494	14 636	21 507
Mean fat equivalent warbles (g)	164	370	543
Maximum ¹ energy cost warbles (kJ)	13 506	33 978	47 437
Maximum fat equivalent warbles (g)	341	858	1198
Mean nose bot number	18 ± 28	37 ± 49	0.3 ± 0.7
Max nose bot number	112	119	2
Mean weight ONE nose bot larva (g)	0.28 ± 0.11	0.3 ± 0.1	0.23 ± 0.25
Mean nose bot total weight (g)	6 ± 10	13 ± 17	0.2 ± 0.2
Mean energy cost nose bots (kJ)	154	317	3
Mean fat equivalent nose bots (g)	4	8	0,1
Maximum energy cost nose bots (kJ)	958	1018	17
Maximum fat equivalent nose bots (g)	24	26	0,4
Warbles & bots combined			
Mean energy cost (kJ)	6648	14 952	21 509
Mean fat equivalent (g)	168	378	543
Maximum energy cost (kJ)	14 465	34 996	47 454
Maximum fat equivalent (g)	365	884	1198
Mean equivalent days of caribou BMR	1	2.3	5.4
Maximum equivalent days of caribou BMR	2.1	5.4	11.8

¹ Maximums were the heaviest infestations observed.

Larvae abundance and weight

Abundance and weight of warble larvae exceeded nose bot larvae in both herds ($P < 0.0001$, $df = 80$, $t = 4.108$ AM; $p < 0.00001$, $df = 78$, $t = 7.088$ KS) (Figs. 4, 5). Adult KS cows carried fewer nose bots ($P = 0.0007$, $df = 79$, $t = 3.533$) and more warbles ($P = 0.006$, $df = 79$, $t = 2.828$) than AM cows; warble number in AM and KS calves were not significantly different ($P = 0.234$, $df = 14$, $t = 1.244$), and KS calves had marginally fewer nose bots than AM calves ($P = 0.0481$, $df = 14$, $t = 1.166$).

Akia-Maniitsoq caribou and warble larvae

Number of warbles differed among reproductive categories ($F_{4,41} = 5.104$, $P = 0.002$) (Figure 4). 10-month old calves-at-heel had significantly higher numbers of warbles than adults ($t = 2.907$, $P = 0.003$). Pregnant cows had fewer warbles than non-pregnant ($t = 1.734$, $P = 0.045$); although the sample size was small and the P -value was close to 0.05. The number of warbles was not influenced by whether a cow was lactating or not ($t = 0.814$, $P = 0.2$). Similarly, weight of warbles differed among the categories ($F_{4,41} = 6.045$, $P = 0.0006$). 10-month old calves-at-heel

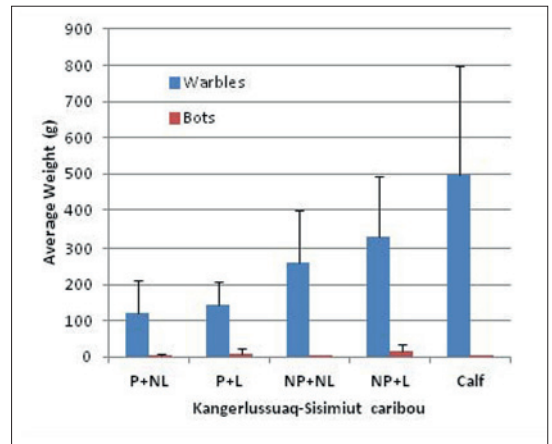
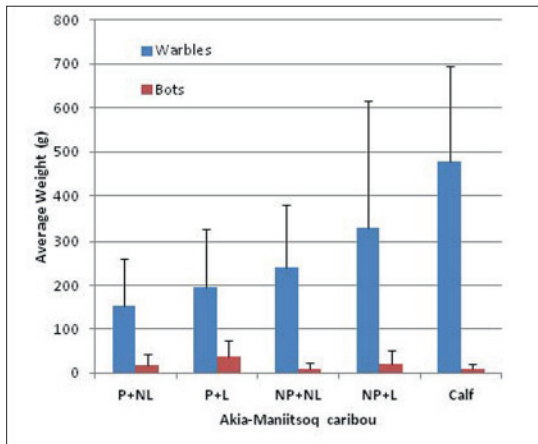
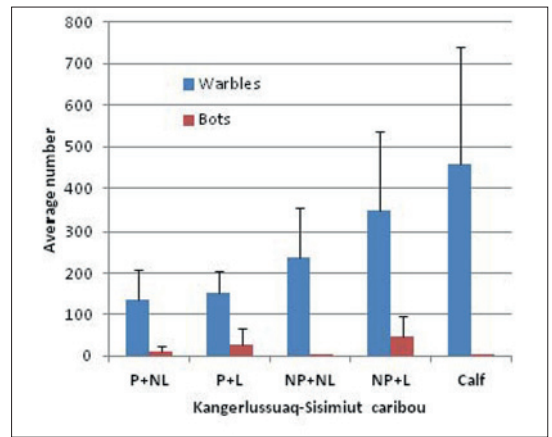
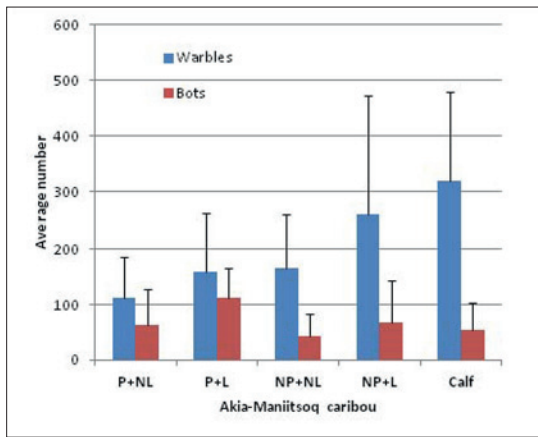


