INTERRELATIONSHIPS BETWEEN WEATHER, PARASITIC INSECTS, AND BARREN-GROUND CARIBOU (*RANGIFER TARANDUS GROENLANDICUS*) BEHAVIOUR IN NORTHWEST TERRITORIES AND NUNAVUT

by

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ABSTRACT

The Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus*) herd decreased by 90% from 1986-2009. Increased intensity of insect harassment due to climatic warming is hypothesized as a factor contributing to the decline. I monitored weather, trapped insects, and recorded caribou behaviour during 2007-2009. Oestrid fly (Oestridae) presence, and mosquito (Culicidae) and black fly (Simuliidae) activity/abundance were best explained by temperature, wind speed, light intensity, barometric pressure, relative humidity, vegetation, topography, and location. Time of day and growing degree days also affected mosquito and black fly levels. Conditions favouring mosquito activity declined, while those favouring black and oestrid fly activity increased since the mid 1980s. Mosquitoes had relatively little effect on caribou behaviour. Insect avoidance increased when oestrids were present or black flies were active at moderate-high levels. Understanding differential effects of macroparasites on *Rangifer* behaviour is necessary to predict herd dynamics in the context of a changing climate across northern Canada.

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CHAPTER 1

General Introduction

Background

Caribou and reindeer (*Rangifer tarandus*) populations are thought to cycle over 40 to 70-yr periods, however, the mechanisms of these patterns are not well understood (Gunn 2003, Zalatan et al. 2006). This is problematic given that many *Rangifer* herds across the circumpolar north are currently in the downward portion of the cycle, and, it is unclear whether natural recovery will be possible in the face of climate change, industrial development, and increased hunting pressure (Forchhammer et al. 2002, Vors and Boyce 2009). The decline of the Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus*) herd in the Northwest Territories and Nunavut, Canada, exemplifies this trend, with numbers dropping from a peak of 472 000 ± 72 000 (SE) in 1986 to 31 900 ± 5 300 in 2009 (Nishi et al. 2010). Continued declines will have consequences for both ecosystem integrity and the livelihoods of northern residents with strong cultural and economic ties to caribou (Lee et al. 2000, Weladji et al. 2002, ACIA 2004, Forchhammer and Post 2004).

Various hypotheses have been proposed to explain recent declines in *Rangifer* populations. Large numbers of caribou/reindeer in the 1990s may have overgrazed summer ranges, leading to density-dependent feedback and current population declines (Skogland 1985, Crête and Huot 1993, Post and Klein 1999). Increased industrial development and human disturbance may also be affecting calving and summer range ecology (Adams 2005, Johnson et al. 2005). Stresses experienced on the summer range could be exacerbated by declines in lichen availability on the winter range due to increased frequency of forest fires (Kumpula et al. 1998, Bathurst Caribou Management Planning Committee 2004). Parasites, disease, predation, and hunting may interact to dampen potential herd recovery further

(Bathurst Caribou Management Planning Committee 2004). Climate change, a major confounding factor, will likely cause increased environmental variability and alter natural dynamics (Brotton and Wall 1997, ACIA 2004).

The post-calving/summer season (June 15 - September 1) is a critical time for caribou/reindeer as they must take advantage of the brief flush of highly nutritious forage and build up energy reserves to survive through the winter (Russell et al. 1993, Mörschel and Klein 1997). Body weight of *Rangifer* is largely determined by summer grazing conditions, and small changes in the pattern, quality, and quantity of forage intake can have multiplicative effects for growth and survival (White 1983, Reimers 1997, Colman et al. 2003). This is especially critical for lactating cows and calves. Females may face a trade-off between lactation and acquiring enough body reserves to survive the winter and reproduce successfully the following spring (Helle and Tarvainen 1984). The potential effects of poor summer-range conditions on both calf survival of the current year and female fecundity the following spring are particularly critical in times of population decline.

Although factors controlling fecundity and recruitment are largely nutritional in origin (Cameron 1994) several stressors may limit the ability of *Rangifer* to meet forage intake requirements. One such factor on the post-calving/summer range is harassment by biting and parasitic insects, including mosquitoes (Culicidae), black flies (Simuliidae), and oestrid flies (Oestridae) (Pruitt 1960, Colman et al. 2003). Biting flies impart costs on caribou/reindeer through blood loss (Syroechkovskii 1995) and act as vectors of blood borne parasites (Glover et al. 1990, Lefebvre et al. 1997, Dubey et al. 2004). The larvae of oestrid flies are obligate mammalian parasites that are a burden on *Rangifer* in terms of resources required for larval growth and development (Nilssen 1997b) and costs associated with immune responses (Gunn and Irvine 2003, Asbakk et al. 2005). In addition to the direct effects of blood loss and parasitic loading, insect harassment alters habitat use and activity budgets of caribou/reindeer (Downes et al. 1986, Mörschel and Klein 1997, Hagemoen and Reimers 2002). Feeding typically dominates *Rangifer* activity budgets, however, animals experiencing insect harassment are reported to decrease time spent foraging and increase time involved in energetically costly behaviours like standing, walking, and running (Roby 1978, Russell et al. 1993, Toupin et al. 1996, Colman et al. 2003). In addition, caribou/reindeer attempting to avoid harassment may frequent insect-relief terrain, which tends to be devoid of vegetative growth or to contain forage of lower quality than surrounding areas (Boertje 1981, Russell et al. 1993, Skarin et al. 2004). Consequent reductions in forage intake can cause *Rangifer* to be in a negative energy balance, with lactating cows and calves being particularly vulnerable (Fancy 1986, Hovey et al. 1989, Russell et al. 1993).

Insect harassment is thought to be the most important causal link between warm summer temperatures and reduced body condition in *Rangifer* (Weladji et al. 2003). The effects of climate change are occurring at an accelerated rate in the Arctic, with a warming of 4-7° C predicted over the coming century (ACIA 2004). Insect harassment experienced by caribou/reindeer may begin earlier in the summer season, last longer, and intensify as summer conditions warm (Brotton and Wall 1997, Callaghan et al. 2004). Our understanding of the potential consequences of warming, however, is hampered by a paucity of information on the effects of changing environmental conditions on the activity/abundance of different families of parasitic insects in the central Arctic. Also, there is insufficient information to determine the differential influence of increased harassment by the various species of insects on the activity patterns and distribution of *Rangifer*. Several studies have examined the behavioural interactions of caribou/reindeer, mosquitoes, and oestrid flies (Dau 1986, Downes et al. 1986, Russell et al. 1993, Hagemoen and Reimers 2002), but results were variable in terms of the relative importance of the different insect species and the environmental thresholds constraining insect activity (Mörschel 1999, Hagemoen and Reimers 2002, Weladji et al. 2003). Additionally, little is known about the distribution and abundance of black flies (Simuliidae) on caribou ranges in North America (Anderson and Nilssen 1996b).

A lack of understanding of the influence of weather on current insect activity/abundance levels makes it difficult to predict the extent to which climate change will affect the distribution and productivity of *Rangifer* populations (Gunn and Skogland 1997, Whitfield and Russell 2005). Identification of trends in disease and parasites, as well as alterations in caribou behaviour in response to environmental change will contribute to understanding the interplay of factors (e.g., disease/parasites, climate change, industrial development, harvest pressure, predation) driving changes in the numbers of Bathurst caribou (Bathurst Caribou Management Planning Committee 2004, NWT CIMP 2007, Chen et al. 2009, TG and GNWT ENR 2010). Increased knowledge of summer-range ecology is critical for developing sustainable harvest levels and management strategies for caribou in the face of global change.

In order to address gaps in our understanding of climate-insect-caribou interactions, I quantified relationships between weather parameters, activity/abundance levels of parasitic insects, and caribou behaviour. During 2007-2009, I recorded weather conditions, used carbon-dioxide baited traps to systematically monitor insect activity, and observed caribou behaviour using group scan and focal individual sampling on the post-calving/summer range of the Bathurst herd. Objectives were to: (1) develop indices representing activity/abundance of parasitic insects (mosquitoes, black flies, oestrid flies) as products of weather, habitat/location, and time; (2) develop a chronology of predicted insect levels since the 1950s; and, (3) define fine-scale functional relationships between caribou behaviour, insect activity/abundance, habitat, and time/date.

In Chapter 2, I developed sets of statistical models that allowed me to test hypotheses about the effects of weather, habitat/location, and date/time on insect activity/abundance. I used multinomial logistic regression (mlogit) to model categorical levels of mosquito and black fly activity, and logistic regression to model oestrid fly presence/absence. I used an Information Theoretic Model Comparison (ITMC) approach to select the best models to describe the ecology and predict the relative abundance of insect family groups. Using indices generated from the best models, along with historical weather data, I developed a chronology of insect activity on the Bathurst range from 1957-2008.

In Chapter 3, I used ITMC to test statistical model sets representing hypotheses about the effects of insects, weather, habitat/location, and date/time on caribou behaviour. I used mlogit to explore factors affecting the relative dominance of behaviour types within groups of caribou. I used a novel statistical approach to behavioural analysis, fractional multinomial logistic regression (fmlogit), to determine factors influencing time allocation by individual caribou. I used fractional logistic regression (flogit) to examine changes in feeding intensity. I concluded with a summary of the main findings of my research, discussion of management implications for the Bathurst caribou herd, and examination of broader applications of this work (Chapter 4).

Study Area

The majority of the Bathurst caribou herd winters below tree line in Northwest Territories and northern Saskatchewan, Canada (Gunn et al. 2001). The northward spring migration begins in mid April (Gunn and Poole 2009). By mid to late May, caribou reach the calving ground near Bathurst Inlet, Nunavut, with peak calving occurring in early June (Gunn et al. 2001). Within a few days of calving, caribou begin the post-calving migration typically following a clockwise pattern of south and southwesterly movement paralleling tree line before heading northwest. During August and September, caribou disperse across the tundra before making their way towards tree line for the rut in October (Gunn et al. 2001).

The post-calving/summer range (June 15 – September 1) of the Bathurst caribou herd covers an area of 46 386 ± 13 725 km^2 of the Slave Geological Province and Southern Arctic Ecozone (Matthews et al. 2001) in the Northwest Territories and Nunavut (Figure 1). Mean annual temperature is -10.5° C, with a summer average of 6° C (Ecological Stratification Working Group 1995). Mean temperatures generally decline from southwest to northeast, with dates of river and lake ice freeze-up and break-up paralleling temperature isotherms (Prowse et al. 2009). The region is semi-arid, receiving 200 to 300 mm mean annual precipitation (Ecological Stratification Working Group 1995). Permafrost is continuous, and the gently rolling landscape consists of largely unvegetated uplands of Canadian Shield rock, and lowlands containing fens, bogs, and tundra lakes (Matthews et al. 2001). Sparsely

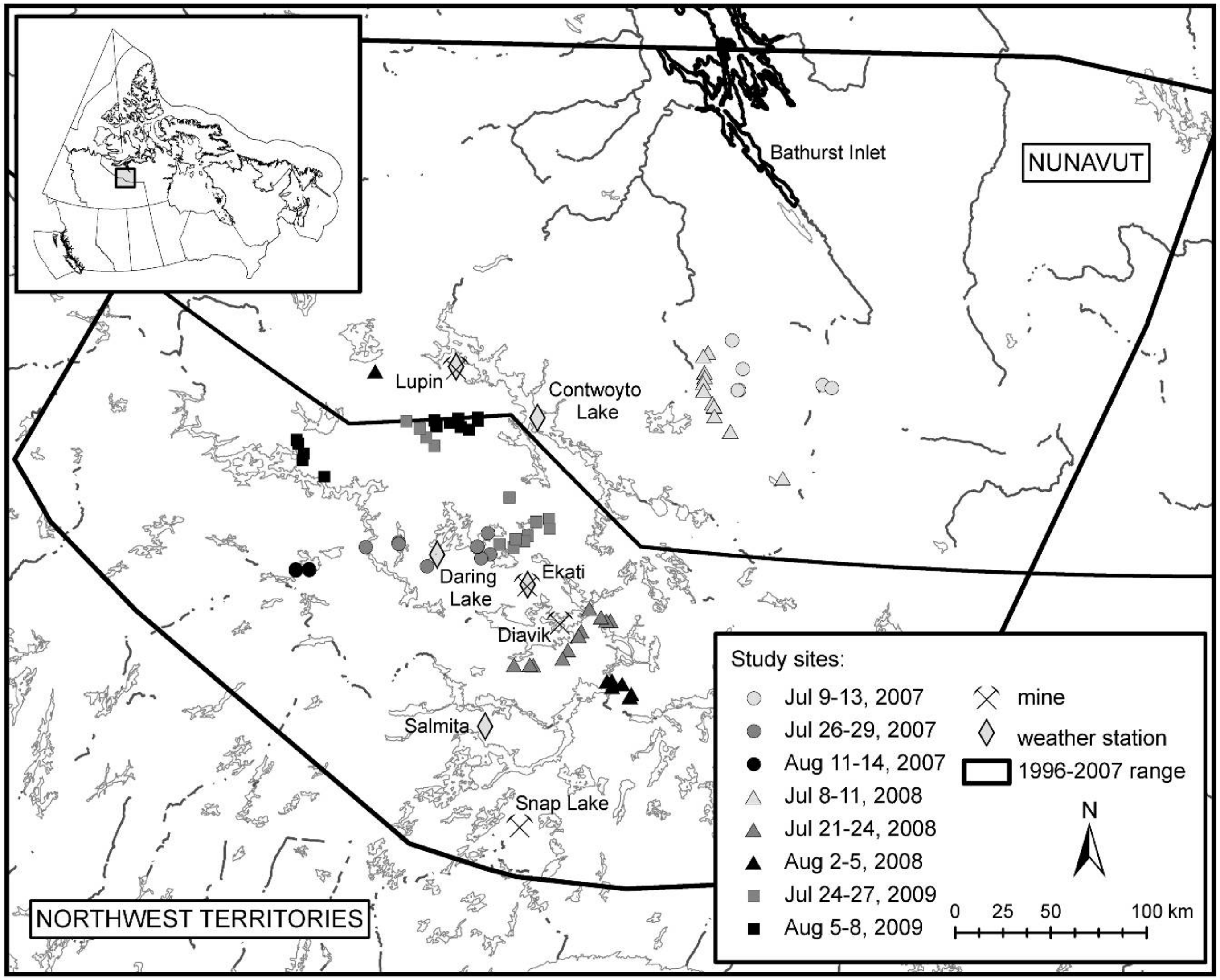


Figure 1. Post-calving/summer range of the Bathurst caribou herd based on locations of satellite-collared cows 1996-2007. Point locations show mines, weather stations, Tundra Ecosystem Research Station at Daring Lake, and intensive session study sites from 2007-2009.

vegetated eskers also provide a significant component of topographic relief in the landscape. Important vegetation types that serve as caribou forage include sedge wetlands dominated by *Carex aquatilis*, *C. bigelowii*, and cotton grass (*Eriophorum angustifolium*), as well as hummocks with tussock cotton grasses (*Eriophorum vaginatum* and *E. russeolum*) (Matthews et al. 2001). Heath tundra consisting of ericaceous mat communities, dwarf birch (*Betula* spp.), and varied amounts of bedrock and boulders is common, along with low shrub (*Betula* spp. and *Salix* spp.) vegetation types.

Aside from caribou, the only large-bodied herbivores on the post-calving/summer range are muskoxen (*Ovibos moschatus*) and moose (*Alces alces*). Muskoxen are common near Queen Maud Gulf and north of Great Bear Lake, but otherwise present in limited numbers across the Bathurst range (GNWT ENR 2008). Historical moose habitat is south of tree line, but since the early 1900s low densities of moose have been seen on the tundra where adequate forage is available (GNWT ENR 2010b). Herbivory by small mammals, especially lemmings (*Lemmus* spp., *Dicrostonyx* spp.), may also affect forage conditions on the post-calving/summer range (Callaghan et al. 2004). Large carnivores include gray wolves (*Canis lupus*), grizzly bears (*Ursus arctos*), and wolverines (*Gulo gulo*). All three hunt caribou and scavenge carcasses to some extent during the post-calving/summer season (Johnson et al. 2005).

Biting and parasitic insects on the Bathurst post-calving/summer range include mosquitoes, black flies, and oestrid flies. The most common mosquito genus in the Arctic, *Aedes* spp., has a single generation per year and overwinters in the egg stage (Twinn 1952). Mosquito larvae require standing water (Wood 1985), and adult emergence typically corresponds with the appearance of the first open water in spring/summer (Haufe and

Burgess 1956). Habitat type also has a marked effect on adult mosquitoes with reduced activity/abundance in stereotypical insect relief terrain such as windswept uplands (Corbet and Danks 1973, Downes et al. 1986). Black flies have one to multiple generations per year (Twinn 1952), and are often associated with habitats near moving water where they breed. Adult black flies are strong fliers, however, and are capable of traveling up to 80 km from their breeding site depending on weather conditions (Williams 1961, Bennett and Fallis 1971, Wenk 1981, Cupp 1981). Two species of oestrid flies are present on the Bathurst range: warble flies (*Hypoderma tarandi*) and nose bot flies (*Cephenemyia trompe*). Unlike mosquitoes and black flies, both oestrid species have larval stages that are obligatory endoparasites of *Rangifer* (Nilssen 1997a). Oestrid larvae overwinter inside the body of the caribou host, feeding on blood and other host secretions (Anderson and Nilssen 1990). Larvae depart from caribou hosts during late April to late June (Nilssen and Haugerud 1994). The southeastern portion of the Bathurst summer range roughly corresponds to the area Bathurst caribou pass through on their northward migration to the calving grounds during the peak oestrid dropping period. After exiting the host, the timing of oestrid pupation and adult emergence varies based on weather conditions (Nilssen 1997a). Adult oestrids are typically active during July and August (Nilssen 1997a) when Bathurst caribou are again in the southern portion of the post-calving/summer range. Other parasitic insects that may be present on the Bathurst post-calving/summer range include horse flies (Tabanidae), muscoid flies (Muscidae), and biting midges (Ceratopogonidae) (Helle et al. 1992, Anderson and Nilssen 1998, Anderson et al. 2001, Hagemoen and Reimers 2002).

Historically, aboriginal peoples occupied the Bathurst post-calving/summer range in low densities, and they continue to engage in subsistence hunting and trapping in the area

(Bathurst Caribou Management Planning Committee 2004, Johnson et al. 2005). Other human developments include mineral exploration and production, winter roads and associated support camps, and outfitter fishing and hunting camps. The Lupin gold mine was active from 1982-2005 in the northern portion of the post-calving/summer range (Johnson et al. 2005, Kitikmeot Corporation 2010). Human development has increased substantially since diamondiferous kimberlite deposits were discovered in 1991, with 3 diamond mines (Diavik, Ekati, Snap Lake) currently operational in the central and southern portions of the range (Johnson et al. 2005, De Beers Canada 2010). A 495-km winter road servicing the diamond mines is active from January-April, and a 29-km, all-season road is associated with the Ekati mine (Johnson et al. 2005). Cumulative sources of human disturbance likely have reduced the area of high-quality caribou habitat on the post-calving/summer range (Johnson et al. 2005, Adamczewski et al. 2009).

CHAPTER 2

Translating the effects of climate change to scales relevant for populations: weather-based indices to predict levels of insect harassment experienced by an arctic ungulate

Abstract

Climate change is occurring at an accelerated rate in the Arctic, and declines in many caribou and reindeer (*Rangifer tarandus*) populations across the circumpolar north are largely contemporaneous to these changes. Insect harassment may be an important link between warm summer temperatures and reduced body condition in *Rangifer*. There is a paucity of information, however, describing regional variation and the effects of changing environmental conditions on the activity and abundance of parasitic insects across the central Arctic. These insects include mosquitoes (Culicidae), black flies (Simuliidae), and oestrid flies (Oestridae); all known to have detrimental impacts on mammalian hosts through both the direct costs of parasitic loading and indirect costs associated with behavioural responses to insect harassment. During 2007-2009, I recorded weather conditions and used carbon-dioxide baited traps to monitor insect activity on the post-calving/summer range of the Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus*) herd in Northwest Territories and Nunavut, Canada. I developed statistical model sets representing hypotheses about the effects of weather, habitat/location, and date/time on insect activity/abundance. I used multinomial logistic regression to model categorical levels of mosquito and black fly activity, and logistic regression to model oestrid fly presence/absence. I used an Information Theoretic Model Comparison approach to select the best models to describe the ecology and predict the relative abundance of insect groups. Using indices generated from the best models, along with historical weather data, I developed a chronology of insect activity on the Bathurst range from 1957-2008. Mosquito and black fly activity levels were best explained by a combination of temperature, wind speed, light intensity, barometric pressure, relative humidity, vegetation type, topography, location, time of day, and growing degree days.

Oestrid presence was best explained by temperature, wind speed, light intensity, barometric pressure, relative humidity, vegetation type, topography, and location. All models had good predictive ability. Retrospective analyses indicated conditions favouring mosquito activity declined since the late 1950s, while predicted levels of black fly and oestrid activity increased. Favourable conditions for black flies and oestrids occurred concurrently with the recent decline in the Bathurst caribou population from 1986 to present. Insect indices can be used as a management tool to predict changes in the activity/abundance of parasitic flies and understand potential repercussions for caribou populations in the context of climatic change. This study exemplifies how indices can be used to link large-scale climate changes to trends relevant to individuals, populations, and ecosystems.

Introduction

Global temperatures have risen by approximately 1.5° C over the past 100 years with Arctic temperatures rising at almost twice the global rate (IPCC 2007). Predictions of continued climatic warming for the near future are widely accepted (ACIA 2004, IPCC 2007). Global climate models, however, have coarse resolutions that do not capture the complexities to which individuals and populations respond at regional scales (Bader et al. 2008, Doherty et al. 2009). To better understand climate change impacts and facilitate appropriate policy and management actions, there is a need for increased understanding of the effects on individuals, populations, communities, and ecosystems, and of the mechanistic processes driving these responses (de Groot et al. 1995, Bale et al. 2002). Knowledge of reference conditions and natural variability is also necessary for predicting and evaluating future change (Linton and Warner 2003, Kutz et al. 2004, Hardman-Mountford et al. 2005, Hodkinson and Jackson 2005). Such baseline knowledge can be used to develop ecological indices and indicators that incorporate multiple sources of information to elucidate trends over time (Fore et al. 1996, Niemi and McDonald 2004, Hardman-Mountford et al. 2005). These tools are critical for cost-effective ecosystem monitoring and adaptive management in the face of global change (McGeoch 1998, Hopkins and Kennedy 2004, Hodkinson and Jackson 2005).

The development of indicators and indices to gauge the response of species and ecosystems to climate change is particularly important in the Arctic, where warming is occurring at an accelerated rate (ACIA 2004) and logistical constraints add to research and monitoring expense. Caribou and reindeer (*Rangifer tarandus*) are important to human and ecological communities across the circumpolar north (Lee et al. 2000, Weladji et al. 2002, ACIA 2004, Forchhammer and Post 2004). Many *Rangifer* herds have declined in population numbers over the past decade (Vors and Boyce 2009), largely contemporaneous with trends of increasing temperatures. Although *Rangifer* populations in the Arctic have experienced fluctuations in the past, the mechanisms are not well understood and it is unclear whether natural recovery will be possible in the face of climate change, industrial development, and increased hunting pressure (Forchhammer et al. 2002).

One hypothesis for the decline in *Rangifer* populations is that warmer summer temperatures may have increased the intensity and duration of harassment by parasitic insects (Brotton and Wall 1997, Mörschel and Klein 1997, Weladji et al. 2003, Callaghan et al. 2004). There is a paucity of information, however, on the types of parasitic insects on caribou/reindeer post-calving/summer ranges in different geographic areas and across the entire season when insects are active (Anderson et al. 2001, Hagemoen and Reimers 2002). Several studies examined the behavioural interactions of caribou/reindeer, mosquitoes (Culicidae), and oestrid (Oestridae) flies (Dau 1986, Downes et al. 1986, Russell et al. 1993, Hagemoen and Reimers 2002), but results in terms of the relative importance of the different insect species and on environmental thresholds constraining insect activity were varied (Mörschel 1999, Hagemoen and Reimers 2002, Weladji et al. 2003). Additionally, little is known about the distribution and abundance of black flies (Simuliidae) on caribou ranges in North America (Anderson and Nilssen 1996b).

Two species of oestrids, warble flies (*Hypoderma tarandi*) and nose bot flies (*Cephenemyia trompe*), are host-specific to caribou and reindeer (Colwell et al. 2006b). Although oestrid adults do not feed, the larval stages of both warbles and nose bots are endoparasitic (Nilssen 1997a). Oestrid infestation is thought to be pervasive in wild

Rangifer populations (Thomas and Kiliaan 1998, Scheer 2008); up to 99.9% of semi-domestic reindeer in Lapland and Norway have been found to be infected (Folstad et al. 1989, Folstad et al. 1991, Colwell et al. 2006a). Oestrids are estimated to cause growth deficits of 20-70 kg/yr in domestic cattle (Gunderson 1945, Campbell et al. 1973), and in caribou/reindeer they negatively affect nutritional balance, trigger immune responses, allergic reactions or infection, and in extreme cases can be a direct mortality factor (Anderson and Luick 1979, Dieterich and Haas 1981). A variety of biting flies, including mosquitoes and black flies, are also prevalent in the Arctic. An individual caribou/reindeer may lose up to 2 L of blood to mosquitoes in a season (Syroechkovskii 1995), and severe effects, including death, in livestock have been attributed to simuliids (Fredeen 1973).

In addition to the direct effects of blood loss and parasitic loading, the behavioural responses of *Rangifer* to abundant and persistent parasitic flies can result in significant energetic and nutritional costs (Downes et al. 1986, Mörschel and Klein 1997, Hagemoen and Reimers 2002, Colman et al. 2003). During times of high insect harassment, caribou/reindeer may reduce both feeding intensity and time spent foraging (Russell et al. 1993, Toupin et al. 1996, Colman et al. 2003). Concurrent with a reduction in feeding, insect harassment results in energetic expenditure via increases in both rate of travel (White et al. 1975, Roby 1978, Dau 1986, Anderson and Nilssen 1998) and time spent walking/running (Russell et al. 1993, Mörschel and Klein 1997, Hagemoen and Reimers 2002, Colman et al. 2003).

Climatic changes, including warmer temperatures throughout the year, increased summer rains, and longer growing seasons, are already being reported in many areas of the Arctic (Dye 2002, IPCC 2007, Environment Canada 2009a). The response of *Rangifer* to these climatic variations will be affected by interactions across multiple trophic levels (Callaghan et al. 2004, Forchhammer and Post 2004). Insect harassment experienced by caribou/reindeer may begin earlier in the summer season, last longer, and intensify as summer conditions warm (Brotton and Wall 1997, Callaghan et al. 2004). The response of insect species to changed conditions will likely be more complex than often suggested (Danks 2004). Many insects in the Arctic exist on the edge of developmental thresholds, and environmental factors may have large effects on egg, larval and pupal life stages as well as on activity of adult insects (Fallis 1964, Danks 2004). Although predictions of species responses to climate change necessarily involve simplification, tools (e.g., ecological indicators and indices) that allow us to anticipate future conditions are crucial to adaptive resource management (Brotton and Wall 1997).

As examples of predictive indices of insect activity/abundance, Russell et al. (1993) correlated mosquito activity with wind speed and temperature, using thresholds levels at which no mosquitoes were caught in sweep net samples on the range of the Porcupine caribou herd in Alaska, USA. Similar indices were also developed for oestrid activity; however, these were based on reported thresholds rather than empirical data collection (Russell et al. 1993). Mörschel (1999) inferred insect activity based on caribou behavioural response, and used daytime temperature and wind speed to develop a simple predictive index of oestrid activity on the range of the Delta caribou herd in Alaska. Weladji et al. (2003) used cloud cover in addition to mid-day temperature and wind speed to develop an index predicting the severity of insect harassment for reindeer on summer pastures in Norway.

The inclusion of local weather conditions within predictive indices provides a link between environmental conditions important at the scale of insects and caribou/reindeer and larger-scale climatic processes (Forchhammer and Post 2004, Whitfield and Russell 2005, LaDeau et al. 2008). In addition to temperature and wind, a number of other biotic and abiotic parameters also may interact to influence occurrence and activity levels of biting and parasitic insects (Danks and Oliver 1972, Clements 1999). In order to gain a better understanding of the influence of a wide range of environmental variables on parasitic fly activity/abundance and to test hypotheses about the potential responses of mosquitoes, black flies, and oestrids to climate change, I systematically trapped insects and monitored local weather conditions on the post-calving/summer range of the Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus*) herd in Northwest Territories and Nunavut, Canada during 2007-2009. Specific objectives were to: (1) determine the effects of weather, habitat/location, and time/date on activity/abundance levels of mosquitoes, black flies, and oestrid flies; (2) use the relationships between insect activity, weather, and time/date to develop indices that can be used to predict trends in insect levels over time; and (3) create a chronology of predicted insect levels on the Bathurst range since the 1950s, with inferences to recorded declines in caribou numbers.

Methods

Data Collection

During 2007-2009, I collected insect trap catch and weather data in the central to southwestern portion of the Bathurst post-calving/summer range (Figure 1). I used locations of collared female caribou to select sites for sampling during intensive sessions chosen to correspond with peak insect season (Roby 1978, Boertje 1981, Dau 1986, Russell et al. 1993). Intensive sessions occurred over a total of 33 days during 2007-2009. Dates were as follows: July 9-13, July 26-29, and August 11-14, 2007; July 8-11, July 21-24, and August 2-5, 2008; July 24-27 and August 5-8, 2009. I accessed sites via helicopter. In order to obtain broader temporal coverage of the insect season, I also collected insect and weather data at the Tundra Ecosystem Research Station at Daring Lake, Northwest Territories from June 29-August 13, 2008, and July 6-August 14, 2009.

I collected weather data, including barometric pressure, relative humidity, temperature, and wind speed at 10-min intervals over each 24-hr period using a portable weather station mounted at a height of 1.0 m above the ground (Kestrel 4500 on Kestrel Portable Vane Mount, Nielsen Kellerman, Boothwyn, PA). I quantified cloud cover by measuring light intensity at 30-min intervals in 2007 (EA30 light meter, Extech, Waltham, MA) and 10-min intervals in 2008-2009 (data-logging light meter, Sper Scientific, Scottsdale, AZ). I calculated mean values of weather variables over each 2-hr trapping session for use in insect models. I used modified Malaise traps baited with carbon dioxide (Anderson et al. 2001) to collect insects. Compressed gas cylinders equipped with Flowset1 valves (Clarke Mosquito Control, Roselle, IL) served as the carbon dioxide source. I regulated carbon dioxide flow at a release rate of 1 L/min; roughly equivalent to the amount emitted by 1-2 caribou (Anderson and Nilssen 1998). During intensive sessions, I monitored traps over the 24-hr period; with insects collected and counted at 2-hr intervals. At Daring Lake, the 24-hr cycle was divided into 4 periods and a 2-hr interval for insect collection was randomly selected within each period. Date, time, location, topography, and vegetation type were recorded at each trap site. I sorted insect catches into female mosquitoes, black flies, oestrid flies, and other. "Other" included male mosquitoes as they are non-hematophagous. Subsamples of mosquito catch were identified to species (Poirier lab, University of Northern

British Columbia) and selected specimens were identified using DNA barcoding (Cywinska et al. 2006). A subsample of 2007 black fly trap catch was sent to D. Currie (Royal Ontario Museum) for identification to species.

Model Development

I developed predictive statistical models of insect activity/abundance based on weather, time/date, and habitat/location. For mosquitoes and black flies, I modeled 4 categories (no, low, moderate, and high) of relative activity/abundance based on hourly trap catch data. Hourly trap catch numbers corresponding to 33.33 and 66.67 centile values were used to determine categorical breaks between low/moderate and moderate/high insect activity (Table 1). Initially, I attempted to fit these data to an ordered logistic regression model. Wald tests (Brant 1990), however, suggested that many environmental parameters violated the proportional odds/parallel regression assumption (i.e., the relationship between a given environmental parameter and insect activity/abundance varied depending on the level of activity/abundance). Thus, I chose to use a nominal non-ordered logistic regression (mlogit; Long and Freese 2001). Mlogits can be thought of as series of logistic regressions for all possible comparisons between categorical outcomes (Long 1997). Here, each binary comparison examined the effect of environmental variables on the probability of a given insect activity level compared to another (e.g., probability of low vs. moderate insect activity). Effects of environmental variables were allowed to vary across the levels of insect activity. Due to low trap catches, I modeled oestrid presence (1) and absence (0) using logistic regression. In all models, I used a robust clustering technique to account for potential autocorrelation among observations at a given trapping site (Nielsen et al. 2002). I used Intercooled Stata 9.2 (Statacorp, College Station, TX) for all statistical analyses.

Table 1. Mosquito and black fly categories used in multinomial logistic regression (mlogit) models of insect activity/abundance on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, 2007-2009.

Category[*]	Mosquitoes/hr	Black flies/hr
None (0)	0	0
Low (1)	0-3.5	0-1.5
Moderate (2)	3.5-42.9	1.5-5.5
High (3)	>42.9	>5.5

[*] For categories 1-3, categorical breaks were based on hourly trap catch numbers corresponding to 33.33 and 66.666 centile values.

Model Parameters

I developed explanatory models that included variables from 3 broad sets of environmental and physiological factors thought to influence the abundance and behaviour of biting and parasitic insects: weather, habitat/location, and time of day/year (Table 2). Weather-related variables included temperature, wind speed, light intensity, barometric pressure, and relative humidity. Habitat-related variables included vegetation type, topography, and location on the Bathurst range. I modified Northern Land Cover/EOSD 30 m vegetation cover data (Wulder and Nelson 2003, Olthof et al. 2008) to create 4 vegetation categories for mosquito and black fly models, and 2 vegetation categories for oestrid models. Topography was classified during site visits. I included easting and northing coordinates (Lambert Conformal Conic projection) of each site to determine if location within the Bathurst post-calving/summer range influenced insect activity/abundance. I also tested for effects of time and date. I used sunrise/set times (National Research Council Canada 2009) to create 5 time of day categories for mosquito and black fly models and 2 categories for oestrid models. As a measure of time of year, I included variables that were specific to the

Table 2. Independent variables and categorical coding used to describe mosquito and black fly activity/abundance and oestrid fly presence/absence on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, 2007-2009.