Fig. 4. Average number and weight of warble and nose bot larvae in Akia-Maniitsoq caribou collected in March/April 2008 in West Greenland: pregnant & not-lactating (P+NL) $n = 23$; pregnant & lactating (P+L) $n = 4$; not-pregnant & not-lactating (NP+NL) $n = 9$; not-pregnant & lactating (NP+L) $n = 4$; calf $n = 6$.

Fig. 5. Average number and weight of warble and nose bot larvae in Kangerlussuaq-Sisimiut caribou, March 2009 in West Greenland: pregnant & not-lactating (P+NL) $n = 12$; pregnant & lactating (P+L) $n = 8$; not-pregnant & not-lactating (NP+NL) $n = 6$; not-pregnant & lactating (NP+L) $n = 14$; calf $n = 10$.

had significantly higher warble weights than adults ($t = 3.611$, $P = 0.0004$). Pregnant cows had lower warble weights than non-pregnant cows ($t = 1.834$, $P = 0.03$). Weight of warbles was not influenced by lactation ($t = 0.496$, $P = 0.3$).

Akia-Maniitsoq caribou and nose bot larvae

The number and weight of nose bot larvae did not differ among categories (Number: $F_{4,41} = 0.9996$, $P = 0.4188$; Weight: $F_{4,41} = 1.267$, $P = 0.2985$). All hypotheses were rejected. Nose bots were not significantly related to age, pregnancy, or lactation in the AM herd.

Kangerlussuaq-Sisimiut caribou and warble larvae

Number of warbles differed between categories ($F_{4,45} = 6.409$, $P = 0.00036$) (Figure 5). 10-month old calves-at-heel had significantly higher numbers of warbles than adults ($t = 3.873$, $P = 0.0002$). Pregnant cows had fewer warbles than non-pregnant cows ($t = 2.569$, $P = 0.007$). Number of warbles did not appear influenced by whether a cow was lactating or not ($t = 0.21$, $P = 0.4$).

The weight of warbles differed among categories ($F_{4,41} = 4.168$, $P = 0.00589$). 10-month old calves-at-heel had significantly ($t = 4.545$, $P = 0.00002$) higher warble weight than adults. Pregnant cows had less warble weight than non-pregnant ($t = 2.825$, $P = 0.0035$). Lactation was not related to the weight of warbles ($t = 0.27$, $P = 0.4$).

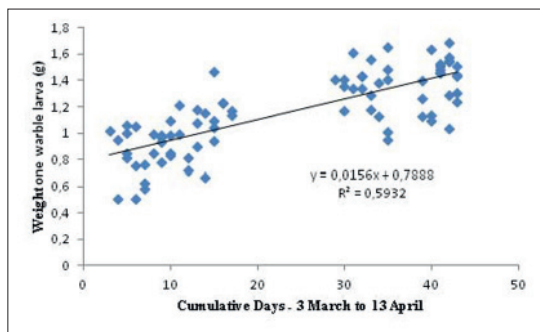


Fig. 6. Individual weight of warble larvae in relation to date from 3 March to 13 April during two sampling years (2008, 2009). Regression slope was significant ($P < 0.0001$).

Kangerlussuaq-Sisimiut caribou and nose bot larvae

Many KS caribou lacked the presence of nose bot larvae (Fig. 5). Number of nose bot larvae was significantly and inversely related to age category ($F_{4,41} = 4.168$, $P = 0.006$). 10-month old calves-at-heel had significantly ($t = -1.822$, $P = 0.037$) fewer nose bots than adults. Pregnancy and lactation were not related to the number of nose bots ($t = 0.341$, $P = 0.35$ and $t = 1.237$, $P = 0.11$ respectively), and nose bot weight was not significant ($F_{4,20} = 2.174$, $P = 0.1090$). Sample size for this data set is small and given the number of animals without nose bot larvae, all hypotheses were rejected.

Warble larvae grow during early spring (Fig. 6), while bot larvae do not (Fig. 7). These data were used to assess minimal average warble and bot larvae of 2.25 g and 0.5 g at shedding for modeling energy costs and a mean growth of warble larvae of 0.016 g/day was assumed. Bot larvae were assumed to make minor growth between sampling and dates of shedding in June.

Metabolic costs of larval growth and metabolism

Basal metabolism of cows and calves-at-heel

Adult KS cows were larger bodied than AM (Tables 1, 2). Mean total body weight of the AM adult cows (age > 3-years) was significantly less than the KS cows, e.g., for pregnant adult cows $P < 0.0001$, $df = 46$, and for non-pregnant cows $P = 0.01$, $df = 22$. Dressed carcass weight for adult pregnant KS cows was also greater than AM ($P < 0.0001$). Within herds, non-pregnant cows weighed significantly less than those pregnant (AM $P = 0.02$, $df = 33$; KS $P < 0.0001$, $df = 35$). For calves-at-heel we found no significant difference in mean total body weight ($P = 0.21$, $df = 15$) between the AM and KS herds. Basal

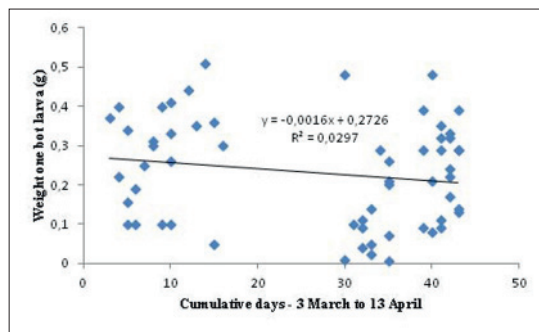


Fig. 7. Individual weight of bot larvae in relation to date from 3 March to 13 April during two sampling years (2008, 2009). Regression slope was not significant ($P = 0.19$).

metabolic rate (BMR) of adult cows was 6250 ± 400 kJ/day for AM and 6723 ± 376 kJ/day for KS, while calves-at-heel were 3936 ± 418 kJ/day (Tables 1, 2).

Warbles and nose bots

Important to estimating a metabolic cost to the host of warble burdens is knowledge of the larval growth functions and the approximate weight of larvae at shedding. Within herds pregnant and non-pregnant adult cows had mean individual warble weight that did not differ significantly, AM ($P = 0.3$, $df = 33$) and KS ($P = 0.06$, $df = 35$). Given the almost one month difference in collection periods between herds, mean individual warble weight in adult pregnant cows at 1.35 g for AM (April) and 0.87 g for KS (March) were different ($P < 0.0001$, $df = 46$). Similarly, mean warble weights in adult non-pregnant cows were 1.28 g for AM and 0.99 g for KS ($P = 0.006$, $df = 22$) (Table 1, 2). Within both herds individual warble weight in calves exceeded that of the adult cows (1.5 g and 1.1 g for AM and KS respectively ($P < 0.02$)). Mean individual nose bot weight in adult cows showed no significant differences ($P > 0.05$), whether within or between herds or between pregnant and non-pregnant. The situation was similar for mean individual nose bot weight in calves versus adults ($P > 0.8$).