Variable	Description and categorical code
Weather	
Temp	Mean air temperature over 2-hr trapping period (°C)
Wind	Mean wind speed over 2-hr trapping period (m/s)
Light	Mean light intensity over 2-hr trapping period (lux)
BP	Mean barometric pressure over 2-hr trapping period (in Hg)
RH	Mean relative humidity over 2-hr trapping period (%)
Habitat	
Vegetation*	
tussock tundra/sedge	Tussock graminoid tundra and sedge (1)
non-tussock tundra	Moist to dry non-tussock graminoid/dwarf shrub tundra (2)
shrub	Low to tall shrub (3)
prostrate shrub	Prostrate dwarf shrub (4)
Topography	
lowland	Topographic depressions and lower slopes (1)
mid-slope/flats	Flat plains and mid-slopes (2)
upland	Ridge or esker tops and upper slopes (3)
Easting	Cartesian coordinates for eastward-measured distance (m)
Northing	Cartesian coordinates for northward-measured distance (m)
Time/date	
Time**	
dawn	1 hr before to 2 hr after sunrise (1)
morning	2 hr after sunrise to local/solar noon (2)
afternoon	Local/solar noon to 2 hr before sunset (3)
dusk	2 hr before sunset to 1 hr after sunset (4)
night	1 hr after sunset to 1 hr before sunrise (5)
Gdd	Growing degree days relevant to insect development
Gdd^2	Quadratic term for growing degree days
Eclosion	Days since predicted eclosion of oestrid flies; calculated using a modification of Nilssen's (1997a) equation
$Eclosion^2$	Quadratic term for days since predicted oestrid eclosion

[*] In oestrid models, vegetation type was collapsed into a binary variable: shrub (0) included prostrate dwarf shrub, low shrub, and tall shrub; and, tundra (1) included tussock tundra, non-tussock tundra, and sedge.
[**] In oestrid models, time was collapsed into a binary variable: dusk/night/dawn/morning (0) and afternoon (1).

emergence biology of the insect species. For mosquitoes and black flies, I calculated growing degree days (gdd) relevant to insect development. Growing degree days were cumulative over the course of each growing season and represented the sum of the mean daily temperatures above 0° C; negative temperature values were set to zero (BC Centre for Disease Control 2009, University of California and California State Department of Agriculture and Natural Resources Integrated Pest Management Program 2009). Adult mosquito emergence typically corresponds with the timing of the first open water in spring (Haufe and Burgess 1956), and black flies appear after mosquito levels have peaked (Wood 1985). I used the ice-free date at Daring Lake (Matthews 2010) as the start date to begin accumulating gdd in order to capture the earliest potential activity of these insect families. Four weather stations (Daring Lake, Ekati, Salmita, and Lupin) on the Bathurst post-calving/summer range (Figure 1; Water Resources Division, Department of Indian Affairs and Northern Development 2009; Environment Canada 2009b) record daily temperatures. Data from the nearest station(s) were used to calculate gdd specific to each sampling location. For oestrid models, I calculated days since predicted eclosion (i.e., emergence of adult flies from the pupal case). I modified an equation developed by Nilssen (1997a) to calculate daily pupal development rates and predicted eclosion date for *C. trompe* based on Julian day, daily mean and maximum temperature, and cloud cover. *C. trompe* larvae develop more rapidly than *H. tarandi*, so calculated eclosion dates should reflect the earliest potential activity of either oestrid species (Nilssen 1997a).

I used a priori knowledge to develop model sets representing biologically plausible hypotheses. I classified models of mosquito and black fly activity, as well as models of oestrid presence/absence, according to 3 explanatory themes: weather, habitat, and time/date. Temperature, wind speed, and light have been consistently cited as important in determining insect activity levels (Russell et al. 1993, Anderson and Nilssen 1996b, Weladji et al. 2003).

I used models within the weather theme to test the influence of these 3 weather variables both on their own and in combination in order to determine their relative importance in influencing insect activity/abundance. I also developed models that included barometric pressure and relative humidity to clarify the importance of these variables in moderating the effects of temperature, wind speed, and light. The timing of life stages of Arctic insects is particularly important as reproduction must be completed during the short summer (Corbet and Danks 1973, Nilssen and Haugerud 1994, Danks 2004). I created models within the time/date theme to test whether the effects of date and seasonality (i.e., gdd, gdd^2, time since predicted oestrid eclosion) might override short-term weather conditions in influencing insect activity/abundance. I included time of day variables to determine if Arctic insects exhibit patterns of strictly programmed diel activity as seen in many temperate species, or, alternatively, become active regardless of time of day given favourable weather conditions (Danks 2004). I created models within the habitat theme to examine the influence of vegetation and topography on insect activity/abundance as differential effects might have consequences for caribou in terms of habitat use and selection of insect relief terrain. Measures of location (i.e., easting and northing) were included in one model in this theme to test whether important habitat variables aside from vegetation and topography might be present in a spatial gradient across the Bathurst range.

By organizing models within the 3 themes, I was able to test if weather, habitat, or time/date was a predominant driver of insect activity/abundance levels as compared to the other themes. I hypothesized, however, that variables within each of the themes would be important in determining insect activity/abundance. Thus, I developed a fourth "combination" theme of models including explanatory variables from the weather, habitat, and time/date categories. I made comparisons among models in each of the explanatory themes, but this does not imply that I captured the full range of model possibilities. I used variance inflation factors to assess collinearity among independent variables (Menard 2001). I parameterized categorical variables using deviation coding to contrast the effect of each level against the overall effect of the categorical variable (Menard 2001).

Model Selection and Predictive Ability

I based model selection on 2 complementary goals: (1) to increase understanding of parasitic fly ecology; and (2) to develop predictive models of insect activity/abundance that can be easily applied by wildlife managers interested in both examining past and monitoring future conditions of insect activity/abundance across the range of Bathurst caribou. To meet the first goal, I considered a set of more complex models that included covariates for habitat type, topography and geographic location across the post-calving/summer range. This information is useful in understanding insect ecology; however, from a management perspective it is necessary to develop predictions that are applicable range-wide. Thus, when identifying the best model for retrospective and prospective applications, I restricted the set to models without habitat/location covariates.

For both modelling objectives, I employed an Information Theoretic Model Comparison (ITMC) approach using Akaike's Information Criteria for small sample sizes (AIC_c) and Akaike weights (w) to select the most parsimonious model (Anderson et al. 2000). I interpreted w as approximating the probability that a given model was the best within a model set. When 2 or more top models had a difference in $AIC_c < 2$, I considered these models to be of near equal parsimony (Burnham and Anderson 1998). For the best models, I generated β-coefficients and 95% confidence intervals for each parameter. To assess model fit I determined the difference between observed and predicted insect activity levels, and calculated Pearson's standardized residuals. During model development, I withheld 20% of the data from each intensive session for use in validation of the final models. I used area under the Receiver Operating Characteristic (ROC) curve (AUC) to assess predictive ability as poor (0.5 – 0.7), reasonable (0.7 – 0.9), or very good (0.9 – 1.0) (Swets 1988). All models were interpreted as predicting activity level or presence/absence relative to the trap catch. Although reflective of insect levels in the environment, trap catches did not measure absolute activity levels or presence/absence.

Retrospective Analysis

I used weather station records dating from 1957-2008 to make predictions about potential insect activity levels on the Bathurst range over the past half century. Retrospective analyses are useful for understanding changes over time, but in attempting such analysis some ecological complexities must necessarily be simplified (Hardman-Mountford et al. 2005). Weather stations in northern Canada are separated by hundreds of km, meaning conditions at varied locations across the Bathurst range must be estimated by those measured at one or a few points. To gain a better understanding of the degree of variation in weather conditions across the range, I calculated the correlation coefficients between meteorological variables recorded at my study sites and at the 4 permanent weather stations currently in operation on the Bathurst range (Figure 1). Strong correlations suggested that measures of a given weather variable at a few monitoring locations were representative of range-wide conditions. To facilitate range-wide predictions for the retrospective analysis, I excluded models from the full set that contained habitat/location covariates.

In the north central portion of the Bathurst range, Contwoyto Lake weather station had records from 1957-1981 and Lupin from 1982-2008 (Environment Canada 2009b). These stations are relatively close together, thus, I compiled these records into a single Lupin/Contwoyto dataset of hourly weather data for 0600-1800 hr DST for the 1957-2008 post-calving/summer seasons. In the south central portion of the range, Daring Lake research station had 24-hr records from 1997-2008; and further south, 24-hr records from the Salmita mine site covered the years from 1998-2008 (Water Resources Division, Department of Indian Affairs and Northern Development 2009).

Weather station records did not contain data on all of the parameters included in predictive models of insect activity. No station recorded barometric pressure, so I used the average value from my 2007-2009 field measurements for all predictions. Lupin/Contwoyto records did not contain data on light intensity; I substituted lux measurements corresponding to average values by time category from my field data. Daring and Salmita records consisted of incoming short wave radiation (Kw/m^2) data instead of light intensity measurements. I multiplied incoming radiation values by 248 756 to get an approximation of lux (Skye Instruments Ltd 2009). For all years, I used the mean ice free date from Daring Lake 1996-2009 records (Julian day 169) as the start date to begin accumulating gdds.

For each of the 3 weather stations (Lupin/Contwoyto, Daring, Salmita), I used insect activity/abundance models to make predictions about mosquitoes, black flies, and oestrids for each hour where weather data were available between June 15-September 1. For mosquitoes and black flies, I calculated the predicted probability of each of the 4 insect activity levels (no, low, moderate, high) for each hourly weather record. I considered insect activity to be the level with the highest predicted probability for the hour. I totalled the number of hours with moderate-high predicted activity across each season and calculated the ratio of moderate-high hours to total number of hourly weather data records. I used this ratio to compare the intensity of insect activity across years. I treated oestrid predictions in a similar manner. I considered the probability of oestrid presence to be high if the predicted probability exceeded 0.13, the 95th centile value of predicted probabilities from my 2007-2009 data set. I calculated the ratio of the number of hours with a high predicted probability of oestrid presence to the total number of hourly data records for each season. I used Spearman's rank correlation to examine potential trends in insect activity over time. The late 1970s/early 1980s were the beginning of a period of increased global temperatures (Jones and Moberg 2003). I used *t*-tests to compare mean Lupin/Contwoyto index values between 2 time periods (1957-1981 and 1982-2008; modified from Gunn 2008). I used Spearman's rank correlation to examine relationships between predicted insect indices and caribou population parameters including estimated population size and late-winter cow:calf ratios (Adamczewski et al. 2009, GNWT ENR 2010a). Other measures of caribou demography (e.g., pregnancy rates) may be more sensitive to the effect of insect harassment; however these data are not available over a long time series for the Bathurst herd.

Results

Weather Conditions and Insect Trap Catch

Weather conditions during the post-calving/summer season varied among the 3 yr of the study (Table 3). On average, temperature was highest in 2008, while 2009 brought

Table 3. Weather conditions by year across trapping sites on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, 2007-2009.

	2007[*] (n=127)	2008[**] (n=411)	2009[**] (n=351)
Temperature (°C)			
minimum	3.81	4.32	1.84
maximum	20.55	26.08	22.77
mean (± SE)	12.50 ± 0.40	13.90 ± 0.19	11.08 ± 0.22
Wind speed (m/s)			
minimum	0.21	0	0
maximum	5.08	7.97	8.81
mean (± SE)	2.40 ± 0.10	2.71 ± 0.071	2.84 ± 0.10
Relative humidity (%)			
minimum	33.68	24.26	38.90
maximum	99.80	100	100
mean (± SE)	70.20 ± 1.70	78.84 ± 0.93	81.67 ± 0.94
Barometric pressure (in Hg)			
minimum	28.30	27.81	27.72
maximum	28.72	29.85	28.77
mean (± SE)	28.46 ± 0.0087	28.27 ± 0.010	28.36 ± 0.011
Light intensity (lux)			
minimum	0	0	0
maximum	91 700	87 750	79 522
mean (± SE)	20 986 ± 1 931	21 633 ± 1 164	21 189 ± 1 199

[*] Includes data from intensive sessions (Jul 9-13, 26-29, and Aug 11-14, 2007)
[**] Includes data from intensive sessions (Jul 8-11, 21-24, and Aug 2-5, 2008; Jul 24-27 and Aug 5-8, 2009) and Daring Lake (Jun 29-Aug 13, 2008; Jul 6-Aug 14, 2009).

cooler temperatures, higher winds, and higher humidity when compared to 2007 and 2008. Onset of spring was also later in 2009; final break-up of ice on Daring Lake occurred on July 10 in 2009 as compared to July 2-3 in 2007-2008 (Matthews 2010). Barometric pressure and light intensity varied little among years. Weather conditions also varied among sampling periods within a year (Table 4). In general, mean temperature declined, while mean wind speed increased over the course of each summer.

Insect trapping effort was similar over the 2007-2008 intensive sessions, and slightly reduced in 2009 when 2 instead of 3 sessions were conducted (Table 5). Notable differences among years included the higher number of black flies trapped in 2007, oestrids in 2008, and

Table 4. Key weather variables ($\bar{x}$ ± SE) by sampling session across trapping sites on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, 2007-2009.

	2007			2008			2009	
	Jul 9-13 (n=32)	Jul 26-29 (n=57)	Aug 11-14 (n=38)	Jul 8-11 (n=59)	Jul 21-24 (n=47)	Aug 2-5 (n=56)	Jul 24-27 (n=59)	Aug 5-8 (n=55)
Temperature (°C)	16.17 ± 0.52	14.17 ± 0.38	6.92 ± 0.28	15.09 ± 0.50	13.65 ± 0.55	13.59 ± 0.34	13.35 ± 0.44	9.65 ± 0.45
Wind speed (m/s)	1.64 ± 0.11	1.97 ± 0.11	3.70 ± 0.13	2.42 ± 0.14	2.91 ± 0.19	2.98 ± 0.16	3.29 ± 0.23	3.39 ± 0.27
Relative humidity (%)	51.94 ± 2.78	69.71 ± 2.33	86.30 ± 1.48	63.73 ± 2.44	88.18 ± 2.20	89.36 ± 2.27	83.75 ± 2.63	90.51 ± 1.75
Barometric pressure (in Hg)	28.56 ± 0.014	28.38 ± 0.0065	28.51 ± 0.0094	28.13 ± 0.021	28.08 ± 0.027	28.22 ± 0.020	28.27 ± 0.020	28.03 ± 0.024
Light intensity (lux)	27 070 ± 4 644	19 687 ± 2 767	17 512 ± 2 936	23 089 ± 2 852	19 036 ± 3 379	15 905 ± 2 592	24 794 ± 3 385	13 665 ± 2 268

mosquitoes in 2009 (Figures 2-3, Table 5). Genetic barcoding of a sample of the 2007 mosquito catch indicated the presence of at least 5 species (A. Cywinska, L. Poirier, personal communications). *Ochlerotatus excrucians*, *O. punctor/absserratus*, and *O. hexodontus* were positively identified. The two remaining species were identified to the genus level (*Ochlerotatus* and *Aedes*); verification of specific identification using morphology was not possible at this point due to degradation of samples in the ethanol storage medium. Species identification of a subsample of black flies trapped during 2007 suggested the presence of common northern species, including *Simulium vittatum*, *S. rostratum*, the *S. venustum* complex, and the *S. arcticum* complex (D. Currie, personal communication). Oestrid flies were positively identified in the 2008-2009 trap catches. In 2008, trapped oestrids included 16 female warble flies, 4 female nose bot flies, and 1 unknown/escaped oestrid fly. Seven female warble flies were trapped in 2009. I failed to catch any oestrids in the Daring Lake traps.

Table 5. Insect trap catch by species grouping and year on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, 2007-2009.

	Intensive sessions 2007	Intensive sessions 2008	Intensive sessions 2009	Daring Lake 2008	Daring Lake 2009
Trap hr	278	319	212	503	493
Total oestrids	0	21	7	0	0
female warbles	-	16	7	-	-
female nose-bots	-	4	0	-	-
unknown/ escaped	-	1	0	-	-
Total female mosquitoes	6 850	9 044	14 258	15 967	38 192
Total black flies	5 765	878	675	2 923	2 749

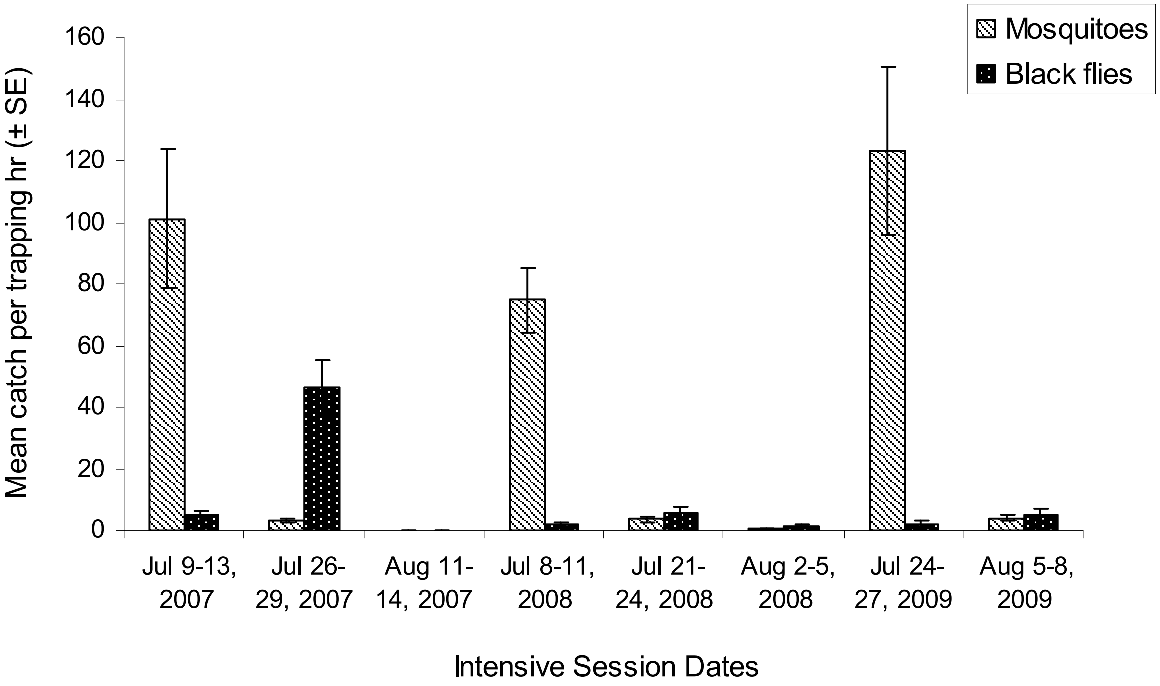


Figure 2. Mean catch ± SE of mosquitoes and black flies per sampling session on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, 2007-2009.

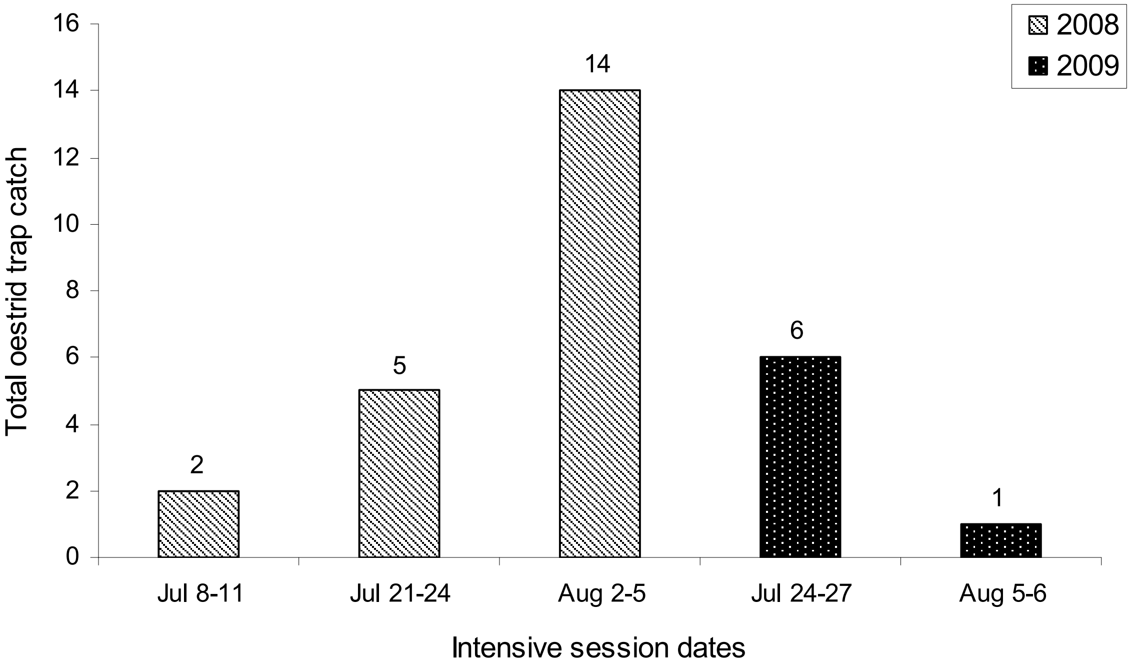


Figure 3. Total oestrid fly catch per sampling session on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, 2008-2009. No oestrids were caught in 2007.

Other hematophagous flies that may affect caribou include muscoid flies (Muscidae), horse and deer flies (Tabanidae), and biting midges (Ceratopogonidae). I trapped a single muscoid fly in 2007. Tabanids were relatively active at Daring Lake (60 tabanids trapped during 2008-2009); however, I trapped only 5 tabanids during the 2007-2009 intensive sessions. I trapped biting midges, but did not separate these from non-biting species caught incidentally. I did not consider these 3 insect species groupings further, however they may be important on the summer ranges of some caribou/reindeer herds.

Mosquito Models

The activity/abundance level of mosquitoes was best explained by a model from the ‘combination’ theme that contained covariates for temperature, wind speed, light, barometric pressure, relative humidity, gdd, time, vegetation type, topography, easting, and northing (Table 6). No other models in the set had comparable AIC_c scores, and the Akaike's *w* indicated there was a 99% chance that this model was the best. The top model had reasonable to very good ability to distinguish between different levels of mosquito activity/abundance. Using independent data, ROC scores for the set of binary logistic regressions that represented the 4 levels of mosquito activity ranged from 0.86-1.00.

Several coefficients from the top-ranked mosquito activity model were statistically significant (Figure 4, Appendix A). All levels of mosquito activity relative to no activity were positively related to temperature and the probability of high relative to moderate mosquito activity also increased significantly as temperatures rose. Wind speed had a consistent negative effect; and, light intensity had a negative, but variable effect on mosquito levels. As barometric pressure rose, the probability of mosquito presence increased; the relationship between barometric pressure and activity level was also positive, but more variable. The relationship between relative humidity and mosquito activity was quite variable, but indicative of increased mosquito levels at higher relative humidity. In addition to the influence of weather, mosquito activity varied with both time of day and season. At dusk, the probability of high mosquito activity increased relative to mosquito absence, and the probabilities of moderate-high levels increased relative to low mosquito activity levels at night. Probabilities of low-moderate as opposed to high levels of activity increased during morning hours. The majority of coefficients relating mosquito activity to gdd were indicative of a quadratic relationship where mosquito activity levels initially increased and then declined as gdd accumulated over the course of the summer. Mosquito activity was not strongly related to vegetation type. Topography, however, influenced activity levels with increased probability of high activity in lowland areas. Many of the relationships between mosquito levels and northing/easting were also strong; indicative of higher activity levels to the north and east within the Bathurst post-calving/summer range.

Table 6. Candidate multinomial logistic regression (mlogit) models of mosquito activity/abundance on the Bathurst caribou post-calving/summer range, 2007-2009; number of parameters (*K*); log-likelihood; Akaike's Information Criterion (AIC_c) scores; differences in AIC_c scores (ΔAIC_c) and AIC_c weights (*w*) for subsets of time/date, weather, habitat, and combinations of time/weather/habitat variables.

Model	*K*	Log-likelihood	AIC_c	ΔAIC_c	*w*
Time/date					
gdd	3	−857.55	1721.14	452.99	<0.001
gdd + gdd^2	6	−780.10	1572.33	304.19	<0.001
gdd + time	15	−843.09	1716.87	448.72	<0.001
gdd + gdd^2 + time	18	−762.04	1561.06	292.92	<0.001
Weather					
temp	3	−956.90	1919.83	651.69	<0.001
wind	3	−849.90	1705.84	437.70	<0.001
light	3	−970.64	1947.31	679.16	<0.001
temp + wind	6	−823.36	1658.84	390.69	<0.001
temp + light	6	−951.25	1914.63	646.49	<0.001
wind + light	6	−842.36	1696.85	428.70	<0.001
temp + wind + light	9	−822.41	1663.08	394.93	<0.001
temp + wind + light + BP + RH	15	−814.71	1660.11	391.97	<0.001
Habitat					
vegetation	9	−964.75	1947.76	679.62	<0.001
topography	6	−958.54	1929.20	661.06	<0.001
vegetation + topography	15	−953.50	1937.69	669.54	<0.001
vegetation + topography + easting + northing	21	−874.66	1792.66	524.51	<0.001
Combination					
gdd + gdd^2 + time + temp + wind + light + BP + RH	33	−619.18	1307.69	39.54[**]	<0.001
gdd + gdd^2 + time + vegetation + topography + easting + northing	39	−727.77	1538.19	270.04	<0.001
temp + wind + light + BP + RH + vegetation + topography + easting + northing	36	−734.60	1545.16	277.01	<0.001
gdd + gdd^2 + time + temp + wind + light + BP + RH + vegetation + topography + easting + northing	54	−575.54	1268.14	0[*]	0.99

[*] To meet the goal of increasing understanding of mosquito ecology, I used the top-ranked model to explore the effects of covariates on mosquito activity/abundance.

[**] I used the second-ranked model to retrospectively analyze weather records and reconstruct a chronology of predicted mosquito levels on the Bathurst range in the past. I did not consider models including habitat/location covariates for use in retrospective analysis due to the need for an index that could be generalized across the Bathurst range.

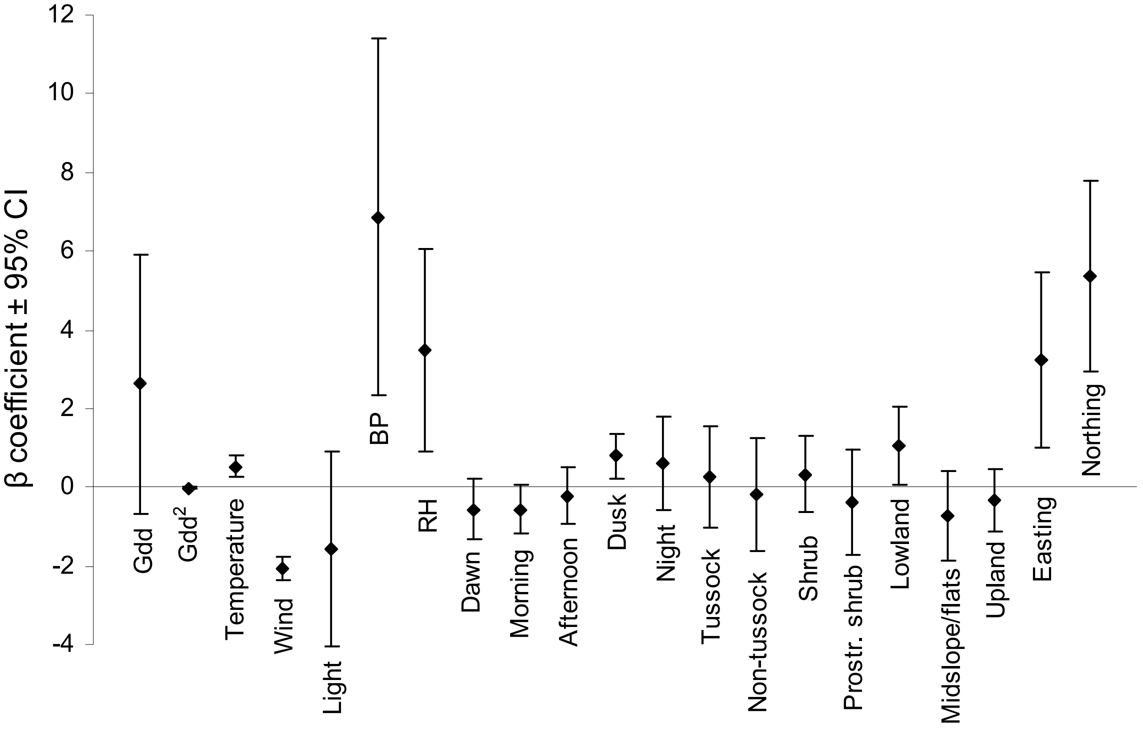


Figure 4. Coefficients (β) from top multinomial logistic regression (mlogit) model for comparison of high relative to no mosquito activity/abundance. Growing degree days (gdd), gdd^2, and relative humidity (RH) multiplied by 100; and, light, easting, and northing multiplied by 100 000 for ease of illustration. Confidence intervals (CI) that do not overlap 0 indicate significant coefficients.

Black Fly Models

Two models of black fly activity had nearly identical AIC$_c$ scores; with the second-ranked model scoring only 0.21 higher than the first (Table 7). The top-ranked model contained covariates related to weather and time/date (K = 33). The second-ranked model contained the same covariates as the first, as well as additional habitat variables (K = 54). In the ITMC framework, model averaging is recommended when a single model is not clearly superior to other models in a set (Burnham and Anderson 1998). There is little guidance, however, on the application of model averaging in a multivariate model framework where the high number of coefficients makes averaging unwieldy. Because of these difficulties, I chose to discuss covariates from the second-ranked model. This model contained all the

Table 7. Candidate multinomial logistic regression (mlogit) models of black fly activity/abundance on the Bathurst caribou post-calving/summer range, 2007-2009; number of parameters (K); log-likelihood; Akaike's Information Criterion (AIC_c) scores; differences in AIC_c scores (ΔAIC_c) and AIC_c weights (w) for subsets of time/date, weather, habitat, and combinations of time/weather/habitat variables.

Model	K	Log-likelihood	AIC_c	ΔAIC_c	w
Time/date					
gdd	3	−877.19	1760.41	489.68	<0.001
gdd + gdd^2	6	−831.03	1674.18	403.45	<0.001
gdd + time	15	−827.66	1686.00	415.27	<0.001
gdd + gdd^2 + time	18	−777.12	1591.24	320.51	<0.001
Weather					
temp	3	−730.75	1467.52	196.80	<0.001
wind	3	−860.36	1726.76	456.03	<0.001
light	3	−858.26	1722.55	451.82	<0.001
temp + wind	6	−675.78	1363.67	92.94	<0.001
temp + light	6	−728.58	1469.28	198.55	<0.001
wind + light	6	−815.21	1642.54	371.81	<0.001
temp + wind + light	9	−675.22	1368.70	97.97	<0.001
temp + wind + RH	9	−670.34	1358.93	88.21	<0.001
temp + wind + light + RH	12	−668.10	1360.64	89.91	<0.001
temp + wind + light + BP + RH	15	−667.36	1365.41	94.68	<0.001
Habitat					
vegetation	9	−878.26	1774.77	504.04	<0.001
topography	6	−879.03	1770.17	499.44	<0.001
vegetation + topography	15	−953.50	1937.69	666.96	<0.001
vegetation + topography + easting + northing	21	−855.14	1753.61	482.89	<0.001
Combination					
gdd + gdd^2 + time + temp + wind + light + BP + RH	33	−600.71	1270.73	0[**]	0.53
gdd + gdd^2 + time + vegetation + topography + easting + northing	39	−743.94	1570.54	299.81	<0.001
temp + wind + light + BP + RH + vegetation + topography + easting + northing	36	−625.36	1326.67	55.94	<0.001
gdd + gdd^2 + time + temp + wind + light + BP + RH + vegetation + topography + easting + northing	54	−576.94	1270.94	0.21[*]	0.47

[*] I used the second-ranked model to explore the effects of covariates on black fly activity/abundance to meet the goal of increasing understanding of black fly ecology.

[**] I used the top-ranked model to retrospectively analyze weather records and reconstruct a chronology of predicted black fly levels on the Bathurst range in the past. I did not consider models including habitat/location covariates for use in retrospective analysis due to the need for an index that could be generalized across the Bathurst range.

covariates that would be included if I adopted a model averaging approach, but did not account for additional weighing of the covariates present in both the first and second-ranked models. The second-ranked model had reasonable to very good ability to distinguish between different levels of black fly activity/abundance. Using independent data, ROC scores for the set of binary logistic regressions that represented the 4 levels of black fly activity ranged from 0.84-1.00.

Temperature had a positive effect on black fly activity, and the majority of coefficients were statistically significant (Figure 5, Appendix A). Wind speed had a consistent negative effect on black fly levels. Coefficients for barometric pressure suggested a negative association with black fly activity, but there was considerable variation in the relationship. The relationships between black fly activity and both light and relative humidity were ambiguous. Coefficients related to time indicated a trend toward increased black fly activity during morning, afternoon, and dusk; and decreased activity at night and dawn. Specifically, the probability of high relative to no-low activity increased during morning, and probability of low-moderate relative to no activity increased at dusk. There was also an increase in the probability of no relative to moderate black fly levels at dawn; and of no relative to low and high activity at night. The majority of coefficients relating black fly activity to gdd were indicative of a quadratic relationship where activity levels initially increased and then declined as gdd accumulated over the course of the summer. Coefficients relating black fly activity to vegetation type exhibited variable direction and strength. One exception was the decreased probability of high black fly activity relative to all other levels in the prostrate dwarf shrub habitat type. Few coefficients relating black fly activity to topographic position were significant; however, there was a weak trend toward increased activity in lowlands.

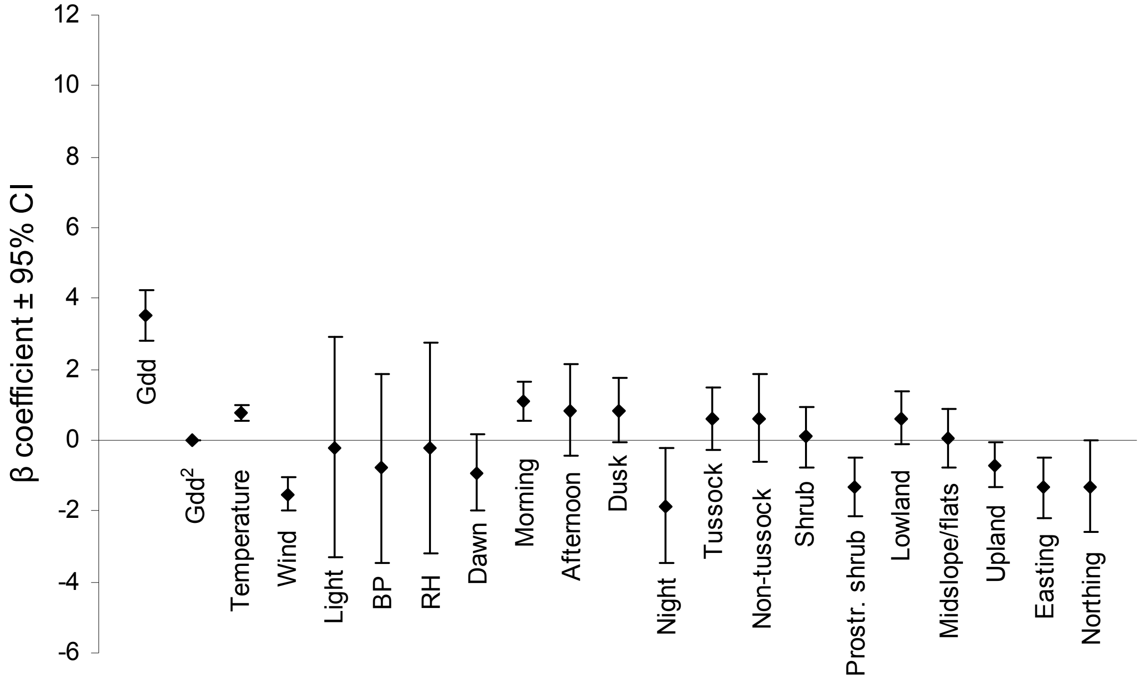


Figure 5. Coefficients (β) from top multinomial logistic regression (mlogit) model for comparison of high relative to no black fly activity/abundance. Growing degree days (gdd), gdd^2, and relative humidity (RH) multiplied by 100; and, light, easting, and northing multiplied by 100 000 for ease of illustration. Confidence intervals (CI) that do not overlap 0 indicate significant coefficients.

Oestrid Models

There was substantial model selection uncertainty in determining the "best" of the set of oestrid presence/absence models (Table 8). The 6 top-ranked models all differed in AIC$_c$ score by less than 2.0. The top-ranked model contained a single covariate for temperature and had good predictive ability (AUC = 0.82 training data; AUC = 0.93 independent data). In addition to temperature, the second-ranked model contained covariates related to other weather and habitat parameters. I chose to use the second-ranked model as my "best" oestrid model as it also had a high predictive ability (AUC = 0.91 training data; AUC = 0.85 independent data) and included information on more variables of potential biological significance. Due to model selection uncertainty, I examined the effects of coefficients from all 6 of the top models to gain a better understanding of oestrid fly biology.

Table 8. Candidate logistic regression models of oestrid fly presence/absence on the Bathurst caribou post-calving/summer range, 2007-2009; number of parameters (*K*); log-likelihood; Akaike's Information Criterion (AIC_c) scores; differences in AIC_c scores (ΔAIC_c); AIC_c weights (*w*); and area under the Receiver Operating Characteristic curve (AUC) calculated using the training data set, for subsets of time/date, weather, habitat, and combinations of time/weather/habitat variables.