Due to differences in sampling date, we used a mature larvae weight of 2.25 g in early June. Expected weight gains between sampling and emergence were similar at approximately 0.016 g/day for warble larvae from both herds (Fig. 6). Estimated peak weight of individual bot larvae at 1 March was approximately 0.5 g (Fig. 7), and we assumed all bot larvae reached this weight at shedding. At shedding, the estimate cost of hosting an individual larva was 17-19 kJ/g of which 54-60% was attributable to NE and 40-46% to the summated support metabolism. Absolute costs to caribou were then assessed from lar-

vae burdens as reported above. Among AM caribou the approximate energy cost associated with larvae burden was a mean 7000 to 11 000 kJ for adult pregnant and non-pregnant cows respectively. Heavily infested cows had energy costs of 17 000 to 30 000 kJ (Table 1). Of these costs only 10-15% were due to bot fly larvae. The energy cost to the most heavily infected cows was equivalent to about 3-5 days BMR. Similarly for the KS caribou (Table 2), larvae burden cost a mean 7000 to 15 000 kJ for adult pregnant and non-pregnant cows respectively, while heavily infested cows had burdens costing 14 000 to 35 000 kJ, which were equivalent to about 2-5 days BMR. Because of the low infestation by bot fly larvae only approximately 2% of this cost was attributable to them. For calves-at-heel larvae burdens were greater and energy costs for mean burdens were 17 000 and 21 000 kJ for AM and KS calves respectively. In the most heavily infested calves, energy costs were about 28 000 kJ and 47 000 kJ for AM and KS respectively. These latter costs were equivalent to about 7-12 days BMR of a calf-at-heel. Again, due to low infestation by bot larvae, the cost for AM calves was only 3% while that for KM calves was less than 0.1%. An alternate expression of the energy cost is to express that cost in terms of forgone fattening. Lowest levels in forgone fattening were for pregnant cows at about 0.1-0.4 kg for the mean and highest infestation rates in both AM and KS females (Table 1, 2). Greatest levels of foregone fattening were estimated in non-pregnant cows at 0.7 and 0.8 kg for respectively the AM and KS herds (Table 1, 2). Foregone fattening was even higher in calves-at-heel at 0.7 kg for the AM and 1.2 kg for the KS animals.

Discussion

Our results were similar to other studies that have found a relationship between warble infection, fat reserves and pregnancy (Thomas & Kiliaan, 1990; Hughes *et al.*, 2009). Further, a recent experimental approach employing removal of warble larvae observed that warbles have a significant negative impact on cow body mass, despite relatively low numbers of larvae (Ballesteros *et al.*, 2011). Our results are also interpreted in relation to a theoretical analysis of energetic costs of hosting variable burdens of warble and bot larvae. For the two herds we examined in West Greenland age was not associated with reproductive status of cows in March-April, however, warble larvae burden was. Pregnant cows had fewer warbles and greater rump fat than non-pregnant cows, and lower energy cost associated with hosting larvae. Cow age was not associated with

rump fat reserves. Adult cows that we examined had rump fat reserves with a mean < 1 cm, compared to pregnant cows, non-pregnant cows had significantly greater number of warbles, and less rump fat, specifically notable in non-pregnant KS cows. Again these findings are consistent with the higher host energy costs and the predicted fat draw-down necessary to meet the oestrid cost when all nutrients are obtained from the host's reserves. Sampled adult KS cows had high warble burdens and a low pregnancy rate of 53%. Relative to KS, the AM cows had lower warble burdens and a pregnancy rate of 82%. Calves-at-heel had zero rump fat and exhibited the highest mean larvae numbers observed. Our findings support those by Hughes *et al.* (2009), who observed that warble abundance was higher in animals with less back fat and that the difference was most apparent in non-pregnant cows, even at lower abundance of warble larvae. Hughes *et al.* (2009) concluded that a negative relationship exists between abundance of warbles and probability of being pregnant. They proposed that high infestations have a cost to the host, reflected in reduced weight gain owing to harassment and reduced time feeding the previous summer. Further, that poor condition or social status of an animal may increase susceptibility to adult fly attack.

Warble load in winter may be influenced by the timing of summer hair shedding among caribou, which occurs in warble fly season (Thomas & Kiliaan, 1990; Syroechkovski, 1995; Bergerud *et al.*, 2008). The successful implant of warble larvae under the hide may be related to the stage of hair loss at the time of peak adult fly harassment, i.e., mid-July to mid-August (Syroechkovski, 1995, p. 162; Josefsen *et al.*, 2006). Lactating cows are actively shedding their winter coat during the height of warble fly season. We suggest that eggs deposited on the winter coat of cows may be lost with shed hair before being able to burrow under the skin. In contrast, calves, juveniles and bulls are well advanced in their hair shedding at peak fly season (Fig. 8), and thus may be more susceptible to successful adherence of eggs to newly growing hair and implantation by warble fly larvae. The warble eggs have a flexible stem which is glued to the hair (Cogley *et al.*, 1981). Thus the eggs lie flat along the hair shaft and would be resistant to grooming but not to loss of the hair shaft. The variation in warble counts may then be related to the timing of hair loss relative to the time adult flies are laying eggs.

Mean numbers of warble larvae in the adult KS cows were 138 ± 64 SD for pregnant and 311 ± 189 SD for non-pregnant, while means in the AM cows were 119 ± 77 SD and 205 ± 186 SD respectively.

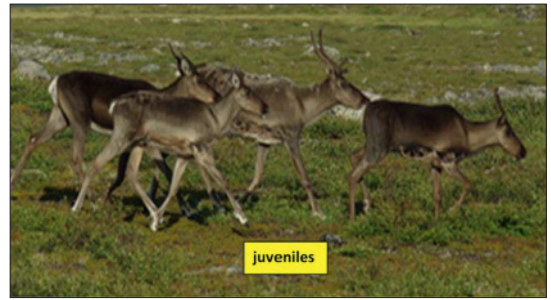
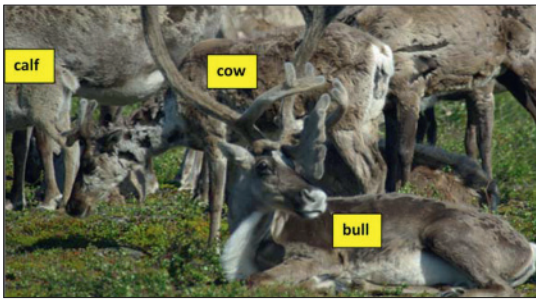


Fig. 8. Differential timing of hair moult among caribou during July (Photo, Leslie Witter).

Table 3. Temperature, precipitation and cumulative oestrid (adult warble & bot fly) index for the period 15 June to 15 August 2007 for Akia-Maniitsoq and 2008 for Kangerlussuaq-Sisimiut.

Population	Daily Temperature (°C) ¹			Mean daily total surface precipitation (kg/m ²)	Warble & Bot Fly Cumulative Index
	Mean	Max	Min		
AM	10.2	20.2	0.1	4.1	5.52
KS	12.9	23.6	1.2	0.8	16.4

¹ Two metres above ground surface.

These means range from roughly double to eight times greater than the 38 ± 43 , 51 ± 4 or median 76 observed in North American caribou (respectively: Thomas & Kiliaan, 1990; Bergerud *et al.*, 2008 Hughes *et al.*, 2009). Even higher were the mean warble larvae number in calves, 457 ± 284 KS, and 318 ± 160 AM. The high larval burdens in Greenland caribou, relative to observations from other CircumArctic herds, may be connected to their short spring migrations (<200 km). Migration can minimize reinfestation by warble and bot flies in wild reindeer and caribou (Thomas & Kiliaan 1990; Folstad *et al.*, 1991) and timing of movement between ranges is recommended as a means of minimizing infestation in domestic reindeer herds (Folstad *et al.*, 1991). The short spring migration distances of the AM and KS herds would not separate them from the areas where the larvae were dropped to pupate, which would put the caribou in close proximity to adult flies when these emerged, promoting high infestations of larvae the following winter.