Model	*K*	Log-likelihood	AIC_c	ΔAIC_c	*w*	AUC
Time/date						
eclosion	1	−45.13	92.28	13.55	<0.001	0.59
eclosion + eclosion^2	2	−43.85	91.73	13.00	<0.001	0.56
eclosion + time	2	−41.15	86.33	7.60	0.005	0.75
eclosion + eclosion^2 + time	3	−40.20	86.48	7.74	0.005	0.73
Weather						
temp	1	−38.36	78.73	0	0.24	0.82
wind	1	−45.08	92.17	13.44	<0.001	0.50
light	1	−42.31	86.64	7.91	0.005	0.69
temp + wind	2	−38.23	80.50	1.76	0.098	0.83
temp + light	2	−38.34	80.73	1.99	0.087	0.82
temp + wind + light	3	−38.16	82.40	3.66	0.038	0.83
temp + wind + light + BP + RH	5	−34.65	79.49	0.75**	0.16	0.87
Habitat						
vegetation	1	−44.79	91.59	12.85	<0.001	0.52
topography	2	−42.45	88.93	10.20	0.001	0.69
vegetation + topography	3	−41.93	89.94	11.21	<0.001	0.71
vegetation + topography + easting + northing	5	−38.58	87.35	8.61	0.003	0.79
Combination						
eclosion + eclosion^2 + time + temp + wind + light + BP + RH	8	−31.92	80.30	1.56	0.11	0.88
eclosion + eclosion^2 + time + vegetation + topography + easting + northing	8	−33.68	83.83	5.09	0.019	0.88
temp + wind + light + BP + RH + vegetation + topography + easting + northing	10	−29.24	79.18	0.45*	0.19	0.91
eclosion + eclosion^2 + time + temp + wind + light + BP + RH + vegetation + topography + easting + northing	13	−27.51	82.21	3.47	0.042	0.91

* I used the second-ranked model to explore the effects of covariates on oestrid presence/absence to meet the goal of increasing understanding of oestrid fly ecology.

** I used the third-ranked model to retrospectively analyze weather records and reconstruct a chronology of predicted probability of oestrid presence on the Bathurst range in the past. I did not consider models including habitat/location covariates for use in retrospective analysis due to the need for an index that could be generalized across the Bathurst range.

Temperature was the covariate with the strongest influence on the presence of oestrids (Figure 6, Appendix A). The probability of oestrid presence increased significantly as temperatures rose. Relative humidity and light had non-significant positive effects on oestrids, while wind speed and barometric pressure had non-significant negative effects. Oestrid presence was weakly related to vegetation type, with increased probability of presence in tundra, as opposed to shrubby vegetation. In lowlands, the probability of oestrid presence increased. Probability of presence increased slightly in the eastern and southern portions of the post-calving/summer range.

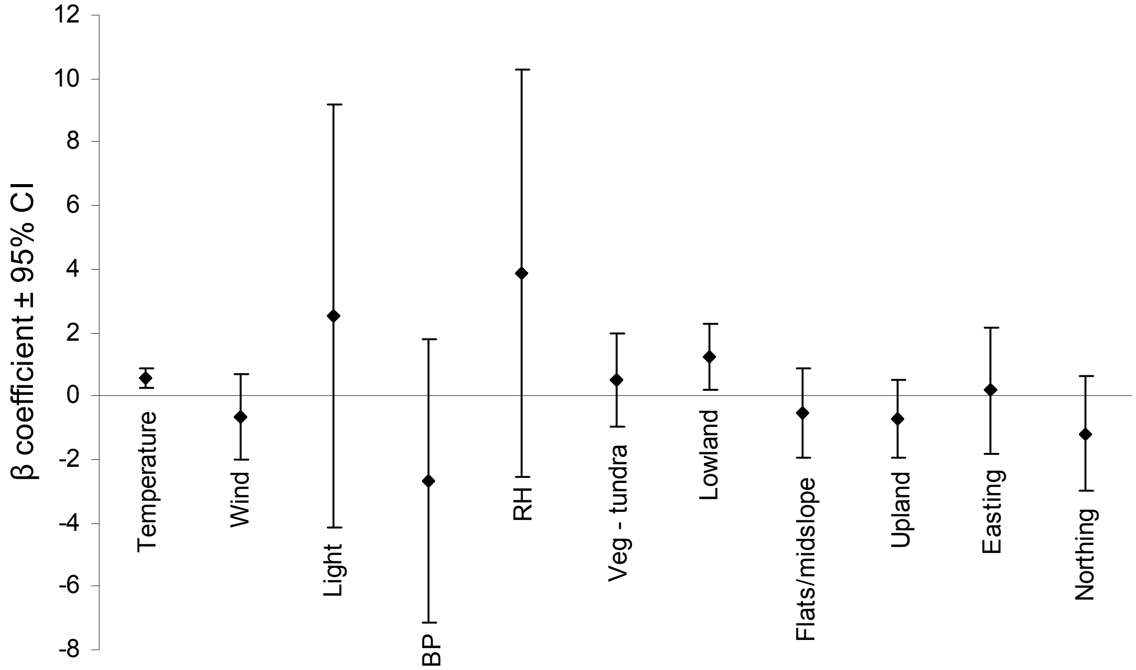


Figure 6. Coefficients (β) from oestrid fly second-ranked logistic regression model for comparison of presence relative to absence. Relative humidity (RH) multiplied by 100; and, light, easting, and northing multiplied by 100 000 for ease of illustration. Confidence intervals (CI) that do not overlap 0 indicate significant coefficients.

Retrospective Analysis

I found strong correlations among temperature, light, and relative humidity for the 4 weather stations across the Bathurst post-calving/summer range; however, wind speed was quite variable among stations. Correlation coefficients for temperature ranged from 0.82-0.97; light from 0.75-0.94; and, relative humidity from 0.67-0.95 (Table 9). Wind speed correlation coefficients varied from 0.37-0.74.

For mosquitoes, the top overall model contained covariates for weather, time/date, and habitat/location (Table 6). I used the second-ranked model, however, for retrospective analysis. This was a simplified version of the top model that excluded site-specific habitat and location covariates and was better suited for general application to the post-calving/summer range. Although the Akaike weight was low, the predictive ability of this model was comparable to that of the top model. Using independent data, ROC scores for the set of binary logistic regressions representing the 4 levels of mosquito activity ranged from 0.84-1.00, indicative of good predictive ability. Furthermore, there were few differences in the sign and significance of coefficients for the covariates in common between the 2 top-ranked mosquito models (Appendices A and B). There were 72 combinations of coefficients shared between the 2 models, only 4 of which differed in sign. Of those coefficients that differed, none were statistically significant.

For black flies, the model ranked second overall contained the same covariates as the top-ranked mosquito model (Table 7). The top-ranked black fly model contained a reduced covariate set that included variables related to weather and time/date. The top and second-ranked black fly models had almost identical AIC_c scores. I focused on the second-ranked model when I discussed ecological relationships in order to capture information on more

Table 9. Correlation of temperature (temp), wind, relative humidity (RH), and light intensity among temporary and permanent weather stations on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, Jul-Aug 2007-2009.

	Daring permanent station				Ekati permanent station				Lupin permanent station				Salmita permanent station			
	temp	wind	RH	light	temp	wind	RH	light	temp	wind	RH	light	temp	wind	RH	light
Intensive session temporary stations	0.89	0.56	0.78	0.83	0.89	0.50	0.77	NA	0.87	0.73	0.84	0.87	0.89	0.64	0.72	0.83
Daring Lake temporary station*	0.95	0.74	0.92	0.77	0.83	0.51	0.66	NA	0.87	0.56	0.77	0.78	0.89	0.62	0.80	0.75
Daring Lake esker temporary station*	0.97	0.72	0.95	0.77	0.82	0.52	0.61	NA	0.90	0.67	0.82	0.76	0.92	0.56	0.80	0.76
Daring permanent station (DIAND)**	1	1	1	1	0.96	0.74	0.92	NA	0.92	0.69	0.90	0.94	0.92	0.67	0.82	0.89
Ekati permanent station (Environment Canada 2009b)	0.96	0.74	0.92	NA	1	1	1	1	0.93	0.60	0.91	NA	0.92	0.37	0.85	NA
Lupin permanent station (DIAND)**	0.92	0.69	0.90	0.94	0.93	0.60	0.91	NA	1	1	1	1	0.89	0.57	0.83	0.91
Salmita permanent station (DIAND)**	0.92	0.67	0.82	0.89	0.92	0.37	0.85	NA	0.89	0.57	0.83	0.91	1	1	1	1

* Data from Daring Lake temporary stations from 2008-2009.

** Water Resources Division, Department of Indian Affairs and Northern Development 2009 variables of potential biological significance. I used the top-ranked model in retrospective analysis as this excluded habitat/location variables. The top-ranked black fly model had good predictive ability (ROC = 0.81-1.00). Of the 72 combinations of coefficients in common between the top 2 black fly models, only 5 differed in sign between the models and none of these were statistically significant (Appendices A and B).

I used the second-ranked oestrid model as the "best" model to explore factors affecting oestrid presence/absence (Table 8). This model contained covariates related to weather and habitat/location. For retrospective analysis, I selected the next best model that did not contain habitat/location covariates. This third-ranked model had good predictive ability (ROC = 0.87 training data; 0.84 independent data). With the exception of relative humidity, the coefficients for the weather covariates in common between the second and third-ranked oestrid models were very similar (Appendices A and B).

Although actual values of the insect indices differed, trends in insect levels were similar among all 3 sites (Lupin/Contwoyto, Daring Lake, Salmita). For example, predicted values for the oestrid index were higher at Daring and Salmita than at Lupin/Contwoyto (Figure 7); but, yearly trends of increase and decrease were consistent. A similar pattern was apparent for mosquito and black fly indices (Appendix C).

Oestrid flies ($t = -2.14$, Df = 50, $p = 0.019$) and black flies ($t = -2.49$, Df = 50, $p = 0.008$) had higher mean index values at the Lupin/Contwoyto weather station during 1982-2008 when compared to 1957-1981. In contrast, mean mosquito index values were higher during 1957-1981 ($t = 3.42$, Df = 50, $p < 0.001$). To further explore trends over time, I examined correlations between year and index levels. There was a weak, but significant, positive correlation between oestrid index values and year ($r_s = 0.34$, $p = 0.001$) and black

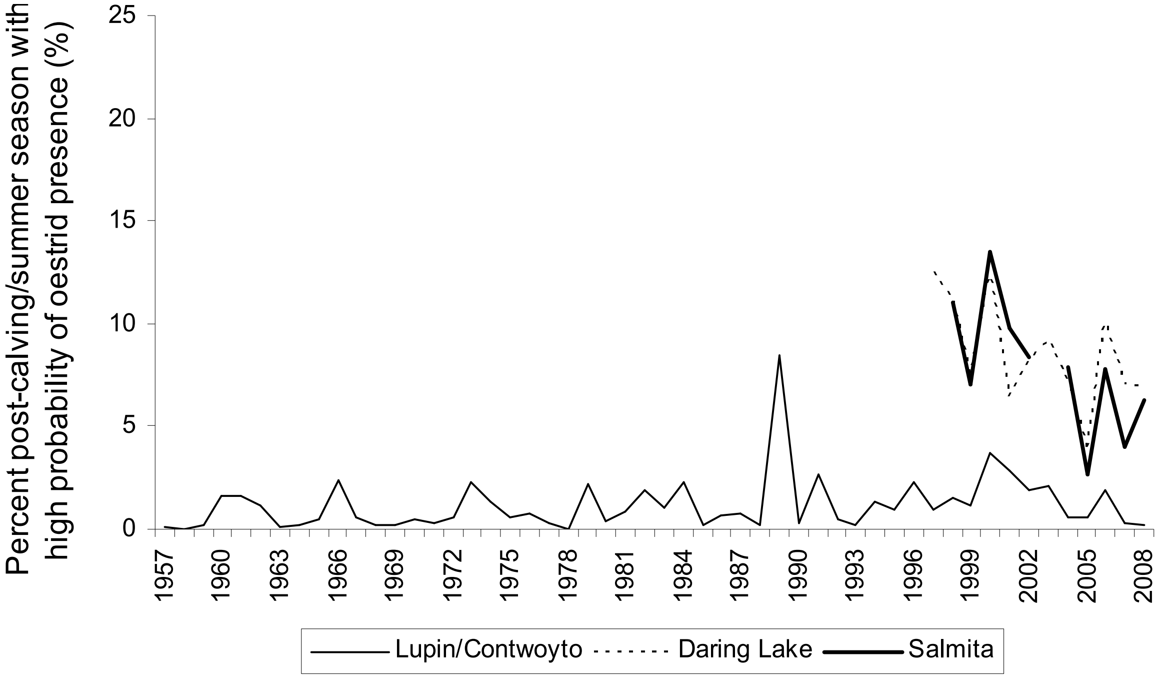


Figure 7. Index representing relative occurrence for oestrid flies at Lupin/Contwoyto, Daring Lake, and Salmita weather stations on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada.

fly predictions and year ($r_s = 0.29$, $p = 0.039$). There was a moderate negative correlation between mosquito index values and year ($r_s = -0.56$, $p < 0.001$), indicative of a trend toward declining mosquito activity over time. There were not strong statistical relationships between caribou population parameters and yearly insect index values (Figure 8). Caribou population estimates and mosquito ($r_s = 0.11$, $p = 0.703$), black fly ($r_s = 0.43$, $p = 0.126$), and oestrid ($r_s = 0.48$, $p = 0.083$) indices were not significantly correlated. Likewise, late-winter cow:calf ratios were not significantly correlated to mosquito ($r_s = 0.33$, $p = 0.18$), black fly ($r_s = -0.29$, $p = 0.24$), or oestrid ($r_s = -0.34$, $p = 0.16$) indices.

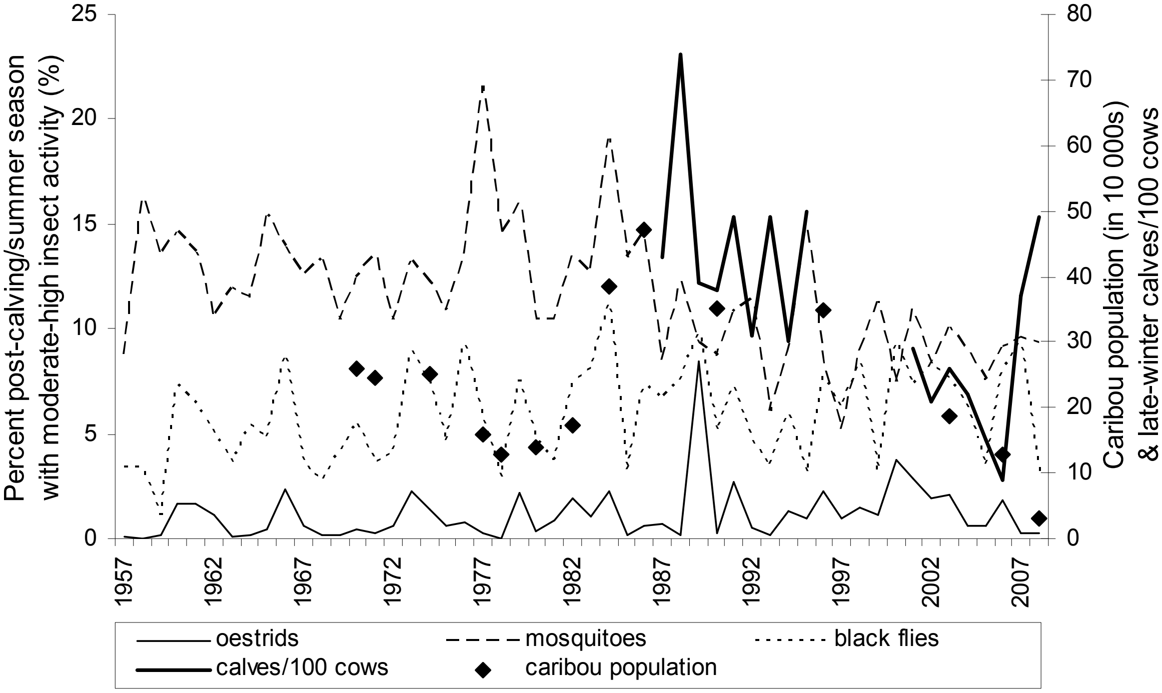


Figure 8. Comparison of population estimates and cow:calf ratios for Bathurst caribou (Adamczewski et al. 2009, GNWT ENR 2010a) relative to indices of activity or occurrence for mosquitoes, black flies, and oestrid flies at Lupin/Contwoyto weather station on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada. Population estimates from 1980-2009 are based on calving ground photographic surveys; numbers prior to 1980 are from visual surveys of the calving ground.

Discussion

I examined the influence of weather, time/date, and habitat on activity/abundance levels of three of the main insect species groupings thought to be responsible for harassment of caribou on the Bathurst post-calving/summer range. Climate change is occurring at an accelerated rate in the Arctic (ACIA 2004). To understand the implications of global change for caribou, we need to account for potential synergistic effects of parasites and climate on caribou population dynamics (Weladji et al. 2002, Forchhammer and Post 2004, Wilmers et al. 2006). Although consideration of large-scale climatic variability is critical, we must translate these changes into an understanding of potential responses at the level of the population (Whitfield and Russell 2005, LaDeau et al. 2008).

Temperature is consistently cited as a key driver of insect activity/abundance (Sommerman et al. 1955, Haufe and Burgess 1956, Danks 2004, Quinlan et al. 2005), and I found it important in predicting mosquito, black fly, and oestrid levels. Mosquito activity was positively related to temperature: I failed to trap mosquitoes at temperatures below 2.7° C and moderate-high activity only occurred above 5.7° C. This corresponds to minimum temperature thresholds of 2-7° C reported in the literature for northern mosquito species (Twinn 1952, Corbet and Danks 1973, Russell et al. 1993, Anderson et al. 2001). I observed high levels of mosquito activity at temperatures up to 22.8° C. I did not trap mosquitoes above 23.5° C, but only experienced temperatures in excess of this on 4 occasions. I did not test for a quadratic relationship between insect activity levels and temperature as current maximum temperatures on the Bathurst range do not approach upper lethal limits (Chapman 1998). It is possible, however, that high temperatures could suppress insect activity (Russell et al. 1993, Hagemoen and Reimers 2002), and I recommend that future studies account for this potentiality. I also found that temperature related positively to black fly activity. I did not trap black flies below 5.8° C, and observed moderate-high activity levels only at temperatures exceeding 8.7° C. Lower thresholds for black fly activity of 6-10° C are reported in the literature (Twinn 1952, McCreadie et al. 1986, Toupin et al. 1996). I did not observe an upper temperature threshold for black fly activity; moderate activity levels occurred up to the highest recorded temperature of 26.1° C. An upper temperature threshold for black fly activity of 22° C was reported in Newfoundland, Canada (McCreadie et al. 1986). Oestrid flies appear least tolerant of low temperatures. I trapped oestrids at temperatures ranging from 14.3-21.5° C roughly corresponding to the reported optimum temperatures for oestrid activity of 15-27° C (Kelsall 1968, White et al. 1975, Anderson and

Nilssen 1996a, Anderson et al. 2001). Due to low sample size of trapped oestrid flies, my measurements should not be construed as upper or lower thresholds.

Wind is another important factor affecting insect activity, and may mediate the effects of temperature (Nielsen and Nielsen 1966, Weladji et al. 2003). Wind negatively affected activity of mosquitoes, black flies, and oestrids. I did not trap mosquitoes at wind speeds over 6.4 m/s; corresponding to reported upper thresholds of 6-10 m/s (Russell et al. 1993, Toupin et al. 1996, Anderson et al. 2001, Hagemoen and Reimers 2002). I recorded high activity levels at winds up to 4.8 m/s, and moderate activity up to 5.6 m/s. Although wind had a stronger effect on mosquitoes, black fly activity also declined as wind speed increased. I recorded moderate activity of black flies at winds up to 6.6 m/s and high activity up to 5.8 m/s. Black fly flight could be possible at higher wind velocities; winds of 6-9 m/s have been reported as having a negative effect (McCreadie et al. 1986, Toupin et al. 1996). Oestrids are larger and stronger fliers than either mosquitoes or black flies. Flight at wind speeds up to 8 m/s is common (Anderson et al. 2001, Hagemoen and Reimers 2002), and flight at winds of 11 m/s was reported in one instance (Mörschel 1999). All of my oestrid trap catch occurred at winds of 1.0-6.4 m/s; although due to small sample size it was unlikely I captured the full range of oestrid tolerance.

In general, I found barometric pressure and relative humidity to have ambiguous or variable effects on insect activity. Exceptions were the strong positive effect of barometric pressure and weak positive effect of relative humidity on mosquito activity. High barometric pressure usually corresponds to warm, clear, and calm conditions that are more favourable for flight. Fournier et al. (2005), however, found that *Trichogramma* wasps responded negatively to rapid changes in barometric pressure, regardless of direction, and did not exhibit changed flight response to stable or slow fluctuations in barometric pressure. Barometric pressure and relative humidity may serve to moderate the response of insects to other meteorological variables, such as temperature. In particular, low relative humidity could compound the risk of desiccation at high temperatures leading to reduced activity levels (Davies 1952, Rowley and Graham 1968).

Solar irradiation is another factor that may moderate the effects of temperature on insect activity by changing the thermal environment of microsites used by insects (Danks 2004). I used light intensity as a measure to quantify cloud cover and solar irradiation. I found little effect of light on mosquito or black fly activity. Light level has been suggested as an important factor affecting oestrids (Anderson and Nilssen 1996a, Weladji et al. 2003). Allotment of energy to flight and basal metabolism is weather dependent, and oestrids may have different temperature thresholds for flight depending on whether or not they are exposed to direct sunlight (Breyev 1961, Nilssen and Anderson 1995). My models indicated light had a weak positive effect on the likelihood of oestrid presence, but there was much variability in this relationship. I trapped oestrids at light intensities ranging from 7 520-78 617 lux. Other studies also report oestrid activity across a range of cloud cover and, thus, light intensity (Dau 1986, Toupin et al. 1996).

Time of day also affected insect activity. The probability of higher levels of mosquito activity increased at dusk/night; but, there was variability in this relationship. This corresponded with reports of increased mosquito activity during evening (Hagemoen and Reimers 2002) and continued activity through the night (Anderson and Nilssen 1998). Some of the ambiguity in this relationship may be due to the opportunistic nature of mosquitoes. Unfed, resting mosquitoes will become active regardless of time of day when potential hosts are nearby (Clements 1999). I observed increased black fly activity at morning, afternoon, and dusk; and, increased probability of oestrid presence during afternoon. This is supported by findings on activity patterns of black flies and oestrids in northern Norway (Anderson and Nilssen 1996b, Anderson et al. 2001). Diel fluctuations in insect activity may be driven by circadian rhythms particular to each species, but also by 24-hr variations in meteorological variables. For black flies and oestrids, temporal patterns in activity may be explained in part by warmer temperatures that I observed during midday.

In addition to intra-day variation in insect activity, levels varied at the larger temporal scale of the post-calving/summer season. Both mosquito and black fly activity showed a pattern of pronounced peak and decline as gdd accumulated over the summer. Peak activity for mosquitoes occurred shortly after lakes became free of ice in early to mid-July. I observed black fly activity peaks in late July/early August after approximately 300 gdd had accumulated. My models did not find the number of days elapsed since predicted eclosion to be a significant predictor of oestrid presence. This could be due to the large potential range of variation in the date at which oestrid larvae drop from caribou, and consequent variation in timing of eclosion among adult oestrids (Anderson and Nilssen 1996b). The lack of a clear relationship may also be an artefact of low oestrid sample size. Although not statistically significant, I trapped more oestrids later in the season, roughly coincident with increased black fly activity and separate from peak mosquito levels. Failure to monitor the entire insect season has been a weakness in many past studies of caribou/reindeer summer range ecology (Anderson et al. 2001). I attempted to cover the entire season by continuing to collect insects at Daring Lake until trap catches showed substantial declines in numbers. Black flies and oestrids, however, may be able to take advantage of short periods of favourable weather after the main insect season has elapsed, thus, I may have missed some instances of late season activity during the end of August/beginning of September (C. Venables, T. Zamin, personal communications).

I did not find strong relationships between activity of any of the 3 insect species groupings and vegetation type. Topography did play a role in moderating activity levels. Mosquito, black fly, and oestrid activity increased in lowlands as compared to both flats/mid-slope and upland topographic positions. This may have been due to decreased wind exposure in low lying areas, and could affect how caribou use the landscape during insect season if they are able to use elevated areas as insect relief terrain. Covariates for easting and northing suggested a slightly increased probability of presence of oestrid flies in the southern and eastern portions of the Bathurst range. Oestrid larvae depart from caribou hosts during late April to late June (Nilssen and Haugerud 1994). The southeastern portion of the summer range roughly corresponded to the area Bathurst caribou passed through on their northward migration to the calving grounds during the peak oestrid dropping period. Oestrids, however, are strong fliers capable of dispersing hundreds of km to find caribou (Nilssen and Anderson 1995). I also found little difference in black fly activity levels across the summer range. Considering the positive correlation among weather data, predicted oestrid and black fly levels should approximate range-wide insect levels. In contrast, mosquito activity was strongly related to location with higher activity levels to the northeast portion of the Bathurst range. Due to patterns of caribou range use, I only trapped insects in the northeast early in the summer at times largely corresponding to peak mosquito activity. Although this could have affected the modeled relationship between mosquito activity and location, the significance of the relationship suggests caution should be taken in extrapolating local mosquito activity to range-wide predictions.

Spatial variation in insect activity levels and weather conditions across the Bathurst post-calving/summer range were a concern in retrospective analysis of weather data. In the 3 yr of my study, oestrid and black fly levels were fairly consistent across the spatial extent of the range, while mosquito levels were more varied. Temperature, relative humidity, and light were also correlated; wind speeds showed high spatial variation. This is consistent with relatively high temperature, but low wind speed, correlations at weather stations across the summer range of the Porcupine caribou herd (Russell et al. 1993). Spatial variation in weather parameters translated into differences in predicted insect index values among the 3 weather stations. Higher temperatures and light levels, and lower wind speeds at Daring Lake and Salmita contributed to consistently higher predictions of the insect indices at these weather stations as compared to Lupin/Contwoyto (Figure 7, Appendix C). Year-to-year trends in insect indices, however, were similar among all 3 stations. Thus, I have confidence that the longer temporal dataset at Lupin/Contwoyto can be considered representative of range-wide trends.

Insect indices calculated at Lupin/Contwoyto indicated that mosquito activity levels on the Bathurst range likely declined since the late 1950s, while conditions became increasingly favourable for black fly and oestrid activity. In particular, mean black fly and oestrid indices were higher during 1982-2008 as compared to 1957-1981. Black fly and oestrid predictions were driven by a trend of increasing summer temperatures since the 1950s. Although temperature positively affects mosquito activity, mosquitoes are also more sensitive to other meteorological variables like wind speed and relative humidity. During

1957-2008, the percent of the post-calving/summer season with relative humidity values over 80% declined while the amount of time wind speeds exceeded 4 m/s increased. Both of these measures are consistent with a declining trend in mosquito index values. Estimates of the number of Bathurst caribou were relatively infrequent during this time period making it difficult to correlate population levels with yearly values of the insect indices. The Bathurst herd declined from a high of 472 000 ± 72 000 ($\bar{x}$ ± SE) in 1986 to 31 900 ± 5 300 animals in 2009 (Nishi et al. 2010). Although correlations among insect indices and caribou population parameters were insignificant, the Bathurst decline roughly corresponded with increased summer temperatures and predicted increases in black fly and oestrid activity from 1982-2008. Late spring cow:calf ratios are indicative of trends in recruitment and calf survival. During the beginning of the decline (1985-1995), ratios ranged from 30-50 calves per 100 cows, dropping to lows of 8.5-30 calves per 100 cows during 2001-2006 before recovering to levels of 37-50 calves per 100 cows in 2007-2008 (Adamczewski et al. 2009). Insect harassment may have contributed to reduced recruitment in the early 2000s. Conditions were favourable for oestrid activity for 4 consecutive summers from 2000-2003 (Figure 8); effects on calf survival would manifest in 2001-2004 cow:calf ratios. With the exceptions of 1999 and 2005, conditions were favourable for moderate-high black fly activity during the summers of 1996-2007 (Figure 8, Appendix C).

Caribou/reindeer have evolved with parasitic flies over the millennia and it is unlikely that insect harassment is a sole cause of *Rangifer* population declines. The direct costs of blood loss and parasitic loading combined with indirect costs of behavioural modification due to insect harassment, however, are stressors that could accelerate population declines or dampen recovery. High pregnancy rates and good calf survival are critical for herd recovery after periods of decline (Adamczewski et al. 2009), and both may be negatively affected by parasites. *Rangifer* make tradeoffs in energetic and nutrient allocation between reproduction and survival in response to parasitism (Albon et al. 2002, Burns et al. 2005). Although immune responses entail energetic costs, healthy adult caribou/reindeer can compensate for the effects of larvae on body condition (Vincente et al. 2004, Scheer 2008). Oestrid infestation may have larger effects on calves experiencing their first exposure to parasites while concurrently facing significant costs of growth and development (Hawlena et al. 2006). Calves lack antibodies against enzymes secreted by warble fly larvae during their migration within the caribou's body (Asbakk et al. 2005). Increased winter mortality rates in *Rangifer* calves may be associated with high oestrid infestation following warm summers favourable for insect activity (Klein 1991). In addition to reduced recruitment rates, cohorts experiencing high parasitism as calves may experience fitness consequences that continue into adulthood. In chipmunks, bot fly (*Cuterebra emasculator*) infestation negatively affected juveniles, and these effects manifested as increased metabolic rates/energetic costs throughout the animal's life even when parasitic infestation did not continue (Careau et al. 2010). Year-to-year variation in levels of parasitic insects means that some cohorts are more affected than others (Hawlena et al. 2006); and, weak cohorts may be a critical factor in *Rangifer* declines (Eberhardt and Pitcher 1992, Coulson et al. 2004, Adamczewski et al. 2009). The negative effects of parasites will be greatest when multiple parasite species are present, during periods of unfavourable environmental or range conditions, and for segments of the population experiencing higher energetic demands for growth or reproduction (Helle and Tarvainen 1984, Albon et al. 2002, Slansky 2007, Careau et al. 2010).

Insect indices can be powerful tools to increase understanding of Bathurst caribou population dynamics, especially when used in conjunction with ongoing caribou demographic and body condition monitoring. To be useful, indices must be grounded in understanding of the ecology of the species they seek to represent (Fore et al. 1996, Linton and Warner 2003). I attempted to provide this foundation by intensively monitoring activity levels of mosquitoes, black flies, and oestrids in conjunction with a wide range of biotic and abiotic factors that may affect insect activity/abundance; and, by continuing this monitoring across the majority of the insect season, over multiple years, and at varied locations across the Bathurst range. I modeled weather conditions at hourly time steps instead of using daily averages in an attempt to capture changes at temporal scales relevant to insects and caribou, and to assess changes in insect activity over the course of the 24-hr period. Although my indices provided more detailed information on the relationships between insects, weather, habitat, and time than many indices constructed in the past, my findings were largely supportive of past conclusions on the importance of temperature and wind in predicting insect activity (Russell et al. 1993, Mörschel 1999, Weladji et al. 2003).

All indices are necessarily simplifications of reality, and there are some important aspects of insect ecology that were not accounted for in my models. One inherent limitation of a short-term study was the inability to observe the full range of natural variability in insect abundance/activity levels and weather conditions that occur over longer time-scales. Additionally, I was not able to distinguish changes in insect abundance from variations in activity levels (Williams 1961). Insect abundance in any given year is affected by insect population size, weather conditions, and host abundance in the previous season, as well as by conditions affecting larval development. Many mosquito and black fly species in the Arctic are facultatively autogenous, and the number of eggs developed may vary widely depending on whether or not a female has access to a blood meal (Corbet 1967, Currie 1997, Danks 2004). Oestrids are highly fecund and populations can rebound quickly following favourable summers (Anderson and Nilssen 1996b, Nilssen 1997a). During summers with unfavourable weather conditions, however, oestrid flight may be limited to 25% of the season, restricting reproductive potential and affecting population levels in the following year (Anderson et al. 1994). I attempted to capture some of the conditions affecting larvae by including covariates for growing degree days and time elapsed since predicted oestrid eclosion in my models, but relationships between larval development and spring conditions are complex. Water temperature has a large effect on mosquito larvae (Corbet and Danks 1973); the temperatures larvae experience are affected by air temperature, solar radiation, and wind chill, as well as by larval behaviour involving movement to areas of cooler or warmer water within a pond (Haufe and Burgess 1956). Water temperature and food availability are also important factors in black fly larval development (Sommerman et al. 1955, Merritt et al. 1982), and requirements differ among species (Currie 1997). Developmental rates of oestrid larvae within caribou/reindeer may vary depending on larval crowding, host immunity, and climatic conditions (Nilssen and Haugerud 1994, Nilssen 2006). Once oestrid larvae leave their hosts, pupal development and eclosion are affected by temperature and humidity at the scale of the microsite; oestrids may also be vulnerable to predation and fungal infection at this time (Nilssen 1997a, Nilssen 2006).

The indices focused on changes in conditions faced by adult insects, but did not account for potential climate change effects on other life-cycle stages that are also important in determining species abundance (Fallis 1964, Hogg and Williams 1996, Danks 2004).

Despite these limitations, indices are means of gauging the potential effects of climate change at the local-scale and allowing adaptive management in the absence of perfect information. The multinomial and binary logistic regression models I used could easily be applied to other species and situations. One benefit of this approach is that it allows assessment of the effects of environmental changes on species abundance in cases when exact numbers are not known or when count models provide poor fit (Long and Freese 2001). In my case, I attempted to predict mosquito and black fly counts, but was unable to make predictions with a high degree of confidence. Models of activity levels and presence/absence, in contrast, provided good fit and predictive ability.

Insect indices can be used as simple and cost-effective tools to translate meteorological data that is collected on a regular basis on the Bathurst range into predictions about the degree to which environmental conditions favour insect activity. In the absence of historical data on insect activity, retrospective indices provide a means of estimating reference insect activity levels against which to compare changes over time (Niemi and McDonald 2004, Hardman-Mountford et al. 2005). Used in conjunction with measures of other potential stressors (e.g., industrial development, hunting pressure, range condition), predictive insect indices can inform ecologically-based management actions for the Bathurst herd. In Arctic ecosystems, parameters of interest cannot always be efficiently and inexpensively measured on a regular basis (McKelvey and Pearson 2001, Hopkins and Kennedy 2004). Thus, tools such as ecological indices with a strong basis in functional ecological relationships are important for detecting trends and understanding the causes and impacts of change over time (McGeoch 1998, Niemi and McDonald 2004). Adaptive management informed by both predictive tools and long-term monitoring will allow us to move beyond the inertia that can hamper decision-making in the face of uncertainties surrounding global change.