KS caribou showed a higher average warble to nose bot ratio by number of larvae than the AM (KS, 3.75-7.5 : 1; AM, 1.42-2.85 : 1). This regional difference suggests that parasite prevalence differs between these two West Greenland populations or differed substantially between the years in which the collections were made. Explanations for the high number of warble larvae in KS relative to AM might include the dissimilarities in topography, weather and cari-

bou density. The sampled KS cows inhabit an area lacking high elevations, while AM habitat includes elevations > 700 metres, which provide options for caribou to reduce the risk of exposure to the adult flies. Recent KS densities are ca. 7 caribou per km² relative to AM's ca. 2 caribou per km² (Cuyler *et al.*, 2011) and spring migration distances are about ½ those of the AM caribou. Both would allow adult flies to easily locate KS caribou. Local weather in the summer preceding the March collections can also explain some of the difference in AM and KS larval burdens. Hot dry summers benefit adult fly activity (Thomas & Kiliaan, 1990) and also could control phenology of shedding or pupation (Nilssen & Haugerud, 1994). The dryer warmer calmer weather at KS resulted in a summer oestrid index of 16.4, in contrast to 5.5 at AM (Table 3).

In adult cows, nose bot larvae were far outnumbered by warble larvae. We do not know why nose bot larvae occurred in lower numbers than warble larvae. Syroechkovski (1995) also found fewer bot larvae in Russian reindeer. At the prevalence and intensity of infection that we recorded, nose bot larvae were not related to reproductive status, although detecting an effect was difficult due to low number or absence of nose bots, which reduced already low sample sizes for some categories in particular. Alternately, these tests may have suffered from low statistical power. Nose bot presence should not yet be rejected as influencing fitness of the host.

In the most heavily infested cows, the energy cost of 'growing' the combined warble and nose bot burdens was equivalent to 2-5 days of the host cow's BMR and foregone body fat reserves of 0.4-0.9 kg. Although these results are modest, any increases in energy expenditure in the three month period prior to parturition, when warble larvae are growing and cows are heavily pregnant, could be critical to fetal development (Roffe, 1993). Maternal condition during late pregnancy influences calf survival (Cameron *et al.*, 1993) and calf birth weight (Russell *et al.*, 2002). Our calculated energy costs for the larvae burden during this period may be a minimum, because we did not account for increased heat loss as the fur surface becomes increasingly disrupted by larger warbles, and increasingly larger "breathing-hole" sizes, or the protein costs of both a heightened immune and inflammatory response by the host to the larvae. Further, calving, specifically 10-days post calving with lactation, is the most energetically demanding period for cows (White & Luick, 1984; Oftedal, 1985; Clutton-Brock *et al.*, 1989; Russell, *et al.*, 1993). This period coincides with peak larvae growth and energy requirements prior to exiting their host (Josefsen *et al.*, 2006). Adverse severe weather events in late winter / spring causing further energy expenditures beyond the already present parasite loads, could negatively affect survival, specifically in malnourished cows (Bergerud *et al.*, 2008). The unusually high warble loads occurring in Greenland cows could intensify the effects of negative weather events on caribou populations in West Greenland. The situation was worse for 10-month old calves-at-heel than for their dams, because calves in addition to being small and having zero rump fat, averaged 320 to 460 warble larvae in AM and KS herds respectively. Calves-at-heel had higher burdens than cows and heavy infestations were over 1000 warbles. Energy costs of the heaviest larvae burdens were equivalent to ca. 7-12 days BMR, and foregone body fat reserves of 0.7 to 1.2 kg. This puts into perspective the minimum energy cost associated with heavy warble infestations in calves, as 1.2 kg fat would raise their body fat by about 3-4%. Although this oestrid fly model addresses an assessment of both the retained energy (NE) and the summated costs of support metabolism, many assumptions are made. We recommend that larvae counts and weights be made throughout the winter to accurately predict growth curves, and to make extensive measurements of nutrient contents (water/dry matter, energy, fat, protein, carbohydrate and ash) be made on larvae from these collections. In addition a more robust measure of the metabolic rate of the growing larva needs to be made. We consider our current estimates

to be minimal. Our finding that the overall cost to the host is almost equally distributed between NE and summated metabolism is novel and requires verification because the balance is dependent on larva composition, growth rate and date of shedding. Thus we have not attempted to relate energy costs on an individual host basis, but have reserved the analysis to gross mean.

The survival to March-April of heavily infested calves-at-heel in this study could be attributed to the high level of extended lactation exhibited by their dams. Given high mean warble numbers, and the March-April timing for our collections we were surprised that several pregnant cows were also nursing their ca. 10-month old calf-at-heel. Sometimes these pregnant lactating cows possessed rump fat greater than average for those sampled. Lactation extending into spring among Greenland cows was rare in a similar 1997 study (C. Cuyler unpubl. data). Extended lactation occurs sporadically in caribou (Bergerud *et al.*, 2008), but is considered a rare event. A four year study of the Porcupine herd showed that extended lactation was associated with infertility, however the authors did not report a weaning time for these cows (Gerhart *et al.*, 1997). Currently, West Greenland caribou are exceptional, since both pregnant and non-pregnant females display extended lactation. Based on the greater incidence of clear liquid in the mammary glands of pregnant KS cows (8 of 19, Fig. 3) collected almost one month earlier than the AM cows (3 of 28, Fig. 2), we suggest weaning following extended lactation had begun in early March for pregnant cows. For non-pregnant cows, however, lactation may be extended beyond mid-April. The likely increased fitness of cows exhibiting extended lactation suggests that they, and their calves-at-heel, would be resilient to survive the energy cost to parturition plus any subsequent restricted forage availability caused by weather. Bergerud *et al.* (2008) argue that overwinter-fat reserves are retained for energy costs of spring migration. However, this is not the case for Greenland caribou because of the short distances. Alternately, White & Luick (1975) suggest that body fat reserves stimulate early post parturient milk secretion. Although our findings are not in conflict with this hypothesis, we suggest that presence of fat reserve in lactating and pregnant cows emphasizes the role of individual variation in caribou populations, possibly driven by responses to parasitism. Individual quality is considered to affect survival and reproduction in semi-domestic reindeer (Weladji *et al.*, 2008) and red deer (Moyes *et al.*, 2011). To capture and measure this variation and to test these hypotheses, we need to increase sample sizes

and to consider more targeted and stratified sampling in order to measure differential effect of parasites on their hosts.

Despite the apparent high level of maternal investment, extended lactation still may not satisfy the energy demands of the most heavily infected calves. Normal autumn weaning or in early winter, or an inability of females to maintain extended lactation, plus unfavourable events creating additional energy expenditures in late winter / spring, separately or in combination, could negatively affect survival of calves with poor body condition and large numbers of warble larvae. This may be a factor behind the observed decreasing trend in late-winter calf-recruitment over the last decade (Cuyler *et al.*, 2005, 2011).

Greenland caribou cows are smaller bodied than other Circumpolar herds, which typically range about 80-90 kg in March-April (Adamczewski *et al.*, 1987; Gerhart *et al.*, 1996; Bergerud *et al.*, 2008). Greenland cow weights are even below Bergerud *et al.*'s (2008) June cows in Ungava, Canada, which were at their lowest annual weight. Pregnancy rates in relation to body weight of Ungava caribou in April (Fig. 9.15, Bergerud *et al.*, 2008) would predict a pregnancy rate of 20-45% based on body weights for AM and KS cows (Table 1, 2). These predictions for light weight cows are low compared with the 53-82% observed for the KS and AM herds. Although these body weight results partially explain the level of fecundity, we cannot discount a bias in sampling and errors associated with small sample sizes. Body size differences between the small AM and KS caribou are best reflected by dressed carcass weight, because KS ingest copious amounts of graminoids (Lund *et al.*, 2000), which cause higher rumen volume and weight (C. Cuyler unpubl.). A comparison of AM and KS calf body and carcass weights clearly confirms a larger alimentary fill in the KS calves compared to AM calves. While pregnant KS cows were larger than AM, their amount of rump fat was the same, making their percentage of fat less than for AM. KS also had greater warble burdens with accompanying greater winter energy costs, and a low pregnancy rate, i.e., 53%. The latter may be another factor behind the decreasing trend in calf-recruitment mentioned above. Regardless, despite their small body size and high warble loads relative to other herds, Greenland cows may maintain extended lactation to their calf-at-heel in addition to being pregnant. Thus to date, it appears that both KS and AM have been able to compensate with adequate winter energy intake. For KS the abundance of readily available graminoids may be the key, while for AM it may be the presence of macro-lichens (albeit reduced in abundance this past

decade, C. Cuyler pers. observation). Until the occurrence of a regional negative stochastic weather event, e.g., severe thaw-refreeze icing restricting forage availability, warbles will not appear detrimental to their hosts, as their effects are subtle. Further analysis for other parasite species will reveal the extent that high oestrid larvae burdens described coincide with elevated levels of gastro-intestinal nematodes that have been implicated in affecting reproduction in Svalbard reindeer (Albon *et al.*, 2004).

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