CHAPTER 3

Behavioural trade-offs in response to external stimuli: time allocation of an arctic ungulate during varying intensities of harassment by parasitic flies

Abstract

Relatively unappreciated until recently, macroparasites may be a major factor shaping animal behaviour. Ecosystems inhabited by caribou and reindeer (*Rangifer tarandus*) are particularly well known for large concentrations of parasitic flies including mosquitoes (Culicidae), black flies (Simuliidae), and oestrid flies (Oestridae). Increased intensity and duration of insect harassment due to climatic warming has been hypothesized as a potential factor in recent declines of *Rangifer* across the circumpolar north. Although there is a well-observed relationship between insect harassment and caribou/reindeer behaviour, the relative influence of different parasitic species is unclear. Climatic changes may favour the activity patterns, distribution, or abundance of certain insect species, thus, understanding the differential effects of macroparasites on the behaviour of *Rangifer* is important. I recorded caribou behaviour using group scan and focal individual sampling methods, while simultaneously trapping insects and recording weather conditions on the post-calving/summer range of the Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus*) herd in Northwest Territories and Nunavut, Canada, during 2007-2009. I developed statistical model sets representing hypotheses about the effects of insects, weather, habitat/location, and date/time on caribou behaviour. I used multinomial logistic regression models (mlogit) to explore factors affecting the relative dominance of behaviour types within groups of caribou. I used a novel approach to behavioural analysis, fractional multinomial logistic regression models (fmlogit), to determine factors influencing time allocation by individual caribou. Finally, I used fractional logistic regression (flogit) to examine changes in feeding intensity. Both the relative dominance of insect avoidance behaviour within caribou groups and time allocation to insect avoidance by individual

caribou increased when oestrid flies were present or black flies were active at moderate-high levels. Mosquito activity had relatively little effect on caribou behaviour. Feeding intensity was influenced to a greater extent by the accumulation of growing degree days over the course of the post-calving/summer season than by insect activity. The methods presented here for exploring behavioural trade-offs are applicable to questions about the influences of environmental variation and human disturbance on behaviour of a variety of wildlife species. Increased understanding of wildlife behavioural ecology is important for effective conservation and management in the context of global change.

Introduction

Activity budgets are driven by demands on individuals to meet life-history requirements for maintenance, growth, and reproduction (Horn and Rubenstein 1984, Maier and White 1998, Ebensperger and Hurtado 2005). As time is a limited resource, animals must make daily compromises about time allocation to different behaviours based on both intrinsic (e.g., metabolic constraints, age, reproductive status, social rank) and external (e.g., forage quality and availability, weather, predators) conditions (Aschoff 1963, Shi et al. 2003, Zhou et al. 2007, Hamel and Côté 2008). Theoretically, animals make trade-offs in relation to the costs and benefits of adopting a particular behaviour (Lima and Dill 1990, Hutchings et al. 2006, Namgail et al. 2007). These changes in activity budgets have fitness consequences at the individual level that may ultimately influence population dynamics (Clutton-Brock et al. 1982, Richner 1998, Rubenstein 1998, Namgail et al. 2007).

Although relatively unappreciated until recently, macroparasites may be a major force shaping animal behaviour (Hart 1990, Fitze et al. 2004). Macroparasites can be a direct mortality factor, but also cause less obvious effects on fitness that manifest when hosts experience additional energetic or nutritional demands associated with immunological responses, reduced food intake, or increased movement and avoidance behaviours (Hart 1990, Lima and Dill 1990, Lochmiller and Deerenberg 2000, Fitze et al. 2004). When parasitism imposes significant costs to hosts, natural selection should favour a set of physiological, morphological, and behavioural responses that optimizes the cost:benefit ratio of parasite defence (Hart 1990, Richner 1998). Activity patterns that avoid or minimize exposure to parasites act as an initial form of protection, complementing the immune responses mounted once parasitism has occurred (Nelson et al. 1975, Hart 1990, Tripet et al. 2002).

A variety of flies (Diptera) have ecto- or endoparasitic life stages that afflict ungulates, and behavioural modifications in response to the risk of fly attack have been observed in species such as cattle (*Bos taurus*), sheep (*Ovis aries*), red deer (*Cervus elaphus*), and reindeer/caribou (*Rangifer tarandus*) (Okumura 1977, Espmark and Langvatn 1979, Harvey and Launchbaugh 1982, Colman et al. 2003). Ecosystems inhabited by caribou and reindeer are particularly well known for large concentrations of parasitic flies including mosquitoes (Culicidae), black flies (Simuliidae), and oestrid flies (Oestridae) during the brief Arctic summer (Russell et al. 1993, Toupin et al. 1996, Anderson et al. 2001, Hagemoen and Reimers 2002). Over the past decade, declining population numbers have been documented in 34 of the 43 regularly monitored *Rangifer* herds across the circumpolar north (Vors and Boyce 2009). A range of hypotheses have been proposed to explain the declines, including shifts in *Rangifer*-parasite dynamics due to environmental change (Mörschel and Klein 1997, Brotton and Wall 1997, Weladji et al. 2003). During the post-calving/summer season, biting and parasitic insects may contribute to reduced *Rangifer* body condition through both the direct costs of blood loss and parasitic loading, and indirect costs of altered activity budgets (Downes et al. 1986, Mörschel and Klein 1997, Hagemoen and Reimers 2002, Colman et al. 2003). Other stressors that may interact with insect harassment and contribute to population declines include decreased forage quality and availability due to overgrazing (Skogland 1985, Crête and Huot 1993, Post and Klein 1999) and increased industrial development and human disturbance (Adams 2005, Johnson et al. 2005).

Insect harassment and variation in forage quality are reported to be the main drivers of *Rangifer* summer-range ecology (Roby 1978, Russell et al. 1993, Skarin et al. 2008). The period from mid June through the end of August is a critical time for caribou/reindeer to exploit the brief flush of highly nutritious forage (Russell et al. 1993, Mörschel and Klein 1997). New growth of preferred forage types such as cottongrass (*Eriophorum* spp.), forbs, and deciduous shrubs is easily digestible, with high nitrogen (N) and phosphorous (P), and low fibre and phenolic content (White et al. 1975, Owen-Smith and Novellie 1982, Kuropat and Bryant 1983, Johnstone et al. 2002). This summer forage is critical for caribou/reindeer in building up nutrient reserves to bolster the N and P-deficient winter diet of lichens (Rognmo et al. 1983, Boertje 1990, Russell et al. 1993, Parker 2003). Harassment by parasitic flies, however, can alter habitat use and activity budgets of caribou/reindeer, potentially leading to reduced forage intake and elevated energy expenditures (Downes et al. 1986, Mörschel and Klein 1997, Hagemoen and Reimers 2002). During times of high insect harassment, caribou may reduce both feeding intensity and time spent foraging (Russell et al. 1993, Toupin et al. 1996, Colman et al. 2003). Insect relief terrain tends to be sparsely vegetated or devoid of vegetation, further precluding grazing activity (Boertje 1981, Hagemoen and Reimers 2002, Skarin et al. 2008). Concurrent with a reduction in energetically beneficial activities such as feeding, insect harassment causes an increase in energetic expenditure via increases in both rate of travel (White et al. 1975, Roby 1978, Dau 1986, Anderson and Nilssen 1998) and time spent walking/running (Russell et al. 1993, Mörschel and Klein 1997, Hagemoen and Reimers 2002, Colman et al. 2003).

Body weight of caribou/reindeer is largely determined by nutrition during the post-calving/summer season. Small changes in pattern, quality, and quantity of forage intake brought about by modifications in time budgets and habitat use can have multiplicative effects on growth, survival, and reproductive potential (White 1983, Reimers 1997, Colman et al. 2003). This is especially critical for lactating cows and calves. Females may face a trade-off between lactation and acquiring enough body reserves to survive the winter and reproduce successfully the following spring (Helle and Tarvainen 1984). Energetically stressed cows may employ strategies that affect calf survival, including post-natal or premature summer weaning (Russell and White 2000). In addition, successful pregnancy is largely determined by autumn breeding condition (Skogland 1985, Cameron et al. 1993, Reimers 1997, Colman et al. 2003). Interactions between insect harassment and forage intake during the post-calving/summer season may have effects on both calf recruitment of the current year and female fecundity in the following spring that are particularly critical in times of population decline.

Despite a well-observed relationship between insect harassment and caribou/reindeer behaviour, there is a lack of agreement on the relative importance of different parasitic species in affecting changes in *Rangifer* activity budgets. Most studies have either used *Rangifer* behaviour to infer the type and level of insect activity (Mörschel and Klein 1997, Hagemoen and Reimers 2002, Colman et al. 2003), used weather conditions as proxies for insect activity (Walsh et al. 1992, Russell et al. 1993), and/or used subjective assessments based on insect activity around human observers (Roby 1978, Mörschel and Klein 1997, Hagemoen and Reimers 2002). The few studies that paired rigorous assessment of insect activity based on trap catch data with behavioural observations of reindeer suggest that it is difficult to determine the identity of parasitic flies based solely on behavioural responses when *Rangifer* are observed from afar (Karter and Folstad 1989, Anderson and Nilssen

1998). Thus, there has been little conclusive differentiation of the effects of the diverse species of parasitic flies attracted to caribou and reindeer. Several studies point to oestrid fly harassment as the main cause of insect-related behavioural alterations in caribou/reindeer (Downes et al. 1986, Mörschel and Klein 1997, Anderson et al. 2001); however, there is a widespread belief in North America that mosquitoes are a major source of persecution (Smith and Cameron 1985, Pollard et al. 1996, Noel et al. 1998, Hagemoen and Reimers 2002). Information distinguishing the effects of black flies and tabanid flies from those of mosquitoes and oestrids is lacking. There is also a paucity of baseline data on the 24-hr activity patterns of caribou/reindeer during the post-calving/summer season (Colman et al. 2001). Caribou/reindeer may be able to compensate for time lost during harassment by parasitic flies by foraging more during the cooler parts of the day and night (Collins and Urness 1982, Colman et al. 2003).

In order to address these knowledge gaps, I systematically trapped insects and monitored weather conditions in the vicinity of groups of caribou while concurrently recording caribou behaviour over the 24-hr period on the post-calving/summer range of the Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus*) herd in Northwest Territories and Nunavut, Canada. My goal was to define fine-scale functional relationships between caribou behaviour, activity/abundance of parasitic flies, and environmental/temporal variables (i.e., weather, habitat, and time/date). Tabanids were not abundant on the Bathurst range, so my study focused on caribou reactions to mosquitoes, black flies, and oestrid flies. Specific objectives were to determine effects of the different families of parasitic flies, levels of insect activity, weather, habitat, and time on: (1) the relative dominance of types of behaviour within caribou groups; (2) time allocation by individual caribou; and (3) feeding intensity.

Methods

Data Collection

I monitored weather conditions, trapped insects, and recorded behavioural observations for caribou of the Bathurst herd over intensive sampling sessions during the 2007-2009 post-calving/summer seasons (see Chapter 2). Groups of caribou were located based on the positions of collared females, and accessed via helicopter. I used portable weather and light meters to record environmental conditions in the vicinity of groups of caribou under observation (Kestrel 4500 on Kestrel Portable Vane Mount, Nielsen Kellerman, Boothwyn, PA; EA30 light meter, Extech, Waltham, MA; data-logging light meter, Sper Scientific, Scottsdale, AZ). I collected insects using modified Malaise traps baited with carbon dioxide (Anderson et al. 2001). Trap catch and weather data were averaged over 2-hr intervals and linked to all caribou observations occurring within the interval. Weather stations and insect traps were generally located 25 m to 2 km from caribou groups, although in some instances caribou came within a few meters of the traps during the natural course of their movements.

I used both group scan and focal individual sampling methods to collect behavioural data (Altmann 1974). I observed caribou for the 24-hr daily period using spotting scopes (Pentax PF-63 Zoom Spotting Scope 20x - 50x zoom, Hoya Corporation, Tokyo, Japan) and classified behaviour as feeding, walking, running, lying, standing/other, and insect avoidance. Insect avoidance was considered as a hierarchical behaviour following the classification of one of the other 5 behaviour types. I defined feeding as standing or walking with the muzzle touching or nearly touching the ground (Griffith et al. 2001). For focal individual sampling, feeding was further broken down into eating and searching (modified from Russell et al. 1993, Griffith et al. 2001). Eating involved actually ingesting forage, while searching encompassed times when caribou had their muzzle near the ground, but did not ingest vegetation. Feeding intensity was calculated as the ratio of time eating to total time eating and searching (Griffith et al. 2001). I defined walking as slow movement with the head in a normal, upright position. Running included trotting and other forms of fast-paced movement with the head in an upright position. Lying included caribou resting or ruminating in a prone position. Standing/other encompassed a range of behaviours such as standing, nursing, social activities, drinking, and playing. Behaviours identified as insect avoidance included: ear flicking, tail wagging, head tossing, body shaking, foot stamping, biting, sneezing, kicking, rearing, bucking, alarm posture, rapid erratic running, and "animal stance" (stationary, with the head touching or close to the ground, and remaining motionless for a period of time) (Downes et al. 1986). Although increases in movement in the absence of the specific avoidance behaviours mentioned above could also be responses to insect harassment, these behaviours were simply classified as walking or running.

I performed instantaneous scan sampling of a randomly selected group of caribou approximately every 30 min. I defined 'group' as socially interacting caribou spatially distinct from other bands of animals in the area (modified from Russell et al. 1993). For groups of <250 caribou, I recorded group size as a total count. For larger groups, I estimated size to the nearest 100 for groups of 250-1000 animals, and the nearest 1000 for groups exceeding 1000 animals. For groups of <250 animals, I recorded the number of caribou per group engaged in each of the behaviour categories. When visibility or movement made this prohibitive, and for group sizes >250, I noted the approximate percentage of animals engaged in the behaviours.

I performed focal individual sampling on randomly selected adult female caribou for intervals of up to 30 min, during which I recorded the behavioural sequence and amount of time spent engaged in each behaviour type (HP 100 LX Palmtop PC, Hewlett Packard, Palo Alto, California; Gillingham 2008). For both group scan and focal individual sampling, I recorded date, time, and location. I noted when caribou reacted to human observers, other human disturbance, or predators, and excluded those observations from further analysis.

Model Development

I examined the effects of insect harassment, weather, time, date, and habitat on 3 aspects of caribou behaviour: relative dominance of behaviour type within caribou groups, time allocation of individual caribou, and feeding intensity of individual caribou. The goal of the first analysis was to understand factors affecting increases or decreases in less common behaviours of caribou, such as insect avoidance. For each group scan, I assigned a percentile value to each of the 6 behaviours (feeding, lying, standing, walking, running, insect avoidance) by comparing the percent of the caribou group engaged in a given behaviour to the observed range of engagement in the behaviour across all scans from the 2007-2009 data set (Table 10). The percentile values of the 6 behaviours were ranked within each group scan, and the behaviour with the highest value was scored as the relatively most dominant. I chose this approach because feeding, walking, and lying tend to dominate caribou activity budgets (White et al. 1975, Roby 1978, Downes et al. 1986, Colman et al.

2003). Thus, rare behaviours with a low absolute prevalence (e.g., under 20% of group engaged in the behaviour) may be masked by more common behaviours even when biologically important changes from typical activity budgets occur. I used multinomial logistic regression (mlogit; Long and Freese 2001) to model the effects of biotic and abiotic variables on the relative dominance of behaviour types. Each binary comparison within the mlogit examined the effect of environmental variables on the probability of a particular behaviour exhibiting relative dominance compared to another (e.g., probability of insect avoidance being relatively more dominant than feeding within a group of caribou).

Table 10. Percent of individuals within a caribou group engaged in each of 6 behaviour types at the 25th, 50th, and 95th centile values. Centile values were calculated based on percents >0, and were used to identify a single dominant behaviour for each group scan sample recorded during 2007-2009 on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada.

% of caribou group	25th centile	50th centile	95th centile
Feeding	27%	50%	100%
Lying	6%	18%	85%
Standing	2%	5%	37%
Walking	9%	20%	100%
Running	5%	20%	100%
Insect avoidance	2%	8%	85%

In the second analysis, I examined factors affecting time allocation by individual caribou using data from focal individual sampling. I used fractional multinomial logistic regression (fmlogit; Buis 2008) to model behaviour choices while recognizing time as a limited resource (Ye and Pendyala 2005). Fmlogit extends the binary approach developed by Papke and Wooldridge (1996) to accommodate multiple proportions as dependent variables. This approach was appropriate for activity budget data as the proportion of time allocated to each of the behaviours was by definition constrained between zero and one; and, all behaviours for a given focal observation were required to sum to one (Buis 2008). Fmlogit models examined the effects of environmental variables on a caribou's allocation of time to each type of behaviour relative to other behaviours for all possible comparisons (e.g., effect of insect activity on the proportion of time spent feeding relative to standing, walking, etc.).

Finally, I used fractional logistic regression (flogit; Papke and Wooldridge 1996) to explore the effects of environmental variables on feeding intensity (measured as a ratio constrained between zero and one of time eating to total time eating and searching). This analysis was restricted to 2008-2009 focal samples; feeding intensity data were not recorded in 2007. In all 3 modeling approaches, I used a robust clustering technique to account for potential autocorrelation among behavioural observations at a given site (Nielsen et al. 2002). I used Intercooled Stata 9.2 (Statacorp, College Station, TX) for all statistical analyses.

Model Parameters

I developed explanatory models that included variables from 3 broad sets of environmental and physiological factors thought to influence caribou behaviour: weather/insects, habitat/location, and time of day/year (Table 11). Weather-related variables included temperature, wind speed, and light intensity. I also modeled variables for activity/abundance of mosquitoes and black flies, and presence/absence of oestrid flies (both nose-bot, *Cephenemia trompe*, and warble flies, *Hypoderma tarandi*). Habitat-related variables included vegetation type and location on the Bathurst range expressed as easting and northing coordinates. I used sunrise/set times (National Research Council Canada 2009) to create 3 categories representing time of day. I parameterized categorical variables using deviation coding to contrast the effect of each level against the overall effect of the

Table 11. Independent variables and categorical coding used to describe behaviour of Bathurst caribou, Northwest Territories and Nunavut, Canada, 2007-2009.

Variable	Description and categorical code
Insect/weather	
Mosquito	Activity/abundance levels of female mosquitoes based on hourly trap catch.
no	0 mosquitoes/hr (0)
low	0-3.5 mosquitoes/hr (1)
moderate	3.5-42.9 mosquitoes/hr (2)
high	>42.9 mosquitoes/hr (3)
Black fly	Activity/abundance levels of black flies based on hourly trap catch.
no	0 black flies/hr (0)
low	0-1.5 black flies/hr (1)
moderate	1.5-5.5 black flies/hr (2)
high	>5.5 black flies/hr (3)
Oestrid	Oestrid flies present (1) or absent (0) in trap catch.
Temp	Mean air temperature over 2-hr trapping period (°C).
Wind	Mean wind speed over 2-hr trapping period (m/s).
Light	Mean light intensity over 2-hr trapping period (lux).
Time/date/habitat	
Time	
morning	2 hr after sunrise to local/solar noon (1)
afternoon	Local/solar noon to 2 hr before sunset (2)
dawn/dusk/night	2 hr before sunset to 2 hr after sunrise (3)
Gdd_{veg}	Total of daily mean temperature accumulation above 0 °C beginning at snow-free date.
Year	2007 (1), 2008 (2), 2009 (3)
Vegetation	Based on dominant type in 500-m radius centered on sampling site.
tussock tundra	Tussock graminoid tundra (0)
shrub	Tall, low, and prostrate dwarf shrub (1)
Easting	Cartesian coordinates for eastward-measured distance (m).
Northing	Cartesian coordinates for northward-measured distance (m).
Group size	Count or estimate of total number of adult caribou in group (scan samples).
Duration	Duration of observation in sec (only used observations >60 sec; focal individual samples)

categorical variable (Menard 2001). As a measure of time of year, I included a growing degree day (gdd) variable based on temperature accumulation above 0° C beginning at the snow-free date (Wielgolaski et al. 1981, Karlsen et al. 2005). I calculated snow-free date as the average value from 4 National Oceanic and Atmospheric Administration (NOAA) monitoring points on the Bathurst post-calving/summer range (Brown et al. 2007). Growing degree days reflected conditions relevant to the developmental biology of green vegetation, allowing me to explore whether caribou may have modified their behaviour as vegetative phenology changed over the course of the post-calving/summer season. I included a variable for year to determine whether there were important annual variations in caribou behaviour not captured by other environmental variables. All models of relative dominance of behaviour from scan samples contained a group-size variable to account for variations in behaviour due to the number of caribou in a group. I did not use focal observations less than 60 sec in length, and included a variable representing duration of the focal observation in all models of individual behaviour and feeding intensity. Inclusion of the group-size and duration variables corrected for some biases in these behavioural sampling methods. I used variance inflation factors to assess collinearity among independent variables (Menard 2001).

Model Selection and Predictive Ability

I used a priori knowledge to develop model sets representing biologically plausible hypotheses. For all 3 behavioural analyses, I classified models according to explanatory themes: insect/weather, time/date/habitat, and combinations of insects and time/date/habitat. Models within the insect/weather theme tested the effects of different parasitic insect families, both alone and in combination, on caribou behaviour. By including weather variables and insect activity covariates in separate models within the theme, I was able to compare the strength of the direct influence of weather (e.g., potential thermal stress) on caribou behaviour to the indirect influence of weather via its effects on insect activity. In the time/date/habitat theme, I created models to determine the influence of circadian and annual cycles, as well as habitat type, on caribou behaviour. I organized models within the insect/weather and time/date/habitat themes in order to test whether 1 of these 2 broad themes might be a predominant driver of caribou behaviour as compared to the other. I hypothesized, however, that variables within each of the themes would be important in determining caribou behaviour. An additional hypothesis was that the indirect effects of weather on insect activity would have a greater influence on caribou behaviour than direct effects of meteorological variables. Thus, I developed a third "combination" theme of models including explanatory variables related to insect activity and time/date/habitat. I made comparisons among models in each of the explanatory themes, but this does not imply that I captured the full range of model possibilities.

I based model selection on an Information Theoretic Model Comparison (ITMC) approach using Akaike's Information Criteria for small sample sizes (AIC_c) and Akaike weights (*w*) to select the most parsimonious model (Anderson et al. 2000). I interpreted *w* as approximating the probability that a given model was the best within a model set. When 2 or more top models had a difference in $AIC_c < 2$, I considered these models to be of near equal parsimony (Burnham and Anderson 1998). For the best models, I generated β-coefficients and 95% confidence intervals for each parameter. I calculated Pearson's standardized residuals to determine the difference between observed and predicted values. I used the area under the Receiver Operating Characteristic (ROC) curve (AUC) and a withheld data set of 20% of the observations to evaluate the predictive ability of mlogit models (Swets 1988). For flogit and fmlogit, I used Spearman's correlations to assess the relationship between the withheld observations and predicted proportions.

Results

Caribou Behaviour

I performed a total of 198 scans in 2007, 450 scans in 2008, and 257 scans in 2009 on groups containing one to >500 caribou (219 ± 532 SD). During focal sampling, I observed 271 (cumulative observation time of 2 614 min), 257 (2 214 min), and 172 (1 689 min) individual caribou in 2007, 2008, and 2009, respectively. Focal observations ranged from one to 30 min in length (9.7 min ± 7.8 SD). In all years, feeding and walking were, on average, the most common behaviours (Figure 9). There was cyclical variation in the percentage of caribou feeding across the 24-hr period. On average, insect avoidance behaviours peaked between 1000-2000 hr.

I observed some differences in caribou activity budgets among sampling sessions; these were generally corroborated by data from both focal individual and group scan sampling (Figure 10). During the July 26-29, 2007, sampling session, for example, caribou fed and rested less, with a concurrent increase in energy intensive behaviours such as walking, running, and insect avoidance. The highest black fly activity levels observed during the study occurred during this session (Chapter 2).

Relative Dominance of Behaviour within Caribou Groups

Two models of relative dominance of behaviour within caribou groups had nearly identical AIC_c scores with the second-ranked model scoring only 0.19 higher than the first (Table 12). Both models included covariates for insect activity levels, time, easting, northing, gdd, year, and group size. The top model, however, contained insect activity covariates for oestrids and black flies, while the second-ranked model included oestrids and mosquitoes. The combined support for the top 2 models was AIC *w* 0.97. Of the 165

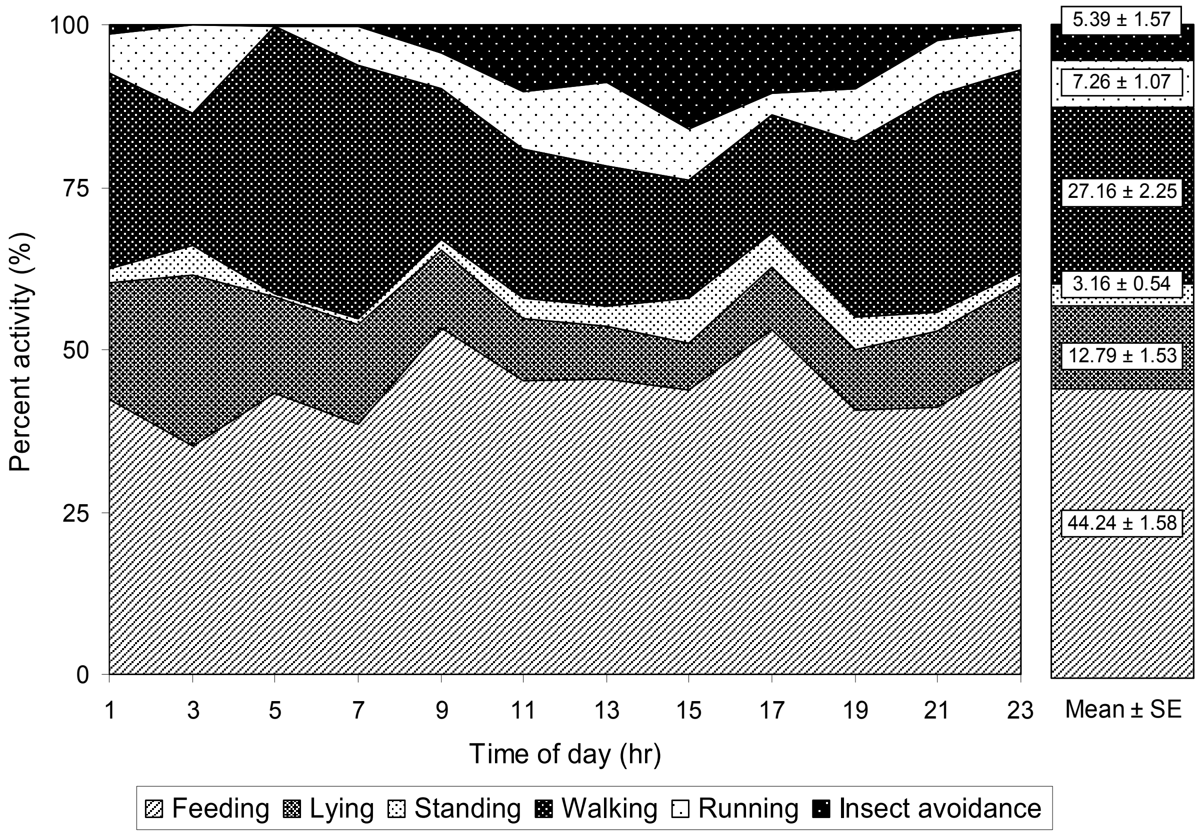
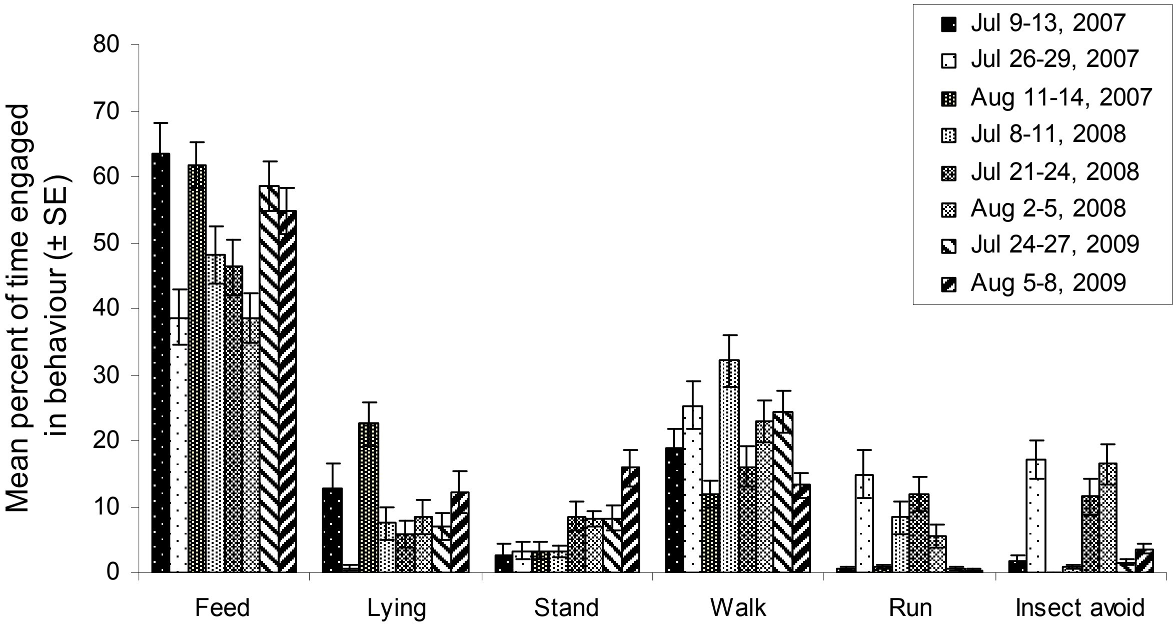


Figure 9. Diurnal pattern of Bathurst caribou activity (from group scans) during the 2007-2009 post-calving/summer seasons, Northwest Territories and Nunavut, Canada.



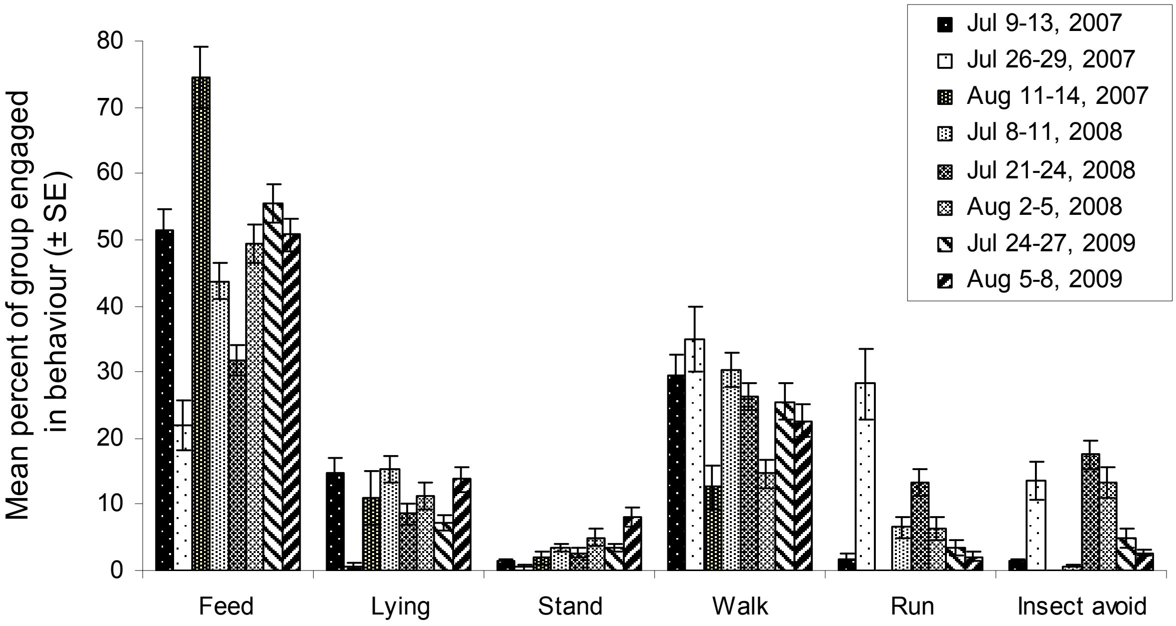


Figure 10. Average time allocation by individual caribou (top) and percent of caribou group (bottom) in each of 6 behaviour types per sampling session on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada, 2007-2009.

Table 12. Candidate multinomial logistic regression (mlogit) models of relative dominance of behaviour type within caribou groups on the Bathurst caribou post-calving/summer range, 2007-2009; number of parameters (*K*); log-likelihood; Akaike's Information Criterion (AIC_c) scores; differences in AIC_c scores (ΔAIC_c) and AIC_c weights (*w*) for subsets of insect/weather, time/date/habitat, and combinations of insect/time/date/habitat variables.

Model	*K*	Log-likelihood	AIC_c	ΔAIC_c	*w*
Insect/weather					
mosquito + group size	20	−1135.79	2312.77	184.11	<0.001
black fly + group size	20	−1127.17	2295.53	166.87	<0.001
oestrid + group size	10	−1134.92	2290.15	161.49	<0.001
mosquito + black fly + group size	35	−1098.46	2270.60	141.93	<0.001
mosquito + oestrid + group size	25	−1105.45	2262.78	134.12	<0.001
black fly + oestrid + group size	25	−1102.55	2256.97	128.31	<0.001
mosquito + black fly + oestrid + group size	40	−1076.90	2238.62	109.96	<0.001
temperature + group size	10	−1129.35	2279.00	150.34	<0.001
temperature + wind + group size	15	−1117.41	2265.50	136.84	<0.001
light + group size	10	−1142.32	2304.95	176.29	<0.001
temperature + light + group size	15	−1119.28	2269.24	140.57	<0.001
temperature + wind speed + light + group size	20	−1114.39	2269.99	141.32	<0.001
Time/date/habitat					
time + group size	15	−1136.13	2302.95	174.28	<0.001
gdd_{veg} + group size	10	−1135.84	2292.00	163.33	<0.001
year + group size	15	−1137.63	2305.94	177.28	<0.001
time + gdd_{veg} + group size	20	−1099.20	2239.60	110.93	<0.001
time + year + group size	25	−1103.13	2258.13	129.47	<0.001
gdd_{veg} + year + group size	20	−1108.99	2259.17	130.51	<0.001
time + gdd_{veg} + year + group size	30	−1073.05	2208.79	80.13	<0.001
vegetation + group size	10	−1153.16	2326.63	197.96	<0.001
vegetation + easting + northing + group size	20	−1082.66	2206.52	77.86	<0.001
vegetation + easting + northing + gdd_{veg} + year + group size	35	−1068.74	2211.16	82.50	<0.001
vegetation + easting + northing + time + gdd_{veg} + year + group size	45	−1023.96	2144.05	15.39	<0.001
Combination					
mosquito + time + easting + northing + gdd_{veg} + year + group size	55	−1008.21	2135.68	7.01	0.015
black fly + time + easting + northing + gdd_{veg} + year + group size	55	−1010.20	2139.67	11.01	0.002
oestrid + time + easting + northing + gdd_{veg} + year + group size	45	−1035.03	2166.20	37.53	<0.001
mosquito + black fly + time + easting + northing + gdd_{veg} + year + group size	70	−993.28	2141.85	13.19	<0.001
mosquito + oestrid + time + easting + northing + gdd_{veg} + year + group size	60	−998.88	2128.85	0.19	0.46
black fly+ oestrid + time + easting + northing + gdd_{veg} + year + group size	60	−998.79	2128.66	0	0.51
mosquito + black fly + oestrid + time + easting + northing + gdd_{veg} + year + group size	75	−984.02	2135.71	7.04	0.015

coefficients in common between the top 2 models, only 18 differed in sign between the models and none of these were statistically significant (Appendix D). Predictive abilities of the top models were reasonable to good: using independent data, ROC scores for the set of binary logistic regressions representing all possible comparisons of relative dominance between behaviours ranged from 0.62-1.00 for the top model, and 0.70-1.00 for the second-ranked model. Both models clearly identified when insect avoidance and running were the dominant behaviours (AUC > 0.90). The models were least predictive when distinguishing between feeding and walking (AUC: 0.62-0.74), and feeding relative to lying (AUC: 0.70-0.72). In all cases except the comparison between feeding and walking in the top model (AUC = 0.62), these ROC scores were still considered "reasonable" (Swets 1988).

Effects of insect activity on the relative dominance of behaviour within caribou groups differed depending on the family and activity level of insects (Figures 11-12, Appendix D). Although not statistically significant, the probability of insect avoidance dominating relative to all other behaviours increased at high mosquito and black fly levels. The other behaviour most likely to dominate at high mosquito levels was walking, while running increased in dominance when black fly activity was high. None of these relationships were significant. Oestrid flies had a larger effect on caribou behaviour. The likelihood of dominance of insect avoidance increased relative to all other behaviours when oestrids were present; the relationships relative to lying and walking were significant. Standing also increased relative to all behaviours other than insect avoidance when oestrids were present, but these relationships were non-significant.

Relative dominance of behaviours varied depending on time of day (Figures 11-12, Appendix D). The likelihood of insect avoidance becoming the dominant behaviour increased during morning. This relationship was significant relative to lying and standing. Feeding and walking were other behaviours likely to dominate in the morning. Although non-significant, both increased relative to lying, standing, and running. In afternoon, insect avoidance also dominated; this was significant relative to all behaviours except standing and running. Standing was also likely to dominate during afternoon. During dawn/dusk/night, the probability of insect avoidance dominating decreased significantly relative to all other behaviours. Lying was the behaviour most likely to dominate at this time.

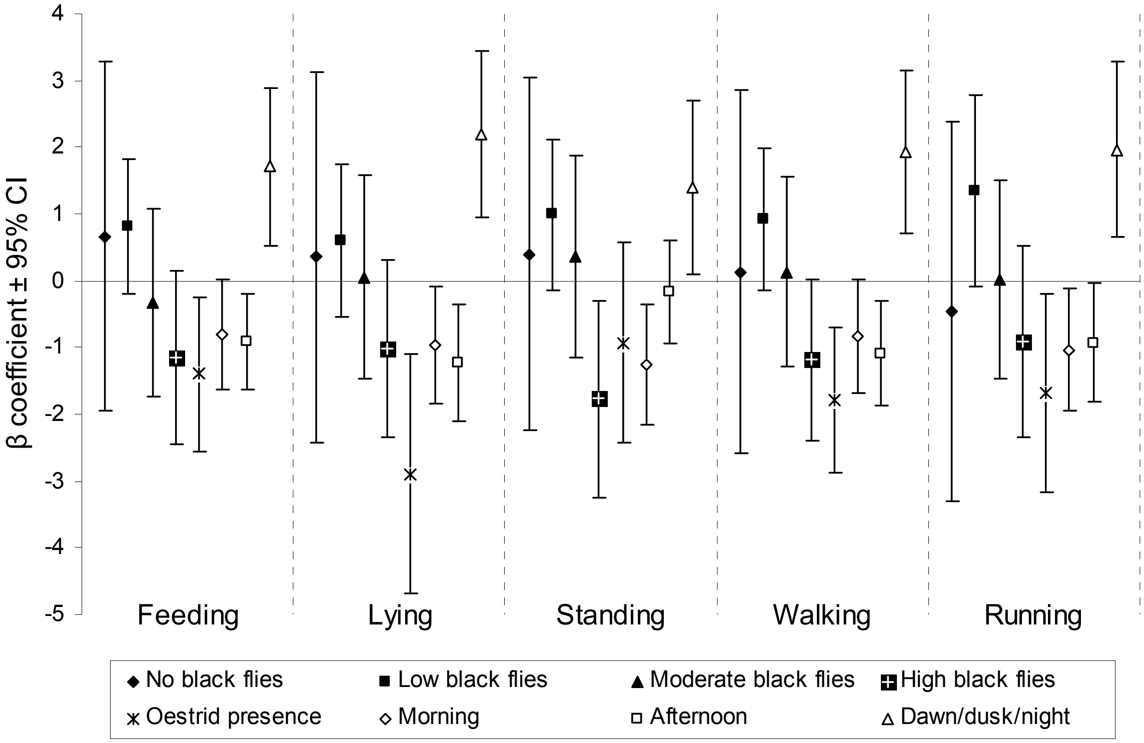


Figure 11. Coefficients (β) for covariates from top-ranked multinomial logistic regression (mlogit) model of dominance of behaviours relative to insect avoidance given black fly activity, oestrid presence, or time of day. Positive coefficients indicate increase in likelihood of dominance of a given behaviour relative to insect avoidance; negative coefficients indicate decrease relative to insect avoidance. Confidence intervals (CI) that do not overlap 0 indicate significant coefficients.

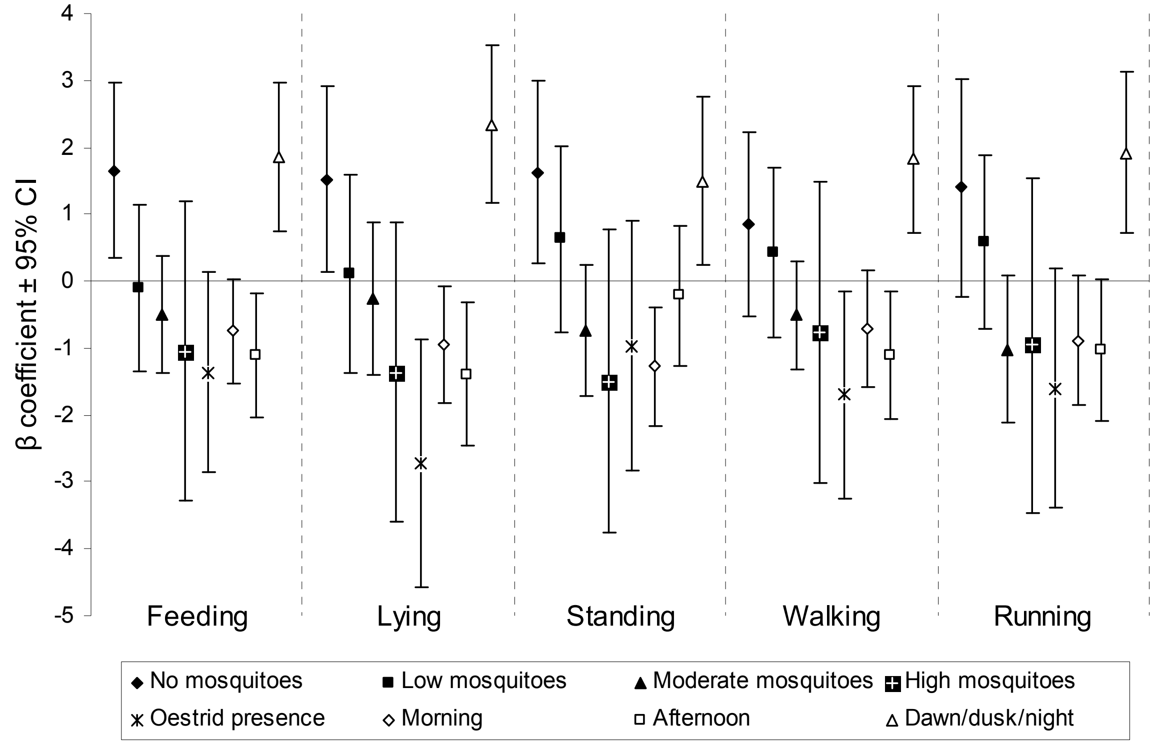


Figure 12. Coefficients (β) for covariates from second-ranked multinomial logistic regression (mlogit) model of dominance of behaviours relative to insect avoidance given mosquito activity, oestrid presence, or time of day. Positive coefficients indicate increase in likelihood of dominance of a given behaviour relative to insect avoidance; negative coefficients indicate decrease relative to insect avoidance. Confidence intervals (CI) that do not overlap 0 indicate significant coefficients.

The relative dominance of behaviours varied throughout the course of the post-calving/summer season and from year to year (Appendix D). As gdd accumulated, the likelihood of lying, feeding, and insect avoidance dominating increased non-significantly relative to walking and running. Year to year variation included increased likelihood of running relative to all other behaviours in both 2007 and 2008; only the relationships relative to feeding and walking in 2008 were significant. In 2009, the likelihood of running decreased relative to all behaviours except insect avoidance; these relationships were statistically significant.

The behaviour of caribou varied slightly across the spatial extent of the post-calving/summer range (Appendix D). Toward the northern extent of the range, feeding and lying were significantly more likely to dominate relative to walking, running, and insect avoidance. The dominance of lying increased relative to running toward the east. Group size had little effect on the relative dominance of behaviour.

Time Allocation by Individual Caribou

The 2 top models describing time allocated by individual caribou to behavioural classes differed by only 0.90 points (Table 13). Both models included covariates for oestrid presence and duration of focal sample; the top model also included black fly activity levels, while the second-ranked model included mosquito activity levels. Combined support or AIC weight for the 2 top models was 0.61. Of the 30 coefficients in common between the 2 models, only 2 differed in direction of effect and neither were significant (Figures 13-14, Appendix E). For both models, Spearman's correlations indicated weak to moderate (r_s = 0.13-0.54; $p \leq 0.05$) correlations between the observed and predicted proportions of time allocated to the 6 behaviours. The models were most successful at predicting proportion of time caribou spent engaged in insect avoidance and lying. Using independent data, the correlation between observed and predicted proportion of time devoted to insect avoidance was 0.54 in the top model and 0.38 in the second-ranked model. Correlation coefficients for lying were 0.44 and 0.45, respectively. The models had difficulty predicting proportions of time caribou spent feeding and running. Correlation coefficients for feeding were 0.20 and 0.13; and, for running were 0.14 and 0.13, for the top and second-ranked models. Residual analysis indicated that both models performed poorly when caribou engaged in a single

Table 13. Candidate fractional multinomial logistic regression (fmlogit) models of time allocation of individual caribou from focal sampling on the Bathurst caribou post-calving/summer range, 2007-2009; number of parameters (*K*); log-likelihood; Akaike's Information Criterion (AIC_c) scores; differences in AIC_c scores (ΔAIC_c) and AIC_c weights (*w*) for subsets of insect/weather, time/date/habitat, and combinations of insect/time/date/habitat variables.

Model	*K*	Log-likelihood	AIC_c	ΔAIC_c	*w*
Insect/weather					
mosquito + duration	20	−629.75	1301.24	9.59	0.003
black fly + duration	20	−629.81	1301.36	9.72	0.003
oestrid + duration	10	−636.64	1293.74	2.09	0.13
mosquito + black fly + duration	35	−612.23	1299.85	8.21	0.006
mosquito + oestrid + duration	25	−619.91	1292.54	0.90	0.24
black fly + oestrid + duration	25	−619.46	1291.64	0	0.37
mosquito + black fly + oestrid + duration	40	−604.25	1295.59	3.95	0.052
temperature + duration	10	−638.44	1297.32	5.68	0.022
temperature + wind + duration	15	−634.06	1299.10	7.46	0.009
light + duration	10	−642.80	1306.05	14.41	<0.001
temperature + light + duration	15	−634.53	1300.04	8.40	0.006
temperature + wind speed + light + duration	20	−631.46	1304.66	13.01	<0.001
Time/date/habitat					
time + duration	15	−641.83	1314.65	23.01	<0.001
gdd_{veg} + duration	10	−645.69	1311.83	20.19	<0.001
year + duration	15	−632.61	1296.20	4.56	0.038
time + gdd_{veg} + duration	20	−634.51	1310.75	19.11	<0.001
time + year + duration	25	−623.81	1300.34	8.70	0.005
gdd_{veg} + year + duration	20	−627.72	1297.18	5.53	0.024
time + gdd_{veg} + year + duration	30	−617.04	1298.02	6.37	0.015
vegetation + duration	10	−646.78	1314.01	22.37	<0.001
vegetation + easting + northing + duration	20	−626.62	1294.98	3.34	0.070
vegetation + easting + northing + gdd_{veg} + year + duration	35	−614.88	1305.14	13.50	<0.001
vegetation + easting + northing + time + gdd_{veg} + year + duration	45	−603.99	1307.03	15.39	<0.001
Combination					
mosquito + time + easting + northing + gdd_{veg} + vegetation +year + duration	60	−586.87	1310.27	18.63	<0.001
black fly + time + easting + northing + gdd_{veg} + vegetation + year + duration	60	−589.09	1314.71	23.07	<0.001
oestrid + time + easting + northing + gdd_{veg} + vegetation + year + duration	50	−598.89	1309.03	17.39	<0.001
mosquito + black fly + time + easting + northing + gdd_{veg} + vegetation + year + duration	75	−576.45	1329.53	37.89	<0.001
mosquito + oestrid + time + easting + northing + gdd_{veg} + vegetation + year + duration	65	−582.74	1315.07	23.43	<0.001
black fly+ oestrid + time + easting + northing + gdd_{veg} + vegetation + year + duration	65	−584.16	1317.90	26.26	<0.001
mosquito + black fly + oestrid + time + easting + northing + gdd_{veg} + vegetation + year + duration	80	−571.98	1334.60	42.96	<0.001

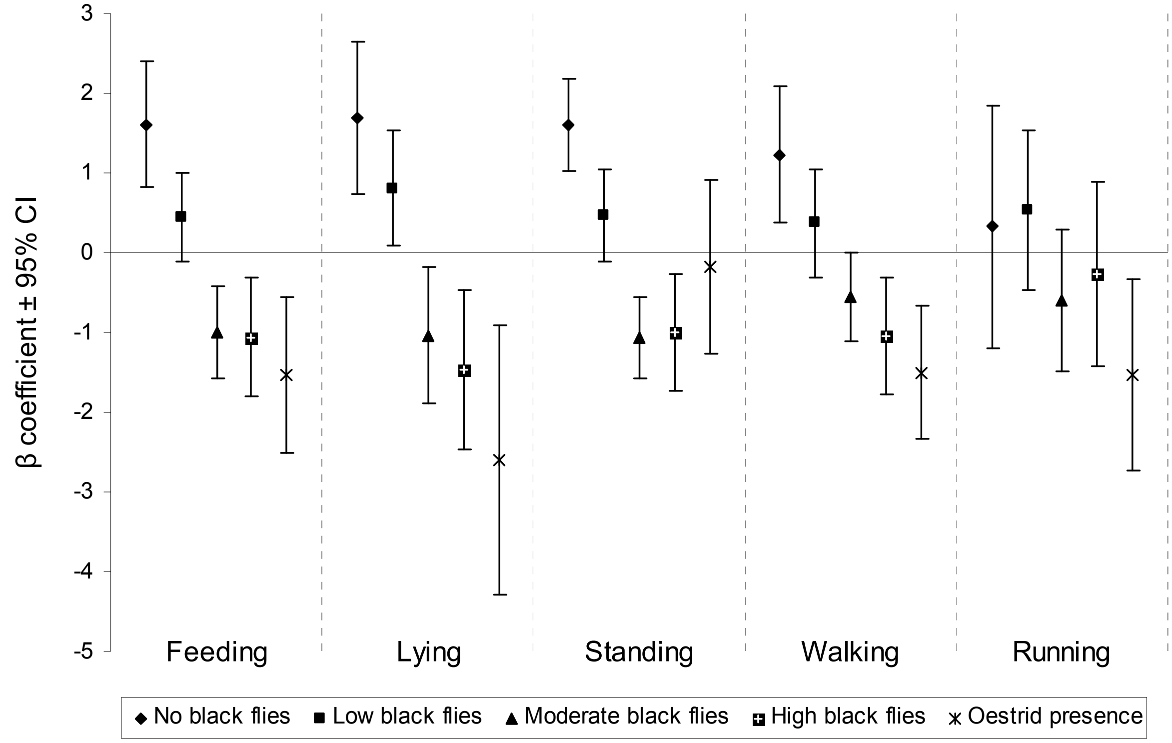


Figure 13. Coefficients (β) from top-ranked fractional multinomial logistic regression (fmlogit) model of tradeoffs in caribou time allocation relative to insect avoidance given black fly activity or oestrid presence. Positive coefficients indicate increase in proportion of time allocated to a given behaviour relative to insect avoidance; negative coefficients indicate decrease relative to insect avoidance. Confidence intervals (CI) that do not overlap 0 indicate significant coefficients.

behaviour for the majority of a focal observation; all models underpredicted the proportion of time caribou engaged in the predominant behaviour. I did not examine covariates from models in the time/date/habitat and combination subcategories as these models did not score well in the ITMC framework; however, it is possible that variables (i.e., time, gdd, year, vegetation type, easting, and northing) in these models influenced the activity budgets of caribou.

Mosquitoes had a variable effect on the behaviour of caribou (Figures 14-15, Appendix E). Counterintuitively, time spent in insect avoidance decreased relative to all other behaviours when mosquito activity was high. The proportion of time spent walking

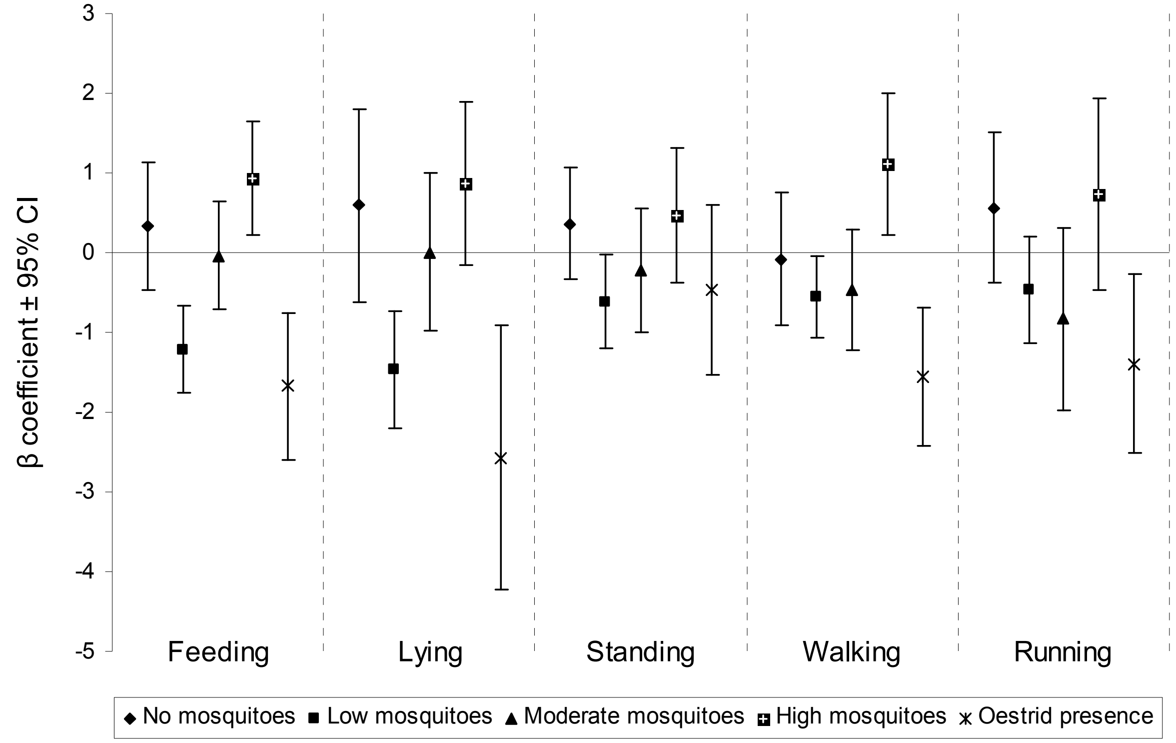


Figure 14. Coefficients (β) from second-ranked fractional multinomial logistic regression (fmlogit) model of tradeoffs in caribou time allocation relative to insect avoidance given mosquito activity or oestrid presence. Positive coefficients indicate increase in proportion of time allocated to a given behaviour relative to insect avoidance; negative coefficients indicate decrease relative to insect avoidance. Confidence intervals (CI) that do not overlap 0 indicate significant coefficients.

increased relative to all other behaviours at high mosquito levels. Other than the relationship between walking and insect avoidance, however, these effects were not statistically significant. Lying and feeding also both increased relative to standing, running, and insect avoidance when mosquito activity was high. With the exception of feeding relative to insect avoidance, these effects were non-significant.

Time allocated to insect avoidance increased when black flies were present at moderate to high levels (Figures 13 and 15, Appendix E). At moderate black fly activity, this increase was significant relative to feeding, lying, and standing. Although non-significant, walking and running also increased relative to feeding, lying, and standing when

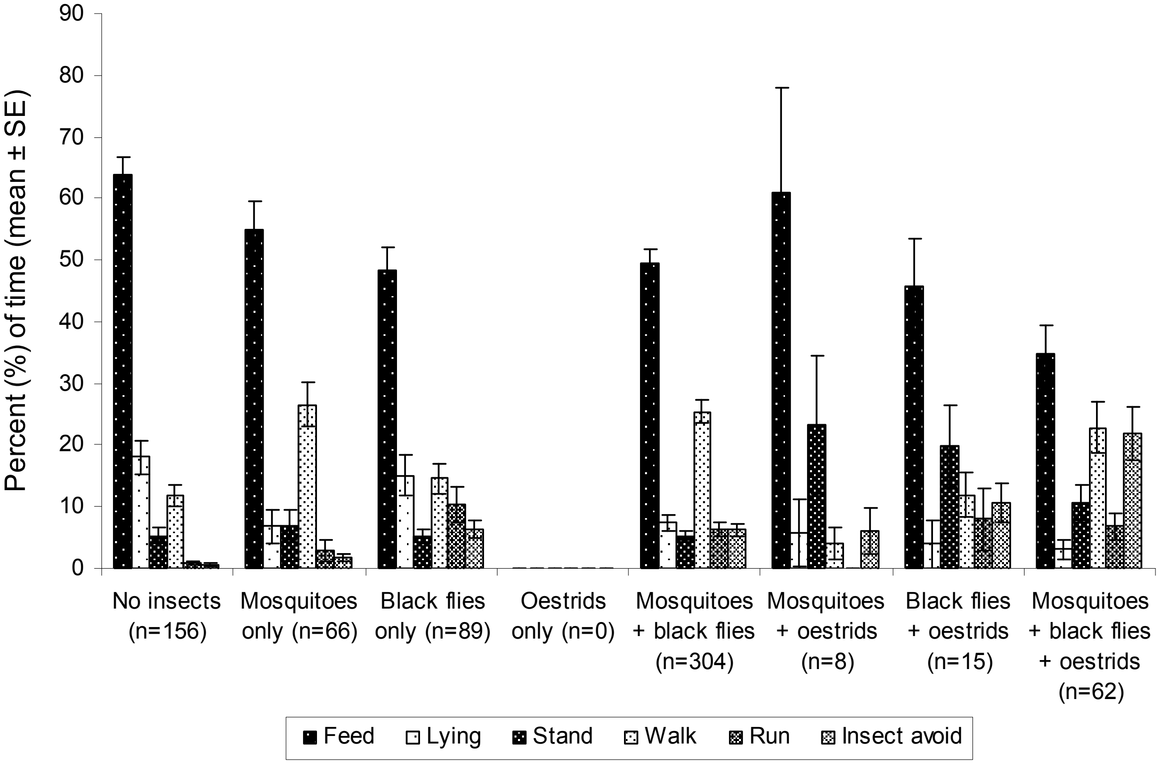


Figure 15. Behaviour of caribou relative to insect presence; data were recorded during focal individual observations 2007-2009 on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada.

black fly levels were moderate. At high black fly activity insect avoidance increased significantly relative to all behaviours except running. Running also increased relative to all behaviours other than insect avoidance, but these relationships were non-significant.

When oestrid flies were present, the proportion of time caribou spent engaged in insect avoidance increased significantly relative to feeding, lying, walking, and running (Figures 13-16, Appendix E). Lying was reduced to a greater degree than the other behaviours. Insect avoidance also increased relative to standing, but this relationship was non-significant. Standing increased relative to all behaviours except insect avoidance. Other than the relationship between standing and running, increases in standing were significant.

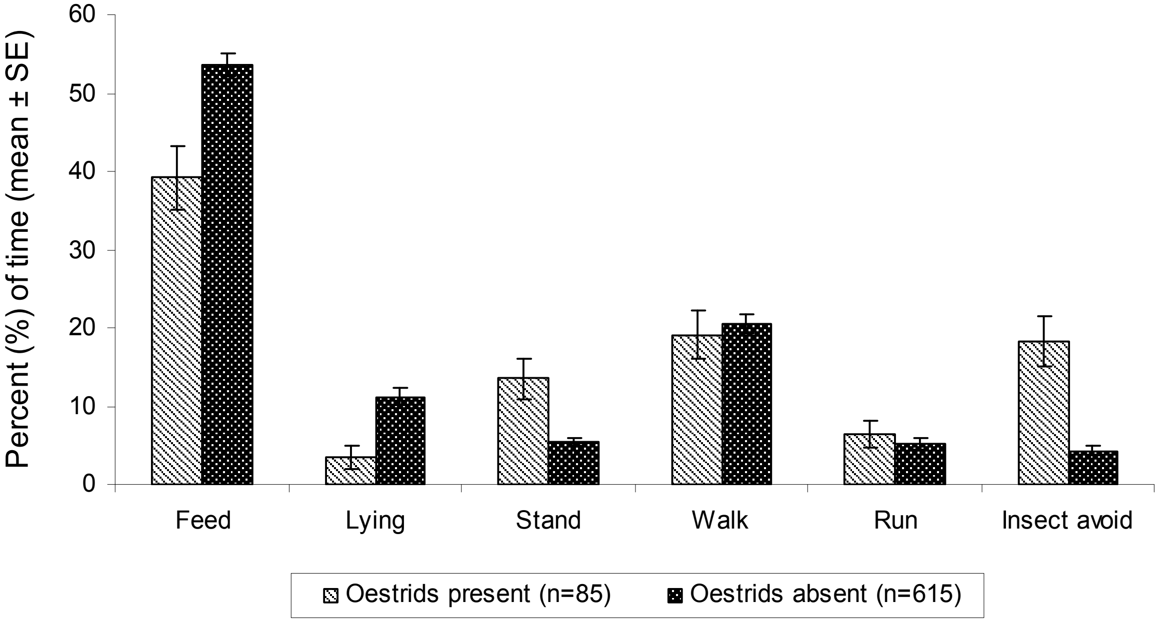


Figure 16. Behaviour of caribou when oestrid flies were present and absent; data were recorded during focal individual observations 2007-2009 on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada.

Duration of the focal observation period was included in all models of time allocation to partially correct for biases in the relative ease of observing different behaviour types using this sampling method. Duration influenced the proportion of time caribou allocated to individual behaviours (Appendix E). As duration of the observation period increased, the proportion of time caribou spent walking and running decreased significantly relative to lying, standing, and insect avoidance. Similarly, as focal duration increased, the proportion of time caribou engaged in lying and insect avoidance increased.

Feeding Intensity

Feeding intensity of individual caribou was best explained by a model from the time/date/habitat theme that contained covariates for year, gdd, and duration (Table 14). No

Table 14. Candidate fractional logistic regression (flogit) models of feeding intensity of individual caribou from focal sampling on the Bathurst caribou post-calving/summer range, 2008-2009; number of parameters (*K*); log-likelihood; Akaike's Information Criterion (AIC_c) scores; differences in AIC_c scores ($\Delta\mathrm{AIC}_c$) and AIC_c weights (*w*) for subsets of insect/weather, time/date/habitat, and combinations of insect/time/date/habitat variables.

Model	*K*	Log-likelihood	AIC_c	$\Delta\mathrm{AIC}_c$	*w*
Insect/weather					
mosquito + duration	4	−139.67	287.49	8.38	0.008
black fly + duration	4	−141.36	290.88	11.76	0.002
oestrid + duration	2	−142.98	290.00	10.88	0.002
mosquito + black fly + duration	7	−138.25	290.92	11.81	0.002
mosquito + oestrid + duration	5	−139.49	289.21	10.10	0.004
black fly + oestrid + duration	5	−140.59	291.41	12.30	0.001
mosquito + black fly + oestrid + duration	8	−137.86	292.26	13.15	<0.001
temperature + duration	2	−142.87	289.78	10.67	0.003
temperature + wind + duration	3	−142.87	291.82	12.71	<0.001
light + duration	2	−143.40	290.85	11.74	0.002
temperature + light + duration	3	−142.82	291.73	12.62	0.001
temperature + wind speed + light + duration	4	−142.82	293.78	14.67	<0.001
Time/date/habitat					
time + duration	3	−142.93	291.94	12.83	<0.001
gdd_{veg} + duration	2	−139.43	282.91	3.80	0.083
year + duration	2	−141.81	287.66	8.54	0.008
time + gdd_{veg} + duration	4	−139.12	286.39	7.27	0.015
time + year + duration	4	−141.18	290.50	11.39	0.002
gdd_{veg} + year + duration	3	−136.51	279.11	0	0.56
time + gdd_{veg} + year + duration	5	−136.21	282.64	3.52	0.096
vegetation + duration	2	−142.88	289.80	10.69	0.003
vegetation + easting + northing + duration	4	−140.29	288.72	9.61	0.005
vegetation + easting + northing + gdd_{veg} + year + duration	6	−134.65	281.61	2.50	0.16
vegetation + easting + northing + time + gdd_{veg} + year + duration	8	−134.39	285.32	6.21	0.025
Combination					
mosquito + time + easting + northing + gdd_{veg} + vegetation + year + duration	11	−133.09	289.18	10.06	0.004
black fly + time + easting + northing + gdd_{veg} + vegetation + year + duration	11	−133.11	289.22	10.11	0.004
oestrid + time + easting + northing + gdd_{veg} + vegetation + year + duration	9	−134.25	287.17	8.06	0.010
mosquito + black fly + time + easting + northing + gdd_{veg} + vegetation + year + duration	14	−132.29	294.18	15.07	<0.001
mosquito + oestrid + time + easting + northing + gdd_{veg} + vegetation + year + duration	12	−132.96	291.10	11.99	0.001
black fly+ oestrid + time + easting + northing + gdd_{veg} + vegetation + year + duration	12	−132.98	291.14	12.03	0.001
mosquito + black fly + oestrid + time + easting + northing + gdd_{veg} + vegetation + year + duration	15	−132.16	296.15	17.04	<0.001

other models in the set had $\Delta AIC_c < 2$; and, Akaike's w indicated there was a 56% chance that this model was the best. Predictive ability of the top model was fair. Using withheld data, I found a moderate positive correlation ($r_s = 0.44$, $p < 0.001$) between observed and predicted records. The most parsimonious model suggested that feeding intensity decreased in 2009 relative to 2008 ($\beta = -0.644$; 95% CI: −1.064 — −0.225) decreased as gdd accumulated over the course of the summer ($\beta = -0.005$; 95% CI: −0.008 — −0.002), and was higher in focal samples of longer duration ($\beta = 0.001$; 95% CI: 0.0002 — 0.001).

Discussion

Rangifer populations are thought to cycle over 40- to 70-yr periods, but the mechanisms of these patterns are not well understood (Gunn 2003, Zalatan et al. 2006). This is problematic given that many herds across the circumpolar north are currently in decline (Vors and Boyce 2009). The Bathurst herd is a case in point, with numbers dropping from a peak of 472 000 ± 72 000 (SE) in 1986 to 31 900 ± 5 300 in 2009 (Nishi et al. 2010). One hypothesis is that increased duration and intensity of insect harassment in response to climatic warming may be contributing to the decline of caribou/reindeer (Brotton and Wall 1997, Mörschel and Klein 1997, Weladji et al. 2003). Insect avoidance behaviours by *Rangifer* are widely reported (Pruitt 1960, Kelsall 1968, Russell et al. 1993, Hagemoen and Reimers 2002); however, in most cases the effects of different parasitic fly families have not been clearly differentiated. Understanding the degree to which different insects affect *Rangifer* behaviour is particularly important as parasitic flies may exhibit dissimilar responses to climate change (Chapter 2). To increase our knowledge of *Rangifer*-parasite dynamics, I examined the effects of mosquitoes, black flies, oestrids, weather, habitat/location, and time/date on the dominance of behaviour within groups of caribou, time allocation by individual caribou, and feeding intensity.

I found that mosquitoes had smaller effects on the dominance of behaviour types within groups of caribou and on activity budgets of individual caribou when compared to black flies and oestrids. Caribou exhibited little increase in stereotypical insect avoidance behaviours when mosquitoes were active. When caribou reacted to mosquitoes, it was by increasing time spent walking, but this relationship was not statistically significant. Although this response was weak, it corresponded to reports of increased walking and increased rate of movement by reindeer in Norway and caribou in Alaska when mosquitoes were present (Dau 1986, Mörschel and Klein 1997, Hagemoen and Reimers 2002). While increases in walking may have energetic implications for caribou, mosquitoes did not seem to be a major stressor of Bathurst caribou on the post-calving/summer range at the activity levels observed during this study. Mosquito activity/abundance, however, may vary across the ranges of different herds and harassment could be a larger factor in post-calving/summer range ecology in other areas.

In contrast to mosquito harassment that has been much commented on in the literature, there is little documentation on the effects of black flies on caribou behaviour. In the few cases where black flies were observed on *Rangifer* post-calving/summer ranges they were present in low numbers, assumed to have little effect, and/or not considered separately from mosquitoes (Roby 1978, Anderson et al. 2001, Hagemoen and Reimers 2002). I found, however, that caribou increased time allocation toward insect avoidance and running when black flies were active at moderate to high levels. These effects were notable even though the absolute number of black flies was relatively low; hourly trap catches >1.5 black flies were classified as moderate. This stands in contrast to mosquitoes which were active in much greater numbers, but had noticeably smaller effects on caribou. To my knowledge this was the first study that directly examined the effects of black flies on caribou behaviour. Based on the results, black fly activity on *Rangifer* post-calving/summer ranges should be considered separately from that of mosquitoes as both the magnitude and type of behavioural response elicited in caribou differed depending on which insect family was present.

The presence of even a single oestrid fly caused larger and more consistent behavioural responses by caribou than either mosquito or black fly activity. This supported reports of alertness and stress spreading through caribou herds when only a few individual caribou were directly attacked by oestrids (Roby 1978, Hagemoen and Reimers 2002). I found that both the relative dominance within caribou groups and the proportion of time individuals spent in insect avoidance and standing behaviours increased when oestrids were present. These behaviours increased at the expense of lying, feeding, walking, and running; however, lying was reduced to a greater degree than the other behaviours. This trade-off was also observed for caribou in Alaska and reindeer in Norway (Russell et al. 1993, Hagemoen and Reimers 2002).

Caribou behavioural responses to particular insect families do not occur in isolation. Alterations in activity budgets are likely magnified when some combination of mosquitoes, black flies, and oestrids are present concurrently. On the Bathurst range, mosquito activity peaked earlier in the season when compared to black flies and oestrids (Chapter 2). Mosquito activity also increased during dawn, dusk, and night whereas black flies and oestrids were more active during morning and afternoon hours. The relationships I observed between dominance of behaviour within caribou groups and time of day were likely related to these diel patterns of insect activity. Prevalence of insect avoidance increased in morning and afternoon, and decreased during dawn/dusk/night. Other studies have also reported more severe *Rangifer* responses to insect harassment during mid-day (Roby 1978, Anderson and Nilssen 1998, Anderson et al. 2001). The relative dominance of feeding did not increase noticeably at dawn/dusk/night, suggesting caribou may not have used this time period to compensate for lost foraging opportunities during morning and afternoon. Colman et al. (2003) also failed to observe grazing compensation at night. Whether or not compensation is necessary for *Rangifer* to maintain adequate forage intake during periods of insect harassment may depend on a variety of factors including reproductive status and the quality and quantity of available forage (Downes et al. 1986, Fancy 1986, Colman et al. 2003). The relative dominance of lying did increase during dawn/dusk/night. This has been observed in other herds (Colman et al. 2001, Loe et al. 2007), and could be due to decreased levels of insect harassment or to intrinsic physiological cues (Colman et al. 2001).

There is some debate over the degree to which weather conditions directly affect caribou/reindeer as opposed to indirect effects via the influence of weather on insect activity (Downes et al. 1986, Mörschel and Klein 1997, Anderson and Nilssen 1998, Skarin et al. 2004). In my analysis, models of caribou behaviour that contained weather variables did not perform as well as those containing covariates related to insect activity. This suggests that the indirect effects were larger than direct effects of weather on caribou behaviour. Other studies have also observed little response by *Rangifer* to weather variables such as temperature, light, and precipitation in the absence of parasitic insects (Hagemoen and Reimers 2002). In some instances, however, caribou/reindeer were found to respond directly to high temperatures by decreasing feeding time (Mörschel and Klein 1997) or altering habitat use by moving to snow patches or higher elevations for thermoregulation (Downes et al. 1986, Anderson and Nilssen 1998, Skarin et al. 2004).

Insect activity levels changed over the course of the summer (Chapter 2), and I also observed trends in caribou behaviour as gdd accumulated over time. Predominance of lying, feeding, and insect avoidance increased, while walking and running decreased over the post-calving/summer season. Increased insect avoidance could have been due to greater black fly and oestrid activity in mid to late summer. The trend toward decreased movement and increased lying and feeding, however, may have been due to variation in factors such as forage quality that were not included in my study. Feeding intensity also declined as gdd accrued; likely also due to factors distinct from insect harassment. Models of feeding intensity that contained covariates representing insect activity did not score as well during model selection as those containing temporal covariates. Although both the predominance of and time allocation toward feeding decreased when oestrids were present or black fly activity was moderate-high, changes in feeding intensity did not appear as drastic. The accumulation of gdd should reflect changes in vegetative phenology throughout the post-calving/summer season. As vegetation senesces later in the summer, caribou may spend more time searching out remaining patches of new green vegetation that is higher in nutrients and lower in fibre and phenolic content (Kelsall 1968, Skoog 1968, White et al. 1975, Russell et al. 1993); thus, feeding intensity might decline. A shift to forage of lower quality or higher fibre content might also explain the increased dominance of lying later in the summer as longer rumination bouts may be required to facilitate digestion (White et al. 1975, Trudell and White 1981, Robbins 1993). Alternatively, caribou may seek out mushrooms in late summer if they are available (Boertje 1981), and time spent searching for this dispersed resource could both increase time allocation to feeding and decrease feeding intensity.

Through the combination of rigorous insect collection methods and caribou behavioural observations, this study was able to refine our knowledge of *Rangifer* response to insect harassment. Field-based behavioural studies, however, have inherent difficulties (Altmann 1974, Martin and Bateson 1993) and interpretation of results and extrapolation to other herds or contexts requires caution. There were times when caribou may have reacted to oestrid flies active in the environment, but traps did not record oestrid presence. This could have led to errors of omission and reduced the predictive ability of behavioural models. Additionally, some types of animal behaviour affect the duration or number of individuals observed (Altmann 1974, Fragaszy et al. 1992). Caribou lying down may be less visible within groups. This is difficult to correct for, and predominance of lying could have been underrepresented in group scan observations. Caribou walking or running were difficult to observe for extended durations. I attempted to account for biases in the length of focal observations by including a variable representing duration in all models of individual time allocation. Temporal coverage throughout the 24-hr period was also a concern (Colman et al. 2001). Logistics of helicopter travel, as well as declining light conditions as day length became shorter in August, resulted in fewer observations being made at night and early morning as compared to other time periods. To prevent small sample sizes during these observation periods, I treated time categorically as morning, afternoon, or dawn/dusk/night. For group scan samples, 31% were observed during morning, 45% during afternoon, and 24% during dawn/dusk/night. For focal observations, the distributions were 39%, 47%, and 14%, respectively. In addition to behavioural differences based on time of day, year to year variation in behaviour may occur. Running was more predominant in group scan samples from 2007-2008, while standing and lying increased in 2009. Feeding intensity also differed between years. There were likely factors driving annual, as well as daily, variations in caribou behaviour that were not accounted for in my models. Additionally, it is unlikely that I captured the full range of caribou response to harassment. The activity/abundance of insects, and thus the magnitude of caribou behavioural response, may vary to a greater extent than I was able to capture in a 3-yr study.

Variations in the quality and quantity of forage are likely major determinants of caribou behaviour and habitat use during the post-calving/summer season (Roby 1978, Russell et al. 1993, Skarin et al. 2008). Poor range quality and severe insect harassment may have cumulative effects on caribou behaviour and body condition, while good forage conditions could mitigate the negative effects of parasitic insects. Although I included vegetation type as a covariate in the model set, it was not in any of the top models of caribou behaviour. This was a coarse measure of habitat based on the dominant type of vegetation within a circle of half km radius surrounding caribou group locations. Caribou may have made habitat use and behavioural decisions at larger and smaller scales, such as the landscape and microsite, which were not represented in my study. The lack of information on forage availability and quality, variation in forage conditions, and diet composition (Appendix F) represents a critical gap in our understanding of the Bathurst herd's post-calving/summer range ecology. Research in this area would complement my study and facilitate increased understanding of range use and population productivity of the Bathurst herd.

Forage conditions and the severity of insect harassment also vary depending on topography (Hall et al. 1991, Russell et al. 1993, Chapter 2), but I was unable to accurately record caribou behaviour relative to topographic variables. Group scan observations often included caribou occupying various topographic positions, and focal individuals moved across a range of topography in the course of an observation period. Degree of topographic relief may also be an important difference among the post-calving/summer ranges of different *Rangifer* herds. Esker tops and upland microsites within the gently rolling tundra habitat of the Bathurst herd provide a degree of insect relief (see Chapter 2). Some *Rangifer* herds, however, inhabit ranges with more extreme topographic variations (Gunn 2003). *Rangifer* in mountainous areas exhibit a pattern of movement from high elevation areas of lower vegetative quality used as insect relief during the day to nearby lower elevation areas of higher quality forage at night (Russell et al. 1993, Anderson et al. 2001, Skarin et al. 2008). Snow patches, glaciers, and coastal relief habitats are also used as insect relief terrain by some herds (Roby 1978, Boertje 1981, Dau 1986, Quayle and Kershaw 1996), but these options are largely unavailable to Bathurst caribou. Differences in forage quality/quantity, availability of insect relief terrain, and identities of parasitic species present mean that each *Rangifer* herd has a unique set of circumstances driving post-calving/summer range dynamics. The relative severity of response to mosquitoes, black flies, and oestrids, however, broadly illustrates the type of behavioural trade-offs faced by caribou experiencing insect harassment and may be applicable to *Rangifer* in other areas. Increased understanding of the behavioural reactions can be paired with ongoing body condition and population monitoring (Adamczewski et al. 2009), as well as energetics modeling (Fancy 1986, Kremsater et al. 1989, Russell et al. 2005), to illuminate potential population-level responses of *Rangifer* to changing levels of insect activity/abundance in the context of climatic variation and industrial development in the circumpolar north.

Populations are composed of individuals, and behavioural choices made at the individual level have repercussions for survival and reproduction that ultimately translate into consequences for population productivity (Clutton-Brock et al. 1982, Richner 1998, Rubenstein 1998, Namgail et al. 2007). The methods presented here for exploring trade-offs may be relevant to a variety of questions in behavioural ecology. In particular, fractional multinomial logistic regression (fmlogit) models are an elegant way to explore factors affecting time budgets. This method is relatively easy to implement and interpret, and also explicitly accounts for the time-constrained nature of activity budgets without requiring additional adjustments to the data (Papke and Wooldridge 1996, Ye and Pendyala 2005). Past studies of time allocation (Mörschel and Klein 1997, Colman et al. 2003, Ebensperger and Hurtado 2005, Shannon et al. 2008) have largely employed approaches based on analysis of variance (e.g., ANOVA, MANOVA) that are appropriate to test for differences in activity budgets, but unable to address the strength of relationships between external or internal factors and changes in time allocation (Tabachnick and Fidell 1989). Recently, ordination methods (e.g., principal components analysis, canonical correlation analysis) have been used to test relationships and explain behavioural patterns (Côté et al. 1997, Kazmaier et al. 2001, Jayakody et al. 2008, Hamel and Côté 2008). Results of such methods, however, can be difficult to interpret (Tabachnick and Fidell 1989) and additional follow-up analyses are often required to determine the influence of explanatory variables of interest (Côté et al. 1997, Hamel and Côté 2008). Fmlogit is an alternative to analysis of variance and ordination methods that is well-suited to exploring trade-offs in time allocation due to a variety of internal or external stimuli. Understanding the influences of human disturbances and environmental variation on animal behaviour will become increasingly important to the development of effective conservation and management strategies in the context of global change.

CHAPTER 4

General Summary

Rangifer populations are known to fluctuate in number and distribution over decadal time scales, however there is little consensus on the factors driving these oscillations (Skoog 1968, Gunn and Skogland 1997, Morneau and Payette 2000, Gunn 2003). Recent declines in *Rangifer* populations across the circumpolar north, including an approximately 90% decrease in the Bathurst barren-ground caribou herd from 1986-2009 (Nishi et al. 2010), are of particular concern. It is unclear whether natural recovery will occur in the face of global change, industrial development, and increased hunting pressure (Forchhammer et al. 2002, Vors and Boyce 2009). Improved understanding of factors influencing caribou/reindeer population dynamics and trophic relationships is needed to facilitate sustainable management of *Rangifer* herds in the context of the changing north.

Some have hypothesized that climatic warming has led to increased intensity and duration of insect harassment resulting in less effective habitat use by *Rangifer* and activity patterns that favour insect avoidance behaviour over foraging (Mörschel and Klein 1997, Brotton and Wall 1997, Weladji et al. 2003). These behavioural and distributional responses to insects may act in isolation or in combination with other factors to reduce the productivity of caribou/reindeer. In order to gain a better understanding of climate-insect-*Rangifer* interrelationships, I monitored weather conditions, trapped insects, and recorded behavioural observations for caribou of the Bathurst herd during the 2007-2009 post-calving/summer seasons. I examined the influence of weather, time/date, and habitat on the activity/abundance levels of 3 of the main parasitic fly families (mosquitoes, black flies, oestrid flies) responsible for harassment of Bathurst caribou. I also explored the relationships between insect activity/abundance and caribou behaviour.

There is a well-observed relationship between *Rangifer* behaviour and insect harassment (Downes et al. 1986, Russell et al. 1993, Mörschel and Klein 1997, Colman et al. 2003). The response of different parasitic fly families to changes in weather parameters and the degree to which these insects affect caribou/reindeer, however, are less clear (Anderson and Nilssen 1998). This study is unique in that it is the first in the central Arctic to employ systematic insect trapping over multiple years and the majority of the season when insects are active. The insect indices I developed include a wide range of weather parameters, allowing for a more nuanced assessment of the effects of changing climate on insect activity/abundance. Additionally, most past studies of insect harassment and *Rangifer* behaviour employed correlative methods and, thus, were not able to identify direct relationships between caribou/reindeer behaviour and insect activity (Walsh et al. 1992, Russell et al. 1993, Mörschel and Klein 1997, Colman et al. 2003). The results of my study clarify the type and severity of *Rangifer* behavioural response to mosquitoes, black flies, and oestrid flies. To my knowledge, this is the first time black flies have been treated separately in developing predictive indices and measuring caribou response to harassment. Finally, my study illustrates a novel approach (fractional multinomial logistic regression; Buis 2008) for conducting time allocation/activity budget analysis that is applicable to other research questions exploring the influence of external or internal stimuli on animal behaviour.

In Chapter 2, I developed statistical models of mosquito and black fly activity/abundance, as well as oestrid fly presence/absence to meet 2 complementary goals: (1) to increase understanding of parasitic fly ecology; and (2) to develop predictive indices of insect activity that can be easily applied by wildlife managers interested in both examining past and monitoring future conditions of insect activity across the post-calving/summer range of Bathurst caribou. Mosquito and black fly levels were best explained by a combination of temperature, wind speed, light intensity, barometric pressure, relative humidity, vegetation type, topography, location, time of day, and growing degree days. Oestrid presence was best explained by temperature, wind speed, light intensity, barometric pressure, relative humidity, vegetation type, topography, and location. Activity of all three insect families increased as temperature rose; oestrids were the least tolerant of low temperatures. Wind speed negatively affected all insect activity, but this effect was strongest for mosquitoes. Time of day and season also affected insect activity/abundance. The probability of high mosquito activity increased during dusk and night, while black flies were most active during morning, afternoon, and dusk. Oestrid presence was most likely during afternoon. Mosquito activity peaked in early to mid July, largely separate from the period of greatest black fly activity in late July to early August. Although I trapped more oestrid flies later in the post-calving/summer season, seasonality of oestrid presence was ambiguous. The activity of all three insect families increased in lowland areas. The best models for mosquitoes, black flies, and oestrids all had good predictive ability.

I used the best models to generate simplified indices that can be used to predict insect activity levels. I tested the strength of correlations among weather measures and insect trap catch collected at different locations across the Bathurst post-calving/summer range in order to determine the efficacy of using indices for range-wide prediction. Temperature, relative humidity, and light intensity were highly correlated, while wind speeds exhibited high spatial variation. There was little difference in black fly activity levels and oestrid presence across the post-calving/summer range, but mosquito activity was strongly related to location. Thus, black fly and oestrid indices calculated based on the conditions at one or a few weather stations should approximate conditions across the range, however, caution should be taken in extrapolating local mosquito activity to range-wide predictions.

I applied the indices to weather data collected on the Bathurst range over the past half century. Retrospective analyses indicated that conditions favouring mosquito activity likely declined since the late 1950s, while predicted levels of black fly and oestrid activity increased. Black fly and oestrid predictions were driven by a trend of increasing summer temperatures. Temperature positively affects mosquito activity, but mosquitoes are also more sensitive to other meteorological variables like wind speed and relative humidity. Increased wind speeds and decreased relative humidity over time are consistent with a declining trend in mosquito index values. Correlations between insect index values and caribou population parameters were insignificant, however, the Bathurst decline roughly corresponded with increased summer temperatures and predicted increases in black fly and oestrid activity from 1982-2008.

Given predicted increases in black fly and oestrid activity levels over time, knowledge of the behavioural responses of caribou to harassment is necessary to determine the potential consequences of increased insect harassment on the productivity of *Rangifer* populations. In Chapter 3, I examined fine-scale functional relationships between caribou behaviour, activity/abundance of parasitic flies, and environmental/temporal variables (i.e., weather, habitat, time/date). I developed statistical models to explain 3 aspects of caribou behaviour: (1) relative dominance of types of behaviour (feeding, lying, standing, walking, running, or insect avoidance) within caribou groups, (2) time allocation by individual caribou, and (3) feeding intensity. When observing caribou in large groups, the predominance of behavioural classes was best described by covariates for mosquito and black fly activity, oestrid presence, time, easting, northing, gdd, year, and group size. Predictive ability was reasonable to good, and the models clearly identified when running and insect avoidance were the dominant behaviours. When considering time allocated by individual caribou to behavioural classes, the best models included covariates for mosquito and black fly activity, oestrid presence, and duration of focal observation. These models were most successful at predicting the proportion of time caribou engaged in insect avoidance and lying. Across all combinations of behaviour, the predictive ability of the individual-based models was weak to moderate; the models performed poorly when caribou engaged in a single behaviour for the majority of the focal observation.

The relative dominance of insect avoidance behaviour within caribou groups and time allocation by individual caribou to insect avoidance increased when oestrid flies were present or black flies were active at moderate to high levels. Standing also increased when oestrids were present, and lying was reduced to a greater degree than other behaviours. Aside from insect avoidance, running also increased when black fly activity was high. Mosquito activity had less effect on caribou behaviour, although walking increased slightly at high mosquito levels. Caribou behaviour was also influenced by time of day. Insect avoidance was more likely to dominate during morning and afternoon, while lying increased at night. Feeding did not increase noticeably in relative dominance during dawn/dusk/night, suggesting that caribou may not have used this time period to compensate for lost foraging opportunities due to insect harassment during the day. Models of caribou behaviour that contained weather variables did not perform as well as those containing covariates related to insect activity. This suggests that the indirect effects of weather on caribou behaviour via insect activity are larger than the direct effects of weather.

Activity levels of mosquitoes, black flies, and oestrids had smaller effects than temporal variables on caribou feeding intensity. The best model of feeding intensity included covariates for year, growing degree days, and duration of focal observation. The most interesting relationship was the decrease in feeding intensity as degree days accumulated over the course of the post-calving/summer season. This model had moderate predictive ability.

Caribou/reindeer have evolved with parasitic flies over the millennia and it is unlikely that insect harassment is a sole cause of *Rangifer* population declines. The direct costs of blood loss and parasitic loading combined with indirect costs of behavioural modification due to insect harassment, however, are stressors that could accelerate population declines or dampen recovery. The predictive indices of insect activity that I developed are easily applied and cost-effective tools wildlife managers can use to monitor levels of insect activity across the Bathurst range. Trap catch data and retrospective predictions from this study can be used together to provide a reference to assess predicted or actual changes in insect activity that may occur in the future. Information on the differential responses of caribou to mosquito, black fly, and oestrid harassment can be combined with predictions of insect indices to help understand behavioural changes over time. Used in conjunction with ongoing caribou demographic and body condition monitoring (Adamczewski et al. 2009) and energetics modeling (Fancy 1986, Kremsater et al. 1989, Russell et al. 2005), these tools can illuminate the potential repercussions of global change for the productivity of Bathurst caribou. Range quality could mitigate or compound the effects of insect harassment and other stressors. The current lack of information on forage availability and quality, variation in forage conditions, and diet composition for the Bathurst herd represent critical gaps in our understanding. Research in this area would complement my study, as well as ongoing monitoring efforts designed to increase our understanding of Bathurst post-calving/summer range ecology and population trends. Although each *Rangifer* herd has a unique ecology, the behavioural responses I observed in Bathurst caribou broadly illustrate the types of trade-offs faced by caribou/reindeer experiencing insect harassment and may be applicable to *Rangifer* in other areas.

In a broader context, my study illustrates several concepts relevant to current issues in wildlife management and ecology. Global change threatens many wildlife populations, and it is increasingly important to incorporate predictions about climatic warming into wildlife management strategies (Weladji et al. 2002, ACIA 2004, Fuller et al. 2008). Global climate models, however, have coarse resolutions that do not capture the complexities to which individuals and populations respond at regional scales (Bader et al. 2008, Doherty et al. 2009). Baseline data, such as insect activity/abundance relative to current weather conditions, can be used to develop ecological indices that elucidate trends over time that are relevant to individuals, populations, and ecosystems (Fore et al. 1996, Niemi and McDonald 2004, Hardman-Mountford et al. 2005). Indices are cost effective tools for directing ecosystem monitoring and adaptive management (McGeoch 1998, Hopkins and Kennedy 2004, Hodkinson and Jackson 2005).

Understanding the influences of human disturbances and environmental variation on animal behaviour is important to the development of effective conservation and management strategies. As time is a limited resource, animals must make daily trade-offs in time allocation to different behaviours based on both intrinsic and extrinsic factors (Aschoff 1963, Shi et al. 2003, Zhou et al. 2007, Hamel and Côté 2008). Fractional multinomial logistic regression models represent a novel approach to behavioural analysis, well-suited for understanding such trade-off decisions relative to internal and external stimuli. This statistical approach is easy to implement, highly flexible, robust to data-related assumptions, and provides an explicit accounting of the time-constrained nature of activity budgets (Papke and Wooldridge 1996, Ye and Pendyala 2005, Buis 2008).

My study provides a detailed and robust assessment of the ecological interrelationships between weather, parasitic insects, and caribou behaviour. This information fills one gap in the broad knowledge set describing factors that may influence the current decline in *Rangifer* populations and future dynamics of this circum-Arctic genus (Vors and Boyce 2009). I documented increases in the time spent by caribou in insect avoidance and other energetically costly behaviours in response to harassment by black flies and oestrids. Climatic warming to date has increased the proportion of the post-calving/summer season during which conditions are favourable for black fly and oestrid activity. Behavioural modifications in response to insect harassment may drive *Rangifer* into a negative energy balance during the post-calving/summer season, with consequences for the population productivity of caribou/reindeer herds (Fancy 1986, Kremsater et al. 1989, Russell et al. 1993).

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Appendix A. Coefficients (β) and 95% confidence intervals (CI) from multinomial logistic regression (mlogit; Tables 3-5) models of mosquito and black fly activity/abundance; and, from logistic regression model of oestrid presence/absence on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada. Coefficients presented are from models selected from the full model sets. Coefficients for growing degree days (gdd^2), light, easting, and northing scaled by a factor of 1000.

Top-ranked mosquito model:

Model coefficients for all other mosquito activity levels relative to absence of mosquitoes:

	Low mosquitoes			Moderate mosquitoes			High mosquitoes		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	0.004	0.001	0.007	0.015	0.007	0.023	0.026	−0.007	0.059
Gdd^2	−0.019	−0.028	−0.011	−0.055	−0.076	−0.033	−0.124	−0.221	−0.028
Temp	0.236	0.104	0.369	0.288	0.088	0.488	0.523	0.253	0.793
Wind	−0.791	−0.943	−0.639	−1.336	−1.512	−1.160	−2.083	−2.376	−1.790
Light	−0.005	−0.024	0.013	−0.013	−0.037	0.010	−0.016	−0.040	0.009
BP	3.415	1.747	5.083	5.828	2.659	8.998	6.865	2.328	11.401
RH	0.025	−0.004	0.053	0.019	−0.003	0.041	0.035	0.009	0.061
Time									
dawn	−0.718	−1.188	−0.248	−0.533	−1.078	0.013	−0.566	−1.319	0.186
morning	0.371	−0.112	0.854	0.020	−0.623	0.664	−0.578	−1.200	0.043
afternoon	0.038	−0.396	0.472	−0.130	−0.846	0.586	−0.234	−0.952	0.485
dusk	0.500	0.064	0.936	0.198	−0.380	0.775	0.782	0.210	1.353
night	−0.192	−0.921	0.538	0.445	−0.380	1.269	0.596	−0.584	1.777
Vegetation									
tussock	0.300	−0.396	0.995	0.043	−0.807	0.894	0.268	−1.024	1.560
non-tussock	−0.409	−1.272	0.455	−0.295	−1.528	0.937	−0.199	−1.641	1.242
shrub	0.145	−0.439	0.730	0.018	−0.842	0.879	0.330	−0.651	1.310
prostr shrub	−0.036	−0.863	0.791	0.234	−0.970	1.440	−0.398	−1.737	0.940
Topography									
lowland	0.175	−0.457	0.807	0.549	−0.392	1.490	1.066	0.066	2.066
mid-slope	−0.085	−0.725	0.555	−0.635	−1.745	0.475	−0.723	−1.845	0.398
upland	−0.090	−0.617	0.436	0.085	−0.622	0.793	−0.342	−1.137	0.452
Easting	0.026	0.010	0.042	0.043	0.024	0.063	0.032	0.010	0.055
Northing	0.029	0.013	0.046	0.039	0.019	0.059	0.054	0.029	0.078

Model coefficients for all other mosquito activity levels relative to low mosquito activity:

	No mosquitoes			Moderate mosquitoes			High mosquitoes		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.004	−0.007	−0.001	0.011	0.003	0.018	0.022	−0.010	0.055
Gdd^2	0.019	0.011	0.028	−0.035	−0.052	−0.019	−0.105	−0.197	−0.013
Temp	−0.236	−0.369	−0.104	0.052	−0.159	0.263	0.287	−0.043	0.616
Wind	0.791	0.639	0.943	−0.545	−0.684	−0.406	−1.292	−1.625	−0.960
Light	0.005	−0.013	0.024	−0.008	−0.023	0.007	−0.011	−0.028	0.007
BP	−3.415	−5.083	−1.750	2.413	−0.801	5.628	3.450	−1.348	8.248
RH	−0.025	−0.053	0.004	−0.005	−0.037	0.027	0.010	−0.032	0.052
Time									
dawn	0.718	0.248	1.188	0.185	−0.282	0.652	0.152	−0.510	0.814
morning	−0.371	−0.854	0.112	−0.351	−0.784	0.082	−0.950	−1.422	−0.478
afternoon	−0.038	−0.472	0.396	−0.168	−0.830	0.493	−0.272	−0.812	0.267
dusk	−0.500	−0.936	−0.064	−0.302	−0.814	0.210	0.282	−0.109	0.673
night	0.192	−0.538	0.921	0.636	0.111	1.161	0.788	0.085	1.492
Vegetation									
tussock	−0.300	−0.995	0.396	−0.256	−1.026	0.514	−0.031	−1.277	1.214
non-tussock	0.409	−0.455	1.272	0.113	−0.875	1.102	0.209	−1.110	1.528
shrub	−0.145	−0.730	0.439	−0.127	−0.802	0.548	0.184	−0.664	1.033
prostr shrub	0.036	−0.791	0.863	0.270	−0.695	1.235	−0.362	−1.529	0.805
Topography									
lowland	−0.175	−0.807	0.457	0.374	−0.355	1.103	0.891	0.056	1.725
mid-slope	0.085	−0.555	0.725	−0.550	−1.453	0.354	−0.639	−1.564	0.286
upland	0.090	−0.436	0.617	0.176	−0.419	0.771	−0.252	−0.952	0.448
Easting	−0.026	−0.042	−0.010	0.018	0.002	0.033	0.006	−0.013	0.026
Northing	−0.029	−0.046	−0.013	<0.001	−0.009	0.028	0.024	0.001	0.047

Model coefficients for all other mosquito activity levels relative to moderate mosquito activity:

	No mosquitoes			Low mosquitoes			High mosquitoes		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.015	−0.023	−0.007	−0.011	−0.018	−0.003	0.011	−0.016	0.039
Gdd^2	0.055	0.033	0.076	0.035	0.019	0.052	−0.070	−0.150	0.011
Temp	−0.288	−0.488	−0.088	−0.052	−0.263	0.159	0.235	0.047	0.423
Wind	1.336	1.160	1.512	0.545	0.406	0.684	−0.747	−1.066	−0.428
Light	0.013	−0.010	0.037	0.008	−0.007	0.023	−0.003	−0.023	0.018
BP	−5.828	−8.998	−2.660	−2.413	−5.628	0.801	1.036	−1.299	3.371
RH	−0.019	−0.041	0.003	0.005	−0.027	0.037	0.015	−0.008	0.039
Time									
dawn	0.533	−0.013	1.078	−0.185	−0.652	0.282	−0.034	−0.606	0.539
morning	−0.020	−0.664	0.623	0.351	−0.082	0.784	−0.599	−1.033	−0.164
afternoon	0.130	−0.586	0.846	0.168	−0.493	0.830	−0.104	−0.751	0.544
dusk	−0.198	−0.775	0.380	0.302	−0.210	0.814	0.584	−0.030	1.199
night	−0.445	−1.269	0.380	−0.636	−1.161	−0.111	0.152	−0.445	0.748
Vegetation									
tussock	−0.043	−0.894	0.807	0.256	−0.514	1.026	0.225	−0.757	1.207
non-tussock	0.295	−0.937	1.528	−0.113	−1.102	0.875	0.096	−0.996	1.188
shrub	−0.018	−0.879	0.842	0.127	−0.548	0.802	0.311	−0.422	1.045
prostr shrub	−0.234	−1.437	0.970	−0.270	−1.235	0.695	−0.632	−1.378	0.114
Topography									
lowland	−0.549	−1.490	0.392	−0.374	−1.103	0.355	0.517	−0.221	1.254
mid-slope	0.635	−0.475	1.745	0.550	−0.354	1.453	−0.089	−0.724	0.547
upland	−0.085	−0.793	0.622	−0.176	−0.771	0.419	−0.428	−0.986	0.131
Easting	−0.043	−0.063	−0.024	−0.018	−0.033	−0.002	−0.011	−0.020	−0.002
Northing	−0.039	−0.059	−0.019	−0.010	−0.028	0.009	0.015	−0.001	0.031

Model coefficients for all other mosquito activity levels relative to high mosquito activity:

	No mosquitoes			Low mosquitoes			Moderate mosquitoes		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.026	−0.059	0.007	−0.022	−0.055	0.010	−0.011	−0.039	0.016
Gdd^2	0.124	0.028	0.221	0.105	0.013	0.197	0.070	−0.011	0.150
Temp	−0.523	−0.793	−0.253	−0.287	−0.616	0.043	−0.235	−0.423	−0.047
Wind	2.083	1.790	2.376	1.292	0.960	1.625	0.747	0.428	1.066
Light	0.016	−0.009	0.040	0.011	−0.007	0.028	0.003	−0.018	0.023
BP	−6.865	−11.40	−2.330	−3.450	−8.248	1.348	−1.036	−3.372	1.299
RH	−0.035	−0.061	−0.009	−0.010	−0.052	0.032	−0.015	−0.039	0.008
Time									
dawn	0.566	−0.186	1.319	−0.152	−0.814	0.510	0.034	−0.539	0.606
morning	0.578	−0.043	1.200	0.950	0.478	1.422	0.599	0.164	1.033
afternoon	0.234	−0.485	0.952	0.272	−0.267	0.812	0.104	−0.544	0.751
dusk	−0.782	−1.353	−0.210	−0.282	−0.673	0.109	−0.584	−1.199	0.030
night	−0.596	−1.777	0.584	−0.788	−1.492	−0.085	−0.152	−0.748	0.445
Vegetation									
tussock	−0.268	−1.560	1.020	0.031	−1.214	1.277	−0.225	−1.207	0.757
non-tussock	0.199	−1.242	1.640	−0.209	−1.528	1.110	−0.096	−1.188	0.996
shrub	−0.330	−1.310	0.650	−0.184	−1.033	0.664	−0.311	−1.045	0.422
prostr shrub	0.398	−0.940	1.737	0.362	−0.805	1.529	0.632	−0.114	1.378
Topography									
lowland	−1.066	−2.066	0.066	−0.891	−1.725	−0.056	−0.517	−1.254	0.221
mid-slope	0.723	−0.398	1.845	0.639	−0.286	1.564	0.089	−0.547	0.724
upland	0.342	−0.452	1.137	0.252	−0.448	0.952	0.428	−0.131	0.986
Easting	−0.032	−0.055	−0.010	−0.006	−0.026	0.013	0.011	0.002	0.020
Northing	−0.054	−0.078	−0.029	−0.024	−0.047	−0.001	−0.015	−0.031	0.001

2nd-ranked black fly model (top 2 models had similar AIC$_c$ scores; selected fuller model to present information on more covariates of potential biological significance)**:**

Model coefficients for all other black fly activity levels relative to absence of black flies:

	Low black flies			Moderate black flies			High black flies		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	0.013	0.008	0.017	0.017	0.013	0.021	0.035	0.028	0.042
Gdd^2	−0.017	−0.023	−0.012	−0.027	−0.038	−0.017	−0.061	−0.074	−0.049
Temp	0.281	0.157	0.405	0.663	0.522	0.803	0.785	0.575	0.996
Wind	−0.577	−0.700	−0.455	−0.967	−1.160	−0.775	−1.522	−1.999	−1.050
Light	0.006	−0.013	0.024	0.013	−0.002	0.029	−0.002	−0.033	0.029
BP	−0.262	−1.495	0.970	−0.240	−2.231	1.751	−0.797	−3.449	1.855
RH	0.001	−0.014	0.017	0.023	−0.007	0.052	−0.002	−0.032	0.027
Time									
dawn	−0.436	−1.011	0.139	−0.871	−1.717	−0.026	−0.928	−2.009	0.153
morning	0.290	−0.147	0.727	0.419	−0.099	0.936	1.086	0.542	1.630
afternoon	0.078	−0.373	0.528	0.253	−0.311	0.816	0.842	−0.438	2.123
dusk	0.569	0.153	0.984	0.773	0.279	1.266	0.852	−0.033	1.737
night	−0.500	−0.954	−0.047	−0.573	−1.502	0.356	−1.852	−3.461	−0.244
Vegetation									
tussock	0.087	−0.451	0.625	0.789	0.033	1.545	0.598	−0.263	1.459
non-tussock	0.322	−0.544	1.189	−0.537	−1.808	0.734	0.627	−0.614	1.869
shrub	0.005	−0.441	0.451	−0.544	−1.145	0.056	0.092	−0.754	0.938
prostr shrub	−0.415	−1.016	0.186	0.292	−0.527	1.112	−1.317	−2.158	−0.475
Topography									
lowland	0.404	−0.234	1.042	0.434	−0.284	1.152	0.622	−0.119	1.364
mid-slope	−0.136	−0.679	0.406	−0.675	−1.460	0.110	0.072	−0.762	0.906
upland	−0.267	−0.749	0.215	0.241	−0.235	0.718	−0.695	−1.342	−0.047
Easting	−0.004	−0.010	0.002	−0.001	−0.007	0.005	−0.013	−0.022	−0.005
Northing	−0.002	−0.010	0.005	−0.005	−0.014	0.005	−0.013	−0.026	<0.001

Model coefficients for all other black fly activity levels relative to low black fly activity:

	No black flies			Moderate black flies			High black flies		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.013	−0.017	−0.008	0.004	−0.002	0.011	0.022	0.015	0.030
Gdd^2	0.017	0.012	0.023	−0.010	−0.022	0.003	−0.044	−0.057	−0.031
Temp	−0.281	−0.405	−0.157	0.382	0.211	0.552	0.504	0.349	0.659
Wind	0.577	0.455	0.700	−0.390	−0.576	−0.204	−0.945	−1.416	−0.474
Light	−0.006	−0.024	0.013	0.007	−0.019	0.034	−0.008	−0.027	0.011
BP	0.262	−0.970	1.495	0.022	−1.700	1.744	−0.534	−2.918	1.849
RH	−0.001	−0.017	0.014	0.021	−0.005	0.047	−0.004	−0.028	0.021
Time									
dawn	0.436	−0.139	1.011	−0.435	−1.317	0.446	−0.492	−1.427	0.442
morning	−0.290	−0.727	0.147	0.129	−0.379	0.637	0.796	0.104	1.488
afternoon	−0.078	−0.528	0.373	0.175	−0.354	0.704	0.765	−0.301	1.831
dusk	−0.569	−0.984	−0.153	0.204	−0.454	0.862	0.283	−0.380	0.947
night	0.500	0.047	0.954	−0.072	−1.028	0.883	−1.352	−3.144	0.441
Vegetation									
tussock	−0.087	−0.625	0.451	0.702	0.039	1.364	0.511	−0.302	1.323
non-tussock	−0.322	−1.189	0.544	−0.859	−2.076	0.357	0.305	−0.735	1.344
shrub	−0.005	−0.451	0.441	−0.549	−1.165	0.066	0.087	−0.767	0.941
prostr shrub	0.415	−0.186	1.016	0.707	−0.222	1.636	−0.902	−1.770	−0.034
Topography									
lowland	−0.404	−1.042	0.234	0.030	−0.646	0.707	0.219	−0.528	0.966
mid-slope	0.136	−0.406	0.679	−0.539	−1.262	0.184	0.208	−0.487	0.904
upland	0.267	−0.215	0.749	0.509	−0.031	1.048	−0.427	−1.120	0.266
Easting	0.004	−0.002	0.010	0.003	−0.003	0.009	−0.009	−0.017	−0.002
Northing	0.002	−0.005	0.010	−0.002	−0.010	0.005	−0.011	−0.023	0.001

Model coefficients for all other black fly activity levels relative to moderate black fly activity:

	No black flies			Low black flies			High black flies		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.017	−0.021	−0.013	−0.004	−0.011	0.002	0.018	0.011	0.025
Gdd^2	0.027	0.017	0.038	0.010	−0.003	0.022	−0.034	−0.047	−0.022
Temp	−0.663	−0.803	−0.522	−0.382	−0.552	−0.211	0.123	−0.047	0.292
Wind	0.967	0.775	1.160	0.390	0.204	0.576	−0.555	−0.944	−0.166
Light	−0.013	−0.029	0.002	−0.007	−0.034	0.019	−0.015	−0.050	0.019
BP	0.240	−1.751	2.231	−0.022	−1.744	1.700	−0.556	−2.279	1.166
RH	−0.023	−0.052	0.007	−0.021	−0.047	0.005	−0.025	−0.050	0.001
Time									
dawn	0.871	0.026	1.717	0.435	−0.446	1.317	−0.057	−0.856	0.742
morning	−0.419	−0.936	0.099	−0.129	−0.637	0.379	0.667	−0.001	1.336
afternoon	−0.253	−0.816	0.311	−0.175	−0.704	0.354	0.590	−0.392	1.571
dusk	−0.773	−1.266	−0.279	−0.204	−0.862	0.454	0.080	−0.940	1.099
night	0.573	−0.356	1.502	0.072	−0.883	1.028	−1.279	−3.001	0.443
Vegetation									
tussock	−0.789	−1.545	−0.033	−0.702	−1.364	−0.039	−0.191	−0.988	0.606
non-tussock	0.537	−0.734	1.808	0.859	−0.357	2.076	1.164	−0.201	2.529
shrub	0.544	−0.056	1.145	0.549	−0.066	1.165	0.636	−0.039	1.311
prostr shrub	−0.292	−1.112	0.527	−0.707	−1.636	0.222	−1.609	−2.383	−0.835
Topography									
lowland	−0.434	−1.152	0.284	−0.030	−0.707	0.646	0.188	−0.478	0.855
mid-slope	0.675	−0.110	1.460	0.539	−0.184	1.262	0.747	0.105	1.390
upland	−0.241	−0.718	0.235	−0.509	−1.048	0.031	−0.936	−1.464	−0.408
Easting	0.001	−0.005	0.007	−0.003	−0.009	0.003	−0.012	−0.019	−0.005
Northing	0.005	−0.005	0.014	0.002	−0.005	0.010	−0.008	−0.018	0.001

Model coefficients for all other black fly activity levels relative to high black fly activity:

	No black flies			Low black flies			Moderate black flies		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.035	−0.042	−0.028	−0.022	−0.030	−0.015	−0.018	−0.025	−0.011
Gdd^2	0.061	0.049	0.074	0.044	0.031	0.057	0.034	0.022	0.047
Temp	−0.785	−0.996	−0.575	−0.504	−0.659	−0.349	−0.123	−0.292	0.047
Wind	1.522	1.045	1.999	0.945	0.474	1.416	0.555	0.166	0.944
Light	0.002	−0.029	0.033	0.008	−0.011	0.027	0.015	−0.019	0.050
BP	0.797	−1.855	3.449	0.534	−1.849	2.918	0.556	−1.166	2.279
RH	0.002	−0.027	0.032	0.004	−0.021	0.028	0.025	<0.001	0.050
Time									
dawn	0.928	−0.153	2.009	0.492	−0.442	1.427	0.057	−0.742	0.856
morning	−1.086	−1.630	−0.542	−0.796	−1.488	−0.104	−0.667	−1.336	0.001
afternoon	−0.842	−2.123	0.438	−0.765	−1.831	0.301	−0.590	−1.571	0.392
dusk	−0.852	−1.737	0.033	−0.283	−0.947	0.380	−0.080	−1.099	0.940
night	1.852	0.244	3.461	1.352	−0.441	3.144	1.279	−0.443	3.001
Vegetation									
tussock	−0.598	−1.459	0.263	−0.511	−1.323	0.302	0.191	−0.606	0.988
non-tussock	−0.627	−1.869	0.614	−0.305	−1.344	0.735	−1.164	−2.529	0.201
shrub	−0.092	−0.938	0.754	−0.087	−0.941	0.767	−0.636	−1.311	0.039
prostr shrub	1.317	0.475	2.158	0.902	0.034	1.770	1.609	0.835	2.383
Topography									
lowland	−0.622	−1.364	0.119	−0.219	−0.966	0.528	−0.188	−0.855	0.478
mid-slope	−0.072	−0.906	0.762	−0.208	−0.904	0.487	−0.747	−1.390	−0.105
upland	0.695	0.047	1.342	0.427	−0.266	1.120	0.936	0.408	1.464
Easting	0.013	0.005	0.022	0.009	0.002	0.017	0.012	0.005	0.019
Northing	0.013	<0.001	0.026	0.011	−0.001	0.023	0.008	−0.001	0.018

Model coefficients for oestrid fly presence relative to absence from 2nd-ranked model (top 2 models had similar AIC$_c$ scores; selected fuller model to present information on more covariates of potential biological significance)**:**

	β	95% CI	
		Lower	Upper
Temp	0.562	0.257	0.867
Wind	−0.642	−1.990	0.706
Light	0.025	−0.042	0.092
BP	−2.666	−7.136	1.804
RH	0.039	−0.026	0.103
Veg - tundra	0.479	−0.994	1.952
Lowland	1.232	0.167	2.297
Mid-slope	−0.529	−1.945	0.887
Upland	−0.703	−1.933	0.527
Easting	0.002	−0.018	0.022
Northing	−0.012	−0.030	0.006

Model coefficients for oestrid fly presence relative to absence from top model in time/date subcategory:

	β	95% CI	
		Lower	Upper
Eclosion	0.130	−0.073	0.333
Eclosion^2	−0.003	−0.008	0.001
Time - afternoon	1.802	0.679	2.925

Appendix B. Coefficients (β) and 95% confidence intervals (CI) from multinomial logistic regression models (mlogit; Tables 3-5) of mosquito and black fly activity/abundance; and from logistic regression model of oestrid presence/absence on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada. Coefficients are from models selected for use as indices in retrospective analysis. Model sets were restricted to those models that did not contain variables for habitat/location. Coefficients for growing degree days (gdd^2) and light scaled by a factor of 1000.

Mosquito index:

Model coefficients for all other mosquito activity levels relative to absence of mosquitoes:

	Low mosquitoes			Moderate mosquitoes			High mosquitoes		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	0.005	0.002	0.009	0.018	0.005	0.030	0.032	−0.001	0.065
Gdd^2	−0.020	−0.029	−0.011	−0.061	−0.095	−0.026	−0.134	−0.229	−0.039
Temp	0.155	0.065	0.245	0.179	−0.013	0.371	0.372	0.097	0.647
Wind	−0.717	−0.835	−0.598	−1.188	−1.403	−0.973	−1.826	−2.143	−1.508
Light	0.002	−0.013	0.018	−0.007	−0.026	0.011	−0.011	−0.032	0.011
BP	0.679	−0.757	2.115	1.588	−1.894	5.070	2.408	−1.641	6.456
RH	0.018	−0.007	0.043	<−0.001	−0.027	0.027	0.013	−0.014	0.039
Time									
dawn	−0.681	−1.167	−0.195	−0.426	−0.922	0.071	−0.488	−1.056	0.080
morning	0.293	−0.146	0.731	0.01	−0.590	0.609	−0.588	−1.133	−0.043
afternoon	−0.039	−0.564	0.487	−0.414	−1.138	0.311	−0.495	−1.418	0.427
dusk	0.504	0.124	0.884	0.190	−0.241	0.620	0.714	0.223	1.205
night	−0.077	−0.813	0.659	0.640	−0.212	1.492	0.857	−0.449	2.164

Model coefficients for all other mosquito activity levels relative to low mosquito activity:

	No mosquitoes			Moderate mosquitoes			High mosquitoes		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.005	−0.009	−0.002	0.012	0.001	0.023	0.027	−0.005	0.058
Gdd^2	0.020	0.011	0.029	−0.041	−0.070	−0.012	−0.114	−0.205	−0.023
Temp	−0.155	−0.245	−0.065	0.024	−0.154	0.203	0.217	−0.087	0.520
Wind	0.717	0.598	0.835	−0.471	−0.614	−0.328	−1.109	−1.393	−0.825
Light	−0.002	−0.018	0.013	−0.009	−0.025	0.006	−0.013	−0.029	0.003
BP	−0.679	−2.115	0.757	0.909	−1.597	3.414	1.729	−1.501	4.958
RH	−0.018	−0.043	0.007	−0.018	−0.050	0.014	−0.005	−0.039	0.028
Time									
dawn	0.681	0.195	1.167	0.256	−0.185	0.697	0.194	−0.425	0.812
morning	−0.293	−0.731	0.146	−0.283	−0.758	0.192	−0.881	−1.399	−0.362
afternoon	0.039	−0.487	0.564	−0.375	−0.968	0.218	−0.457	−1.117	0.204
dusk	−0.504	−0.884	−0.124	−0.314	−0.802	0.173	0.209	−0.171	0.590
night	0.077	−0.659	0.813	0.717	0.148	1.286	0.934	0.103	1.766

Model coefficients for all other mosquito activity levels relative to moderate mosquito activity:

	No mosquitoes			Low mosquitoes			High mosquitoes		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.018	−0.030	−0.005	−0.012	−0.023	−0.001	0.014	−0.012	0.040
Gdd^2	0.061	0.026	0.095	0.041	0.012	0.070	−0.073	−0.148	0.001
Temp	−0.179	−0.371	0.013	−0.024	−0.203	0.154	0.192	−0.012	0.396
Wind	1.188	0.973	1.403	0.471	0.328	0.614	−0.638	−0.891	−0.384
Light	0.007	−0.011	0.026	0.009	−0.006	0.025	−0.003	−0.027	0.020
BP	−1.588	−5.070	1.894	−0.909	−3.414	1.597	0.820	−0.957	2.597
RH	<0.001	−0.027	0.027	0.018	−0.014	0.050	0.013	−0.011	0.036
Time									
dawn	0.426	−0.071	0.922	−0.256	−0.697	0.185	−0.062	−0.657	0.532
morning	−0.010	−0.609	0.590	0.283	−0.192	0.758	−0.598	−1.045	−0.151
afternoon	0.414	−0.311	1.138	0.375	−0.218	0.968	−0.082	−0.675	0.511
dusk	−0.190	−0.620	0.241	0.314	−0.173	0.802	0.524	−0.124	1.172
night	−0.640	−1.492	0.212	−0.717	−1.286	−0.148	0.218	−0.410	0.845

Model coefficients for all other mosquito activity levels relative to high mosquito activity:

	No mosquitoes			Low mosquitoes			Moderate mosquitoes		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.032	−0.065	0.001	−0.027	−0.058	0.005	−0.014	−0.040	0.012
Gdd^2	0.134	0.039	0.229	0.114	0.023	0.205	0.073	−0.001	0.148
Temp	−0.372	−0.647	−0.097	−0.217	−0.520	0.087	−0.192	−0.396	0.012
Wind	1.826	1.508	2.140	1.109	0.825	1.393	0.638	0.384	0.891
Light	0.011	−0.011	0.032	0.013	−0.003	0.029	0.003	−0.020	0.027
BP	−2.408	−6.456	1.641	−1.729	−4.958	1.501	−0.820	−2.597	0.957
RH	−0.013	−0.039	0.014	0.005	−0.028	0.039	−0.013	−0.036	0.011
Time									
dawn	0.488	−0.080	1.056	−0.194	−0.812	0.425	0.062	−0.532	0.657
morning	0.588	0.043	1.133	0.881	0.362	1.399	0.598	0.151	1.045
afternoon	0.495	−0.427	1.418	0.457	−0.204	1.117	0.082	−0.511	0.675
dusk	−0.714	−1.205	−0.223	−0.209	−0.590	0.171	−0.524	−1.172	0.124
night	−0.857	−2.164	0.449	−0.934	−1.766	−0.103	−0.218	−0.845	0.410

Black fly index:

Model coefficients for all other black fly activity levels relative to absence of black flies:

	Low black flies			Moderate black flies			High black flies		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	0.014	0.010	0.018	0.018	0.012	0.023	0.046	0.029	0.062
Gdd^2	−0.018	−0.024	−0.013	−0.028	−0.038	−0.017	−0.075	−0.099	−0.050
Temp	0.248	0.145	0.351	0.631	0.490	0.771	0.768	0.551	0.985
Wind	−0.520	−0.642	−0.397	−0.905	−1.077	−0.734	−1.429	−1.879	−0.978
Light	0.006	−0.011	0.023	0.012	−0.005	0.029	0.002	−0.024	0.028
BP	−0.260	−1.741	1.220	−0.327	−2.372	1.718	−0.634	−3.255	1.988
RH	0.005	−0.011	0.021	0.028	−0.003	0.059	0.015	−0.016	0.047
Time									
dawn	−0.426	−0.964	0.112	−0.886	−1.749	−0.024	−0.857	−1.813	0.099
morning	0.208	−0.208	0.624	0.413	−0.094	0.920	0.837	0.288	1.386
afternoon	0.118	−0.307	0.542	0.305	−0.179	0.788	0.832	−0.241	1.905
dusk	0.561	0.176	0.945	0.705	0.222	1.188	0.903	0.176	1.629
night	−0.460	−0.949	0.030	−0.536	−1.486	0.413	−1.715	−3.239	−0.191

Model coefficients for all other black fly activity levels relative to low black fly activity:

	No black flies			Moderate black flies			High black flies		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.014	−0.018	−0.010	0.004	−0.002	0.010	0.032	0.015	0.049
Gdd^2	0.018	0.013	0.024	−0.009	−0.022	0.003	−0.056	−0.082	−0.030
Temp	−0.248	−0.351	−0.145	0.383	0.219	0.546	0.520	0.344	0.697
Wind	0.520	0.397	0.642	−0.386	−0.531	−0.240	−0.909	−1.316	−0.502
Light	−0.006	−0.023	0.011	0.006	−0.021	0.032	−0.004	−0.021	0.014
BP	0.260	−1.220	1.741	−0.067	−1.681	1.548	−0.373	−2.445	1.698
RH	−0.005	−0.021	0.011	0.023	−0.001	0.047	0.01	−0.014	0.035
Time									
dawn	0.426	−0.112	0.964	−0.460	−1.373	0.453	−0.431	−1.315	0.454
morning	−0.208	−0.624	0.208	0.206	−0.329	0.740	0.630	−0.039	1.299
afternoon	−0.118	−0.542	0.307	0.187	−0.295	0.669	0.715	−0.249	1.678
dusk	−0.561	−0.945	−0.176	0.144	−0.492	0.781	0.342	−0.216	0.900
night	0.460	−0.030	0.949	−0.077	−1.054	0.900	−1.256	−3.008	0.496

Model coefficients for all other black fly activity levels relative to moderate black fly activity:

	No black flies			Low black flies			High black flies		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.018	−0.023	0.012	−0.004	−0.010	0.002	0.028	0.014	0.042
Gdd^2	0.028	0.017	0.038	0.009	−0.003	0.022	−0.047	−0.067	−0.027
Temp	−0.631	−0.771	−0.490	−0.383	−0.546	−0.219	0.137	−0.044	0.319
Wind	0.905	0.734	1.077	0.386	0.240	0.531	−0.523	−0.913	−0.133
Light	−0.012	−0.029	0.005	−0.006	−0.032	0.021	−0.009	−0.039	0.021
BP	0.327	−1.718	2.372	0.067	−1.548	1.681	−0.307	−2.027	1.414
RH	−0.028	−0.059	0.003	−0.023	−0.047	0.001	−0.013	−0.033	0.007
Time									
dawn	0.886	0.024	1.749	0.460	−0.453	1.373	0.030	−0.664	0.723
morning	−0.413	−0.920	0.094	−0.206	−0.740	0.329	0.424	−0.207	1.055
afternoon	−0.305	−0.788	0.179	−0.187	−0.669	0.295	0.527	−0.368	1.423
dusk	−0.705	−1.188	−0.222	−0.144	−0.781	0.492	0.198	−0.666	1.061
night	0.536	−0.413	1.486	0.077	−0.900	1.054	−1.179	−2.874	0.516

Model coefficients for all other black fly activity levels relative to high black fly activity:

	No black flies			Low black flies			Moderate black flies		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	−0.046	−0.062	−0.029	−0.032	−0.049	−0.015	−0.028	−0.042	−0.014
Gdd^2	0.075	0.050	0.099	0.056	0.030	0.082	0.047	0.027	0.067
Temp	−0.768	−0.985	−0.551	−0.520	−0.697	−0.344	−0.137	−0.319	0.044
Wind	1.429	0.978	1.879	0.909	0.502	1.316	0.523	0.133	0.913
Light	−0.002	−0.028	0.024	0.004	−0.014	0.021	0.009	−0.021	0.039
BP	0.634	−1.988	3.255	0.373	−1.698	2.445	0.307	−1.414	2.027
RH	−0.015	−0.466	0.016	−0.010	−0.035	0.014	0.013	−0.007	0.033
Time									
dawn	0.857	−0.099	1.813	0.431	−0.454	1.315	−0.030	−0.723	0.664
morning	−0.837	−1.386	−0.288	−0.630	−1.299	0.039	−0.424	−1.055	0.207
afternoon	−0.832	−1.905	0.241	−0.715	−1.678	0.249	−0.527	−1.423	0.368
dusk	−0.903	−1.629	−0.176	−0.342	−0.900	0.216	−0.198	−1.061	0.666
night	1.715	0.191	3.239	1.256	−0.496	3.008	1.179	−0.516	2.874

Oestrid index (model coefficients for oestrid presence relative to absence)**:**

	β	95% CI	
		Lower	Upper
Temp	0.597	0.330	0.864
Wind	−0.528	−1.498	0.441
Light	0.026	−0.035	0.086
BP	−1.180	−4.925	2.565
RH	0.063	0.012	0.113

Appendix C. Retrospective analysis of mosquito and black fly activity/abundance and oestrid occurrence indices using weather data collected from Lupin/Contwoyto, Daring Lake, and Salmita stations on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada. Insect indices represent the percent of the post-calving/summer season predicted to have moderate-high mosquito and black fly activity levels or a high probability of oestrid presence.

Lupin/Contwoyto insect indices 1957-2008:

Year	Mosquito index	Black fly index	Oestrid index
1957	8.81	3.40	0.11
1958	16.26	3.36	0
1959	13.52	1.15	0.14
1960	14.59	7.33	1.65
1961	13.66	6.47	1.65
1962	10.56	5.06	1.10
1963	11.95	3.68	0.08
1964	11.50	5.39	0.22
1965	15.46	4.82	0.43
1966	13.95	8.77	2.37
1967	12.51	3.59	0.58
1968	13.30	2.80	0.14
1969	10.50	4.17	0.22
1970	12.44	5.54	0.43
1971	13.59	3.67	0.29
1972	10.50	4.10	0.58
1973	13.23	8.99	2.30
1974	12.22	7.48	1.37
1975	10.86	4.60	0.58
1976	13.52	9.35	0.79
1977	21.64	5.75	0.29
1978	14.45	2.95	0
1979	16.03	7.62	2.16
1980	10.50	4.67	0.36
1981	10.42	3.74	0.86
1982	13.53	7.41	1.94
1983	12.72	8.12	1.01
1984	19.05	11.21	2.30
1985	13.44	3.24	0.14
1986	14.52	7.33	0.65
1987	8.55	6.69	0.72
1988	12.29	7.55	0.14
1989	9.35	9.85	8.48
1990	8.70	5.10	0.29
1991	10.78	7.33	2.66
1992	11.43	4.74	0.50
1993	6.12	3.45	0.22
1994	8.99	6.04	1.29
1995	15.08	3.13	0.95
1996	8.36	7.77	2.29
1997	5.27	6.29	0.95
1998	9.00	8.49	1.52
1999	11.36	3.18	1.16
2000	7.36	9.38	3.75
2001	10.96	7.35	2.88
2002	8.35	8.35	1.94
2003	10.06	7.69	2.08

2004	8.99	6.26	0.58
2005	7.55	3.52	0.58
2006	9.13	7.98	1.87
2007	9.59	9.44	0.29
2008	9.30	3.12	0.22

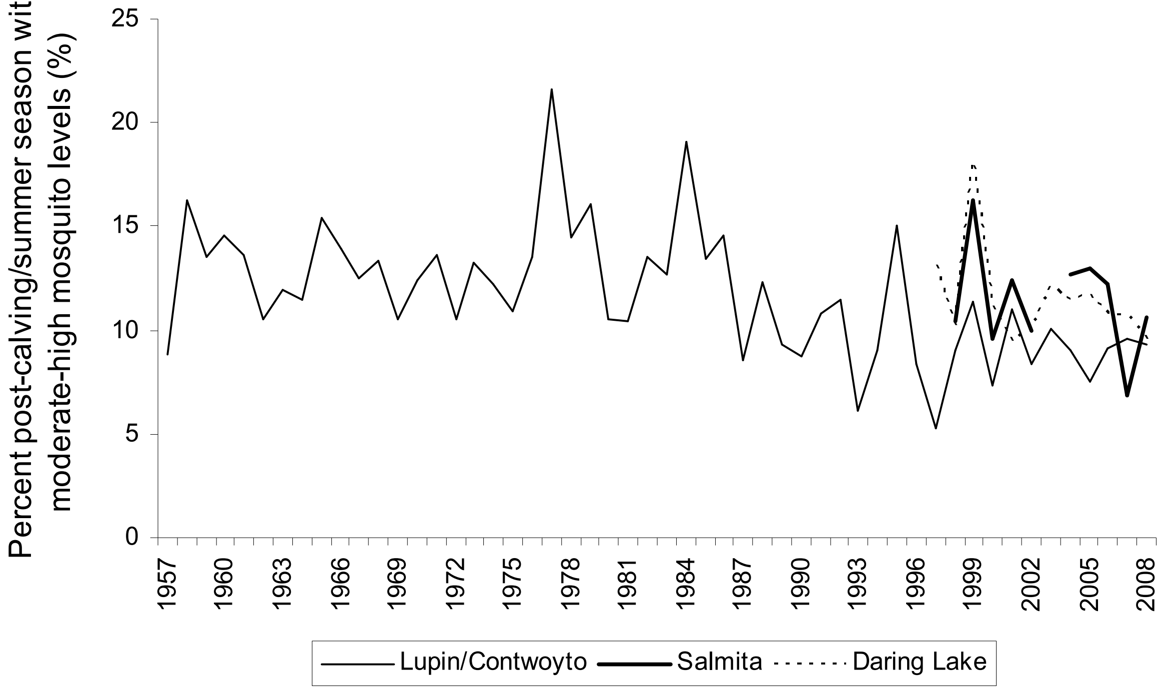
Daring Lake insect indices 1997-2008:

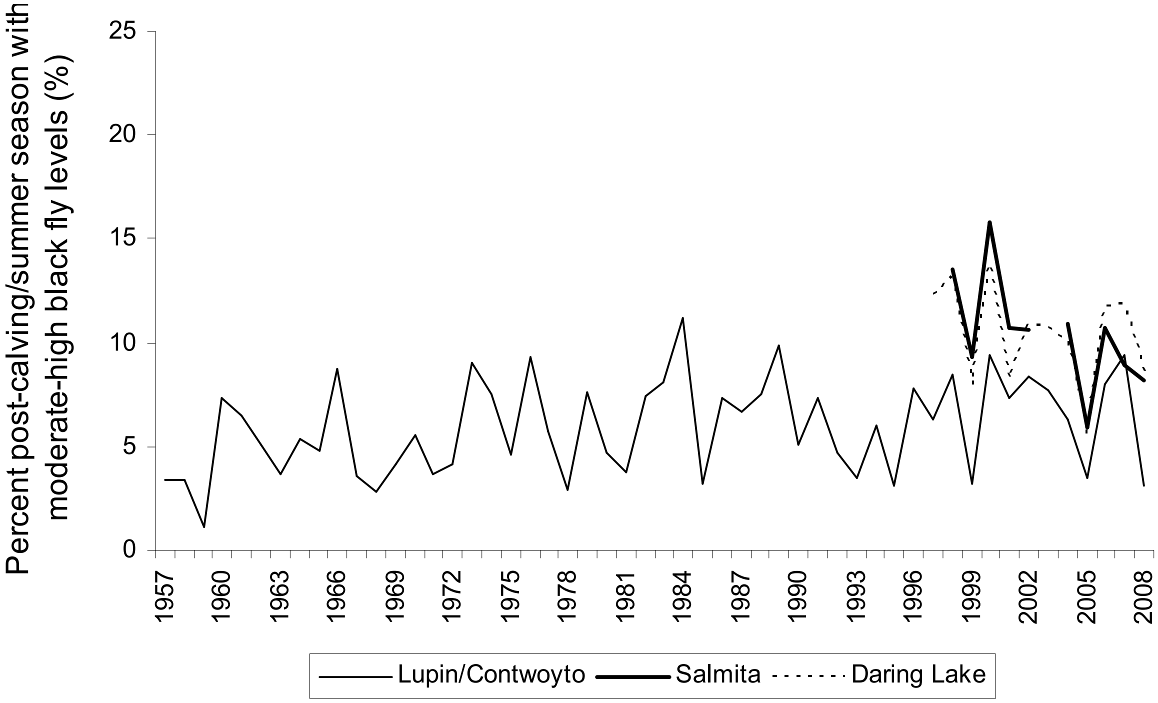
Year	Mosquito index	Black fly index	Oestrid index
1997	13.20	12.34	12.54
1998	10.16	13.16	11.14
1999	18.19	7.98	7.36
2000	11.15	13.78	12.36
2001	9.45	8.27	6.49
2002	9.94	10.88	8.19
2003	12.15	10.67	9.23
2004	11.49	10.09	7.17
2005	11.76	5.69	3.78
2006	10.83	11.72	10.05
2007	10.71	11.84	7.05
2008	9.54	8.64	6.85

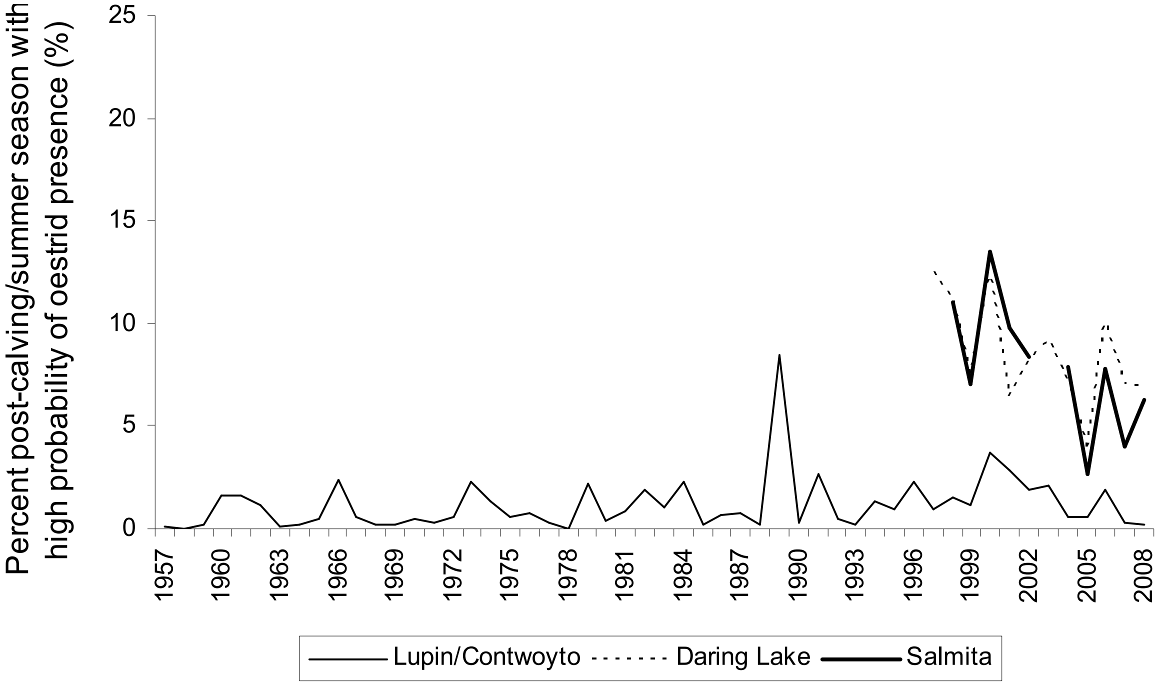
Salmita insect indices 1998-2008 (index values not calculated for 2003 due to incomplete weather records)**:**

Year	Mosquito index	Black fly index	Oestrid index
1998	10.46	13.58	11.01
1999	16.24	9.35	7.01
2000	9.62	15.81	13.51
2001	12.42	10.71	9.81
2002	9.93	10.59	8.41
2003	**--**	**--**	**--**
2004	12.73	10.86	7.87
2005	13.00	5.91	2.64
2006	12.23	10.75	7.75
2007	6.85	8.96	3.97
2008	10.63	8.22	6.23

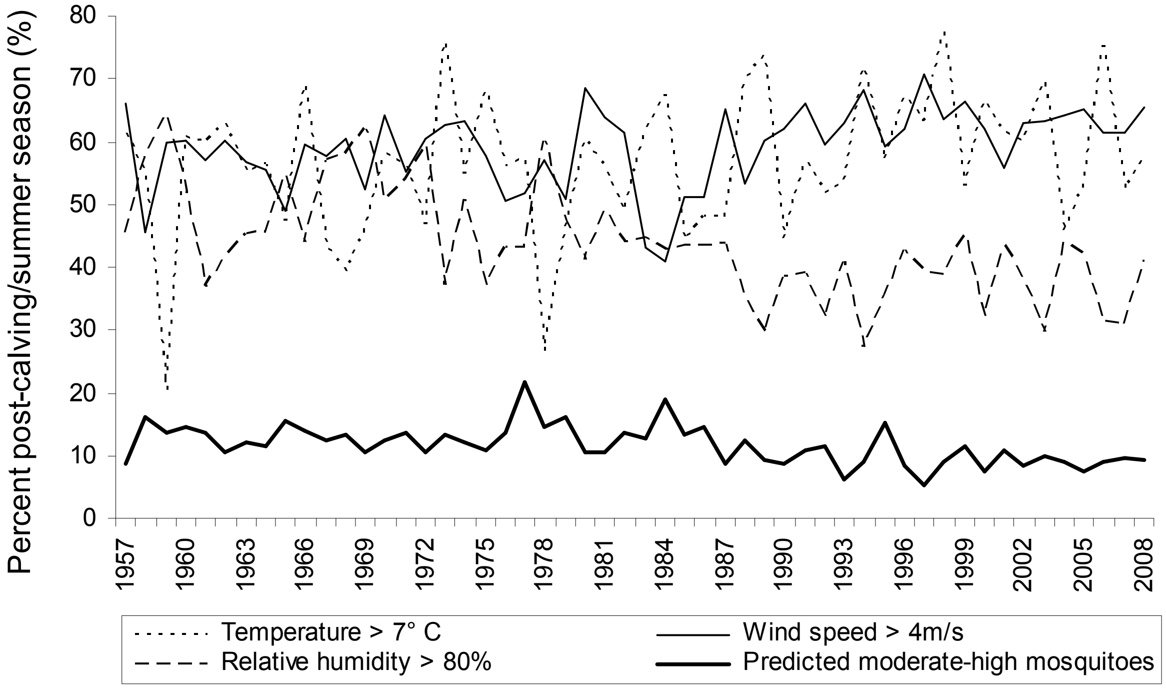
Comparison of insect indices between Lupin/Contwoyto, Daring Lake, and Salmita:

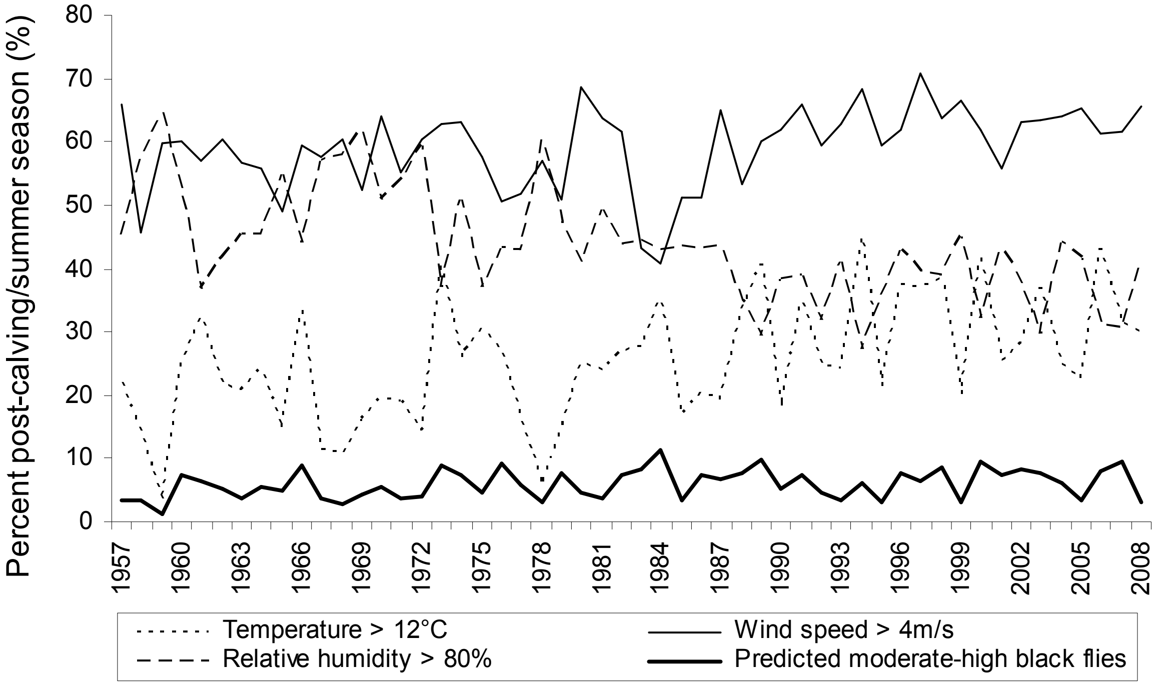




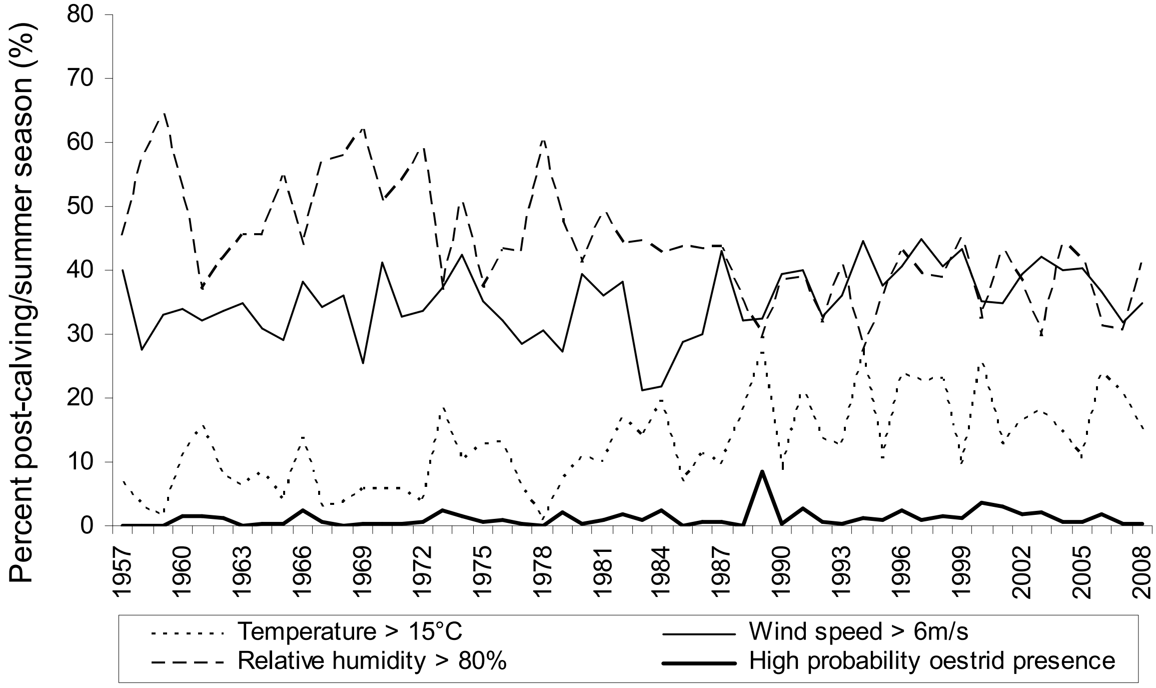


Comparison of weather trends and insect indices at Lupin/Contwoyto:





Percent post-calving/summer season (%)
80
70
60
50
40
30
20
10
0
1957
1960
1963
1966
1969
1972
1975
1978
1981
1984
1987
1990
1993
1996
1999
2002
2005
2008
Temperature > 12°C
Wind speed > 4m/s
Relative humidity > 80%
Predicted moderate-high black flies



Percent post-calving/summer season (%)
80
70
60
50
40
30
20
10
0
1957
1960
1963
1966
1969
1972
1975
1978
1981
1984
1987
1990
1993
1996
1999
2002
2005
2008
Temperature > 15°C
Wind speed > 6m/s
Relative humidity > 80%
High probability oestrid presence

Appendix D. Coefficients (β) and 95% confidence intervals (CI) from the top and second-ranked multinomial logistic regression models (mlogit; Table 12) of relative dominance of behaviour types within caribou groups on the Bathurst caribou post-calving/summer range, Northwest Territories and Nunavut, Canada. The top 2 models differed in AIC$_c$ scores by 0.19. Coefficients for easting and northing were scaled by a factor of 1000; group size was scaled by a factor of 100.

Top-ranked mlogit model

Model coefficients for dominance of all other behaviours relative to feeding within caribou groups:

	Lying			Standing			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	−1.500	−3.454	0.453	0.469	−0.489	1.427	−0.384	−1.526	0.758	−0.273	−2.055	1.510	1.398	0.236	2.561
Black fl.															
no	−0.313	−0.859	0.233	−0.261	−0.823	0.300	−0.527	−1.071	0.017	−1.122	−2.662	0.419	−0.664	−3.277	1.950
low	−0.204	−0.764	0.356	0.177	−0.515	0.869	0.102	−0.460	0.663	0.526	−0.521	1.574	−0.816	−1.823	0.191
mod.	0.377	−0.389	1.142	0.696	0.149	1.244	0.455	−0.115	1.025	0.346	−0.611	1.303	0.322	−1.086	1.730
high	0.140	−0.417	0.697	−0.612	−1.266	0.042	−0.030	−0.672	0.612	0.249	−0.784	1.282	1.158	−0.144	2.459
Time															
morn.	−0.154	−0.530	0.222	−0.446	−1.017	0.125	−0.028	−0.399	0.343	−0.234	−0.831	0.362	0.805	−0.006	1.616
aft.	−0.325	−0.863	0.213	0.752	0.302	1.203	−0.177	−0.638	0.283	−0.018	−0.627	0.592	0.911	0.185	1.636
night	0.479	0.069	0.890	−0.307	−0.893	0.279	0.205	−0.198	0.608	0.252	−0.489	0.993	−1.716	−2.896	−0.535
Year															
2007	−0.302	−0.821	0.218	−0.689	−1.025	−0.354	0.238	−0.354	0.831	0.629	−0.500	1.758	0.257	−0.766	1.281
2008	0.085	−0.439	0.609	0.205	−0.322	0.732	0.084	−0.477	0.645	0.998	0.168	1.827	0.019	−1.324	1.362
2009	0.217	−0.470	0.904	0.484	−0.091	1.060	−0.323	−1.012	0.366	−1.627	−2.766	−0.487	−0.276	−1.500	0.947
Gdd	0.003	−0.003	0.010	0.002	−0.003	0.008	−0.007	−0.014	<0.001	−0.007	−0.017	0.004	−0.001	−0.012	0.010
Easting	0.005	−0.002	0.013	−0.003	−0.011	0.004	−0.003	−0.012	0.006	−0.010	−0.024	0.003	−0.009	−0.027	0.008
Northing	0.007	−0.003	0.017	0.004	−0.005	0.012	−0.010	−0.018	−0.002	−0.007	−0.016	0.001	−0.038	−0.070	−0.006
Grp-size	0.034	−0.050	0.118	−0.018	−0.179	0.143	−0.039	−0.105	0.027	−0.048	−0.216	0.119	0.020	−0.071	0.110

Model coefficients for dominance of all other behaviours relative to lying within caribou groups:

	Feeding			Standing			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	1.500	−0.453	3.454	1.970	−0.044	3.983	1.116	−0.306	2.539	1.228	−1.232	3.688	2.899	1.107	4.691
Black fl.															
no	0.313	−0.233	0.859	0.051	−0.783	0.886	−0.214	−0.890	0.462	−0.809	−2.286	0.668	−0.351	−3.126	2.424
low	0.204	−0.356	0.764	0.381	−0.357	1.119	0.305	−0.277	0.888	0.73	−0.281	1.742	−0.612	−1.756	0.531
mod.	−0.377	−1.142	0.389	0.320	−0.524	1.163	0.078	−0.756	0.913	−0.031	−1.156	1.094	−0.055	−1.586	1.477
high	−0.140	−0.697	0.417	−0.752	−1.460	−0.043	−0.169	−0.695	0.356	0.110	−0.852	1.071	1.018	−0.306	2.341
Time															
morn.	0.154	−0.222	0.530	−0.291	−0.904	0.321	0.126	−0.347	0.599	−0.080	−0.731	0.570	0.959	0.085	1.833
aft.	0.325	−0.213	0.863	1.077	0.443	1.711	0.148	−0.463	0.759	0.307	−0.443	1.058	1.236	0.356	2.115
night	−0.479	−0.890	−0.069	−0.786	−1.312	−0.260	−0.274	−0.733	0.185	−0.227	−0.977	0.522	−2.195	−3.455	−0.935
Year															
2007	0.302	−0.218	0.821	−0.388	−0.950	0.175	0.540	−0.204	1.284	0.931	−0.222	2.084	0.559	−0.552	1.669
2008	−0.085	−0.609	0.439	0.120	−0.533	0.774	>−0.001	−0.595	0.594	0.913	−0.028	1.854	−0.066	−1.422	1.291
2009	−0.217	−0.904	0.470	0.267	−0.595	1.130	−0.540	−1.406	0.326	−1.844	−3.114	−0.574	−0.493	−1.797	0.811
Gdd	−0.003	−0.010	0.003	−0.001	−0.010	0.008	−0.011	−0.020	−0.001	−0.010	−0.022	0.002	−0.005	−0.018	0.009
Easting	−0.005	−0.013	0.002	−0.008	−0.019	0.002	−0.008	−0.019	0.003	−0.015	−0.030	−0.001	−0.015	−0.031	0.002
Northing	−0.007	−0.017	0.003	−0.003	−0.015	0.009	−0.017	−0.030	−0.004	−0.014	−0.026	−0.002	−0.044	−0.078	−0.010
Grp-size	−0.034	−0.118	0.050	−0.052	−0.211	0.108	−0.073	−0.157	0.011	−0.082	−0.243	0.078	−0.014	−0.115	0.086

Model coefficients for dominance of all other behaviours relative to standing within caribou groups:

	Feeding			Lying			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	−0.469	−1.427	0.489	−1.097	−3.983	0.044	−0.853	−2.201	0.495	−0.742	−2.783	1.300	0.929	−0.567	2.425
Black fl.															
no	0.261	−0.300	0.823	−0.051	−0.886	0.783	−0.266	−0.950	0.419	−0.860	−2.310	0.590	−0.402	−3.035	2.230
low	−0.177	−0.869	0.515	−0.381	−1.119	0.357	−0.075	−0.777	0.626	0.349	−0.675	1.374	−0.993	−2.122	0.135
mod.	−0.696	−1.244	−0.149	−0.320	−1.163	0.524	−0.241	−0.925	0.442	−0.350	−1.320	0.619	−0.374	−1.885	1.137
high	0.612	−0.042	1.266	0.752	0.043	1.460	0.582	−0.099	1.264	0.861	−0.225	1.947	1.770	0.299	3.240
Time															
morn.	0.446	−0.125	1.017	0.291	−0.321	0.904	0.418	−0.095	0.930	0.211	−0.471	0.894	1.251	0.352	2.150
aft.	−0.752	−1.203	−0.302	−1.077	−1.711	−0.443	−0.930	−1.450	−0.409	−0.770	−1.352	−0.188	0.158	−0.613	0.930
night	0.306	−0.279	0.893	0.786	0.260	1.312	0.512	−0.168	1.191	0.559	−0.151	1.269	−1.409	−2.707	−0.110
Year															
2007	0.689	0.354	1.025	0.388	−0.175	0.950	0.928	0.301	1.555	1.318	0.178	2.459	0.947	−0.116	2.009
2008	−0.205	−0.732	0.322	−0.120	−0.774	0.533	−0.121	−0.659	0.418	0.793	−0.078	1.664	−0.186	−1.497	1.125
2009	−0.484	−1.060	0.091	−0.267	−1.130	0.595	−0.807	−1.574	−0.040	−2.111	−3.329	−0.894	−0.761	−2.035	0.514
Gdd	−0.002	−0.008	0.003	0.001	−0.008	0.010	−0.010	−0.018	−0.001	−0.009	−0.021	0.003	−0.004	−0.015	0.008
Easting	0.003	−0.004	0.011	0.008	−0.002	0.019	0.000	−0.010	0.011	−0.007	−0.023	0.009	−0.006	−0.024	0.011
Northing	−0.004	−0.012	0.005	0.003	−0.009	0.015	−0.014	−0.022	−0.005	−0.011	−0.022	<0.001	−0.041	−0.074	−0.009
Grp-size	0.018	−0.143	0.179	0.052	−0.108	0.211	−0.021	−0.189	0.146	−0.031	−0.256	0.194	0.037	−0.138	0.213

Model coefficients for dominance of all other behaviours relative to walking within caribou groups:

	Feeding			Lying			Standing			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	0.384	−0.758	1.526	−1.116	−2.539	0.306	0.853	−0.495	2.201	0.112	−1.827	2.050	1.783	0.687	2.878
Black fl.															
no	0.527	−0.017	1.071	0.214	−0.462	0.890	0.266	−0.419	0.950	−0.595	−2.107	0.918	−0.137	−2.856	2.583
low	−0.102	−0.663	0.460	−0.305	−0.888	0.277	0.075	−0.626	0.777	0.425	−0.618	1.467	−0.918	−1.981	0.145
mod.	−0.455	−1.025	0.115	−0.078	−0.913	0.756	0.241	−0.442	0.925	−0.109	−0.937	0.719	−0.133	−1.545	1.280
high	0.030	−0.612	0.672	0.169	−0.356	0.695	−0.582	−1.264	0.099	0.279	−0.568	1.126	1.187	−0.031	2.405
Time															
morn.	0.028	−0.343	0.399	−0.126	−0.599	0.347	−0.418	−0.930	0.095	−0.206	−0.799	0.386	0.833	−0.026	1.692
aft.	0.177	−0.283	0.638	−0.148	−0.759	0.463	0.930	0.409	1.450	0.160	−0.503	0.822	1.088	0.310	1.866
night	−0.205	−0.608	0.198	0.274	−0.185	0.733	−0.512	−1.191	0.168	0.047	−0.776	0.870	−1.921	−3.144	−0.697
Year															
2007	−0.238	−0.831	0.354	−0.540	−1.284	0.204	−0.928	−1.555	−0.301	0.391	−0.669	1.450	0.019	−1.119	1.156
2008	−0.084	−0.645	0.477	<0.001	−0.594	0.595	0.121	−0.418	0.659	0.913	0.064	1.763	−0.065	−1.395	1.264
2009	0.323	−0.366	1.012	0.540	−0.326	1.406	0.807	0.040	1.574	−1.304	−2.371	−0.236	0.047	−1.185	1.278
Gdd	0.007	>−0.00	0.014	0.011	0.001	0.020	0.010	0.001	0.018	0.001	−0.008	0.009	0.006	−0.008	0.020
Easting	0.003	−0.006	0.012	0.008	−0.003	0.019	0.000	−0.011	0.010	−0.007	−0.018	0.003	−0.007	−0.023	0.009
Northing	0.010	0.002	0.018	0.017	0.004	0.030	0.014	0.005	0.022	0.003	−0.007	0.012	−0.028	−0.060	0.005
Grp-size	0.039	−0.027	0.105	0.073	−0.011	0.157	0.021	−0.146	0.189	−0.010	−0.187	0.168	0.059	−0.047	0.164

Model coefficients for dominance of all other behaviours relative to running within caribou groups:

	Feeding			Lying			Standing			Walking			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	0.273	−1.510	2.055	−1.228	−3.688	1.232	0.742	−1.300	2.783	−0.112	−2.050	1.827	1.671	0.186	3.156
Black fl.															
no	1.122	−0.419	2.662	0.809	−0.668	2.286	0.860	−0.590	2.310	0.595	−0.918	2.107	0.458	−2.387	3.304
low	−0.526	−1.574	0.521	−0.730	−1.742	0.281	−0.349	−1.374	0.675	−0.425	−1.467	0.618	−1.343	−2.779	0.094
mod.	−0.346	−1.303	0.611	0.031	−1.094	1.156	0.350	−0.619	1.320	0.109	−0.719	0.937	−0.024	−1.516	1.469
high	−0.249	−1.282	0.784	−0.110	−1.071	0.852	−0.861	−1.947	0.225	−0.279	−1.126	0.568	0.908	−0.529	2.345
Time															
morn.	0.234	−0.362	0.831	0.080	−0.570	0.731	−0.211	−0.894	0.471	0.206	−0.386	0.799	1.039	0.128	1.950
aft.	0.018	−0.592	0.627	−0.307	−1.058	0.443	0.770	0.188	1.352	−0.160	−0.822	0.503	0.928	0.049	1.808
night	−0.252	−0.993	0.489	0.227	−0.522	0.977	−0.559	−1.269	0.151	−0.047	−0.870	0.776	−1.968	−3.274	−0.661
Year															
2007	−0.629	−1.758	0.500	−0.931	−2.084	0.222	−1.318	−2.459	−0.178	−0.391	−1.450	0.669	−0.372	−2.025	1.282
2008	−0.998	−1.827	−0.168	−0.913	−1.854	0.028	−0.793	−1.664	0.078	−0.913	−1.763	−0.064	−0.979	−2.524	0.566
2009	1.627	0.487	2.766	1.844	0.574	3.114	2.111	0.894	3.329	1.304	0.236	2.371	1.350	−0.138	2.839
Gdd	0.007	−0.004	0.017	0.010	−0.002	0.022	0.009	−0.003	0.021	−0.001	−0.009	0.008	0.006	−0.009	0.020
Easting	0.010	−0.003	0.024	0.015	0.001	0.030	0.007	−0.009	0.023	0.007	−0.003	0.018	0.001	−0.016	0.017
Northing	0.007	−0.001	0.016	0.014	0.002	0.026	0.011	0.000	0.022	−0.003	−0.012	0.007	−0.030	−0.063	0.002
Grp-size	0.048	−0.119	0.216	0.082	−0.078	0.243	0.031	−0.194	0.256	0.010	−0.168	0.187	0.068	−0.116	0.252

Model coefficients for dominance of all other behaviours relative to insect avoidance within caribou groups:

	Feeding			Lying			Standing			Walking			Running		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	−1.398	−2.561	−0.236	−2.899	−4.691	−1.107	−0.929	−2.425	0.567	−1.783	−2.878	−0.687	−1.671	−3.156	−0.186
Black fl.															
no	0.664	−1.950	3.277	0.351	−2.424	3.126	0.402	−2.230	3.035	0.137	−2.583	2.856	−0.458	−3.304	2.387
low	0.816	−0.191	1.823	0.612	−0.531	1.756	0.993	−0.135	2.122	0.918	−0.145	1.981	1.343	−0.094	2.779
mod.	−0.322	−1.730	1.086	0.055	−1.477	1.586	0.374	−1.137	1.885	0.133	−1.280	1.545	0.024	−1.469	1.516
high	−1.158	−2.459	0.144	−1.018	−2.341	0.306	−1.770	−3.240	−0.299	−1.187	−2.405	0.031	−0.908	−2.345	0.529
Time															
morn.	−0.805	−1.616	0.006	−0.959	−1.833	−0.085	−1.251	−2.150	−0.352	−0.833	−1.692	0.026	−1.039	−1.950	−0.128
aft.	−0.911	−1.636	−0.185	−1.236	−2.115	−0.356	−0.158	−0.930	0.613	−1.088	−1.866	−0.310	−0.928	−1.808	−9.049
night	1.716	0.535	2.896	2.195	0.935	3.455	1.409	0.110	2.707	1.921	0.697	3.144	1.968	0.661	3.274
Year															
2007	−0.257	−1.281	0.766	−0.559	−1.669	0.552	−0.947	−2.009	0.116	−0.019	−1.156	1.119	0.372	−1.282	2.025
2008	−0.019	−1.362	1.324	0.066	−1.291	1.422	0.186	−1.125	1.497	0.065	−1.264	1.395	0.979	−0.566	2.524
2009	0.276	−0.947	1.500	0.493	−0.811	1.797	0.761	−0.514	2.035	−0.047	−1.278	1.185	−1.350	−2.839	9.138
Gdd	0.001	−0.010	0.012	0.005	−0.009	0.018	0.004	−0.008	0.015	−0.006	−0.020	0.008	−0.006	−0.020	9.009
Easting	0.009	−0.008	0.027	0.015	−0.002	0.031	0.006	−0.011	0.024	0.007	−0.009	0.023	−0.001	−0.017	0.016
Northing	0.038	0.006	0.070	0.044	0.010	0.078	0.041	0.009	0.074	0.028	−0.005	0.060	0.030	−0.002	0.063
Grp-size	−0.020	−0.110	0.071	0.014	−0.086	0.115	−0.037	−0.213	0.138	−0.059	−0.164	0.047	−0.068	−0.252	0.116

Second-ranked mlogit model

Model coefficients for dominance of all other behaviours relative to feeding within caribou groups:

	Lying			Standing			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	−1.360	−3.106	0.386	0.394	−0.608	1.396	−0.342	−1.524	0.840	−0.238	−1.943	1.466	1.362	−0.143	2.866
Mosquito															
no	−0.138	−0.817	0.541	−0.027	−0.800	0.745	−0.808	−1.518	−0.099	−0.258	−1.220	0.704	−1.653	−2.960	−0.346
low	0.213	−0.473	0.899	0.731	0.073	1.390	0.533	−0.005	1.071	0.691	−0.108	1.490	0.105	−1.137	1.347
mod.	0.238	−0.385	0.861	−0.248	−0.934	0.437	−0.008	−0.537	0.522	−0.522	−1.382	0.338	0.499	−0.366	1.365
high	−0.313	−0.987	0.360	−0.455	−1.437	0.526	0.283	−0.571	1.137	0.089	−1.135	1.313	1.049	−1.192	3.289
Time															
morn.	−0.207	−0.621	0.207	−0.530	−1.101	0.040	0.035	−0.361	0.430	−0.141	−0.796	0.514	0.746	−0.035	1.527
aft.	−0.272	−0.757	0.214	0.902	0.495	1.309	0.011	−0.413	0.435	0.094	−0.472	0.659	1.118	0.188	2.048
night	0.479	0.035	0.922	−0.372	−0.896	0.153	−0.045	−0.512	0.421	0.047	−0.659	0.753	−1.864	−2.977	−0.752
Year															
2007	−0.261	−0.645	0.122	−0.819	−1.252	−0.386	0.104	−0.382	0.590	0.417	−0.659	1.494	0.079	−1.190	1.349
2008	0.152	−0.376	0.680	0.148	−0.423	0.720	0.157	−0.380	0.694	1.101	0.283	1.918	0.477	−0.716	1.670
2009	0.109	−0.545	0.763	0.671	−0.022	1.364	−0.261	−0.851	0.329	−1.518	−2.663	−0.373	−0.556	−1.788	0.675
Gdd	0.002	−0.003	0.008	0.004	−0.003	0.011	−0.005	−0.012	0.002	−0.007	−0.017	0.003	0.002	−0.012	0.016
Easting	0.005	−0.003	0.013	0.003	−0.005	0.011	−0.001	−0.009	0.007	−0.008	−0.021	0.004	−0.014	−0.033	0.004
Northing	0.006	−0.003	0.014	0.005	−0.003	0.012	−0.012	−0.019	−0.004	−0.011	−0.019	−0.002	−0.035	−0.057	−0.013
Grp-size	0.029	−0.055	0.113	−0.005	−0.154	0.144	−0.038	−0.109	0.032	−0.054	−0.237	0.129	0.026	−0.081	0.133

Model coefficients for dominance of all other behaviours relative to lying within caribou groups:

	Feeding			Standing			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	1.360	−0.386	3.106	1.754	0.018	3.490	1.019	−0.024	2.061	1.122	−1.082	3.326	2.722	0.866	4.578
Mosquito															
no	0.138	−0.541	0.817	0.111	−0.771	0.992	−0.670	−1.631	0.290	−0.120	−1.123	0.883	−1.515	−2.906	−0.125
low	−0.213	−0.899	0.473	0.518	−0.466	1.502	0.320	−0.487	1.126	0.478	−0.380	1.336	−0.108	−1.579	1.363
mod.	−0.238	−0.861	0.385	−0.486	−1.346	0.373	−0.246	−1.066	0.575	−0.760	−1.660	0.140	0.261	−0.867	1.390
high	0.313	−0.360	0.987	−0.142	−1.135	0.851	0.596	−0.270	1.463	0.403	−0.946	1.752	1.362	−0.867	3.591
Time															
morn.	0.207	−0.207	0.621	−0.323	−0.957	0.311	0.242	−0.253	0.737	0.066	−0.667	0.799	0.953	0.071	1.836
aft.	0.272	−0.214	0.757	1.174	0.584	1.763	0.282	−0.243	0.807	0.365	−0.272	1.003	1.390	0.317	2.463
night	−0.479	−0.922	−0.035	−0.851	−1.383	−0.318	−0.524	−1.028	−0.020	−0.432	−1.148	0.284	−2.343	−3.517	−1.170
Year															
2007	0.261	−0.122	0.645	−0.558	−1.181	0.065	0.365	−0.238	0.967	0.678	−0.418	1.775	0.341	−0.963	1.645
2008	−0.152	−0.680	0.376	−0.004	−0.761	0.753	0.005	−0.602	0.612	0.949	<0.001	1.897	0.325	−0.950	1.600
2009	−0.109	−0.763	0.545	0.562	−0.447	1.570	−0.370	−1.212	0.472	−1.627	−2.959	−0.295	−0.665	−2.026	0.695
Gdd	−0.002	−0.008	0.003	0.002	−0.006	0.009	−0.008	−0.016	0.001	−0.010	−0.020	0.001	>−0.001	−0.015	0.015
Easting	−0.005	−0.013	0.003	−0.002	−0.013	0.009	−0.006	−0.017	0.005	−0.013	−0.027	<0.001	−0.020	−0.039	<0.001
Northing	−0.006	−0.014	0.003	−0.001	−0.011	0.009	−0.017	−0.028	−0.006	−0.016	−0.028	−0.005	−0.041	−0.065	−0.017
Grp-size	−0.029	−0.113	0.055	−0.034	−0.182	0.114	−0.068	−0.157	0.022	−0.084	−0.253	0.085	−0.003	−0.119	0.112

Model coefficients for dominance of all other behaviours relative to standing within caribou groups:

	Feeding			Lying			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	−0.394	−1.396	0.608	−1.754	−3.490	−0.018	−0.735	−2.062	0.591	−0.632	−2.671	1.407	0.968	−0.903	2.839
Mosquito															
no	0.027	−0.745	0.800	−0.111	−0.992	0.771	−0.781	−1.630	0.068	−0.231	−1.331	0.870	−1.626	−2.988	−0.264
low	−0.731	−1.390	−0.073	−0.518	−1.502	0.466	−0.198	−0.863	0.467	−0.040	−0.973	0.892	−0.626	−2.015	0.763
mod.	0.248	−0.437	0.934	0.486	−0.373	1.346	0.241	−0.466	0.948	−0.274	−1.266	0.719	0.748	−0.229	1.724
high	0.455	−0.526	1.437	0.142	−0.851	1.135	0.739	−0.158	1.635	0.545	−0.758	1.847	1.504	−0.758	3.767
Time															
morn.	0.530	−0.040	1.101	0.323	−0.311	0.957	0.565	0.057	1.072	0.389	−0.320	1.099	1.277	0.396	2.157
aft.	−0.902	−1.309	−0.495	−1.174	−1.763	−0.584	−0.891	−1.358	−0.424	−0.808	−1.376	−0.240	0.216	−0.822	1.255
night	0.372	−0.153	0.896	0.851	0.318	1.383	0.326	−0.339	0.992	0.419	−0.258	1.095	−1.493	−2.744	−0.242
Year															
2007	0.819	0.386	1.252	0.558	−0.065	1.181	0.923	0.268	1.577	1.236	−0.039	2.512	0.899	−0.440	2.237
2008	−0.148	−0.720	0.423	0.004	−0.753	0.761	0.009	−0.570	0.587	0.952	0.030	1.875	0.328	−0.860	1.517
2009	−0.671	−1.364	0.022	−0.562	−1.570	0.447	−0.931	−1.702	−0.161	−2.189	−3.516	−0.861	−1.227	−2.583	0.129
Gdd	−0.004	−0.011	0.003	−0.002	−0.009	0.006	−0.009	−0.017	−0.001	−0.011	−0.023	0.001	−0.002	−0.016	0.013
Easting	−0.003	−0.011	0.005	0.002	−0.009	0.013	−0.004	−0.013	0.005	−0.012	−0.026	0.003	−0.018	−0.037	0.002
Northing	−0.005	−0.012	0.003	0.001	−0.009	0.011	−0.016	−0.024	−0.008	−0.015	−0.027	−0.004	−0.040	−0.062	−0.018
Grp-size	0.005	−0.144	0.154	0.034	−0.114	0.182	−0.034	−0.191	0.123	−0.050	−0.283	0.183	0.031	−0.135	0.197

Model coefficients for dominance of all other behaviours relative to walking within caribou groups:

	Feeding			Lying			Standing			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	0.342	−0.840	1.524	−1.019	−2.061	0.024	0.735	−0.591	2.062	0.103	−1.756	1.962	1.703	0.160	3.246
Mosquito															
no	0.808	0.099	1.518	0.670	−0.290	1.631	0.781	−0.068	1.630	0.550	−0.347	1.447	−0.845	−2.226	0.537
low	−0.533	−1.071	0.005	−0.320	−1.126	0.487	0.198	−0.467	0.863	0.158	−0.569	0.885	−0.428	−1.700	0.844
mod.	0.008	−0.522	0.537	0.246	−0.575	1.066	−0.241	−0.948	0.466	−0.514	−1.397	0.369	0.507	−0.304	1.318
high	−0.283	−1.137	0.571	−0.596	−1.463	0.270	−0.739	−1.635	0.158	−0.194	−1.355	0.967	0.766	−1.481	3.012
Time															
morn.	−0.035	−0.430	0.361	−0.242	−0.737	0.253	−0.565	−1.072	−0.057	−0.175	−0.782	0.432	0.712	−0.169	1.593
aft.	−0.011	−0.435	0.413	−0.282	−0.807	0.243	0.891	0.424	1.358	0.083	−0.503	0.669	1.107	0.151	2.064
night	0.045	−0.421	0.512	0.524	0.020	1.028	−0.326	−0.992	0.339	0.092	−0.614	0.798	−1.819	−2.923	−0.716
Year															
2007	−0.104	−0.590	0.382	−0.365	−0.967	0.238	−0.923	−1.577	−0.268	0.314	−0.728	1.355	−0.024	−1.356	1.308
2008	−0.157	−0.694	0.380	−0.005	−0.612	0.602	−0.009	−0.587	0.570	0.944	0.072	1.815	0.320	−0.855	1.495
2009	0.261	−0.329	0.851	0.370	−0.472	1.212	0.931	0.161	1.702	−1.257	−2.363	−0.151	−0.296	−1.540	0.949
Gdd	0.005	−0.002	0.012	0.008	−0.001	0.016	0.009	0.001	0.017	−0.002	−0.011	0.007	0.007	−0.010	0.025
Easting	0.001	−0.007	0.009	0.006	−0.005	0.017	0.004	−0.005	0.013	−0.007	−0.018	0.003	−0.013	−0.033	0.006
Northing	0.012	0.004	0.019	0.017	0.006	0.028	0.016	0.008	0.024	0.001	−0.010	0.012	−0.024	−0.047	<0.001
Grp-size	0.038	−0.032	0.109	0.068	−0.022	0.157	0.034	−0.123	0.191	−0.016	−0.211	0.179	0.064	−0.053	0.182

Model coefficients for dominance of all other behaviours relative to running within caribou groups:

	Feeding			Lying			Standing			Walking			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	0.238	−1.466	1.943	−1.122	−3.326	1.082	0.632	−1.407	2.671	−0.103	−1.962	1.756	1.600	−0.196	3.395
Mosquito															
no	0.258	−0.704	1.220	0.120	−0.883	1.123	0.231	−0.870	1.331	−0.550	−1.447	0.347	−1.395	−3.014	0.224
low	−0.691	−1.490	0.108	−0.478	−1.336	0.380	0.040	−0.892	0.973	−0.158	−0.885	0.569	−0.586	−1.880	0.708
mod.	0.522	−0.338	1.382	0.760	−0.140	1.660	0.274	−0.719	1.266	0.514	−0.369	1.397	1.021	−0.070	2.112
high	−0.089	−1.313	1.135	−0.403	−1.752	0.946	−0.545	−1.847	0.758	0.194	−0.967	1.355	0.960	−1.545	3.464
Time															
morn.	0.141	−0.514	0.796	−0.066	−0.799	0.667	−0.389	−1.099	0.320	0.175	−0.432	0.782	0.887	−0.072	1.846
aft.	−0.094	−0.659	0.472	−0.365	−1.003	0.272	0.808	0.240	1.376	−0.083	−0.669	0.503	1.024	−0.029	2.078
night	−0.047	−0.753	0.659	0.432	−0.284	1.148	−0.419	−1.095	0.258	−0.092	−0.798	0.614	−1.911	−3.118	−0.705
Year															
2007	−0.417	−1.494	0.659	−0.678	−1.775	0.418	−1.236	−2.512	0.039	−0.314	−1.355	0.728	−0.338	−2.194	1.518
2008	−1.101	−1.918	−0.283	−0.949	−1.897	−0.001	−0.952	−1.875	−0.030	−0.944	−1.815	−0.072	−0.624	−2.006	0.759
2009	1.518	0.373	2.663	1.627	0.295	2.959	2.189	0.861	3.516	1.257	0.151	2.363	0.962	−0.618	2.542
Gdd	0.007	−0.003	0.017	0.010	−0.001	0.020	0.011	−0.001	0.023	0.002	−0.007	0.011	0.009	−0.009	0.027
Easting	0.008	−0.004	0.021	0.013	<0.001	0.027	0.012	−0.003	0.026	0.007	−0.003	0.018	−0.006	−0.024	0.012
Northing	0.011	0.002	0.019	0.016	0.005	0.028	0.015	0.004	0.027	−0.001	−0.012	0.010	−0.024	−0.047	−0.001
Grp-size	0.054	−0.129	0.237	0.084	−0.085	0.253	0.050	−0.183	0.283	0.016	−0.179	0.211	0.080	−0.121	0.282

Model coefficients for dominance of all other behaviours relative to insect avoidance within caribou groups:

	Feeding			Lying			Standing			Walking			Running		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Oestrid	−1.362	−2.866	0.143	−2.722	−4.578	−0.866	−0.968	−2.839	0.903	−1.703	−3.246	−0.160	−1.600	−3.395	0.196
Mosquito															
no	1.653	0.346	2.960	1.515	0.125	2.906	1.626	0.264	2.988	0.845	−0.537	2.226	1.395	−0.224	3.014
low	−0.105	−1.347	1.137	0.108	−1.363	1.579	0.626	−0.763	2.015	0.428	−0.844	1.700	0.586	−0.708	1.880
mod.	−0.499	−1.365	0.366	−0.261	−1.390	0.867	−0.748	−1.724	0.229	−0.507	−1.318	0.304	−1.021	−2.112	0.070
high	−1.049	−3.289	1.192	−1.362	−3.591	0.867	−1.504	−3.767	0.758	−0.766	−3.012	1.481	−0.960	−3.464	1.545
Time															
morn.	−0.746	−1.527	0.035	−0.953	−1.836	−0.071	−1.277	−2.157	−0.396	−0.507	−1.318	0.304	−0.887	−1.846	0.072
aft.	−1.118	−2.048	−0.188	−1.390	−2.463	−0.317	−0.216	−1.255	0.822	−1.107	−2.064	−0.151	−1.024	−2.078	0.029
night	1.864	0.752	2.977	2.343	1.170	3.517	1.493	0.242	2.744	1.819	0.716	2.923	1.911	0.705	3.118
Year															
2007	−0.079	−1.349	1.190	−0.341	−1.645	0.963	−0.899	−2.237	0.440	0.024	−1.308	1.356	0.338	−1.518	2.194
2008	−0.477	−1.670	0.716	−0.325	−1.600	0.950	−0.328	−1.517	0.860	−0.320	−1.495	0.855	0.624	−0.759	2.006
2009	0.556	−0.675	1.788	0.665	−0.695	2.026	1.227	−0.129	2.583	0.296	−0.949	1.540	−0.962	−2.542	0.618
Gdd	−0.002	−0.016	0.012	<0.001	−0.015	0.015	0.002	−0.013	0.016	−0.007	−0.025	0.010	−0.009	−0.027	0.009
Easting	0.014	−0.004	0.033	0.020	<0.001	0.039	0.018	−0.002	0.037	0.013	−0.006	0.033	0.006	−0.012	0.024
Northing	0.035	0.013	0.057	0.041	0.017	0.065	0.040	0.018	0.062	0.024	<0.001	0.047	0.024	0.001	0.047
Grp-size	−0.026	−0.133	0.081	0.003	−0.112	0.119	−0.031	−0.197	0.135	−0.064	−0.182	0.053	−0.080	−0.282	0.121

Appendix E. Coefficients (β) and 95% confidence intervals (CI) from the top and second-ranked fractional multinomial logistic regression models (fmlogit; Table 13) representing time allocation by focal individual caribou observed on the Bathurst post-calving/summer range, Northwest Territories and Nunavut, Canada. The top 2 models differed in AIC_c scores by 0.90.

Top-ranked fmlogit model

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to feeding:

	Lying			Standing			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Black fl.															
no	0.089	−0.321	0.499	0.003	−0.442	0.448	−0.374	−0.654	−0.093	−1.272	−2.666	0.123	−1.603	−2.390	−0.816
low	0.362	−0.186	0.911	0.024	−0.411	0.458	−0.081	−0.567	0.406	0.089	−0.844	1.023	−0.447	−1.010	0.115
mod.	−0.045	−0.853	0.764	−0.081	−0.602	0.441	0.439	−0.062	0.940	0.389	−0.442	1.220	0.991	0.414	1.568
high	−0.407	−0.971	0.158	0.054	−0.354	0.461	0.015	−0.378	0.408	0.794	−0.304	1.891	1.059	0.312	1.807
Oestrid	−1.077	−2.650	0.497	1.352	0.721	1.984	0.019	−0.741	0.779	0.002	−1.512	1.516	1.527	0.550	2.503
Duration	0.002	0.001	0.003	<0.001	>−0.001	0.001	−0.002	−0.002	−0.001	−0.001	−0.003	<0.001	0.001	<0.001	0.001

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to lying:

	Feeding			Standing			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Black fl.															
no	−0.089	−0.499	0.321	−0.086	−0.757	0.585	−0.463	−0.875	−0.051	−1.361	−2.834	0.112	−1.692	−2.645	−0.739
low	−0.362	−0.911	0.186	−0.339	−1.034	0.357	−0.443	−1.152	0.266	−0.273	−1.366	0.819	−0.810	−1.532	−0.088
mod.	0.045	−0.763	0.853	−0.036	−0.882	0.810	0.484	−0.391	1.358	0.434	−0.769	1.636	1.035	0.185	1.885
high	0.407	−0.158	0.971	0.461	−0.237	1.158	0.422	−0.214	1.058	1.201	−0.067	2.468	1.466	0.460	2.472
Oestrid	1.077	−0.497	2.650	2.429	0.985	3.872	1.096	−0.570	2.761	1.078	−1.148	3.304	2.603	0.921	4.286
Duration	−0.002	−0.003	−0.001	−0.002	−0.002	0.001	−0.004	−0.004	−0.003	−0.003	−0.005	−0.002	−0.001	−0.002	−0.001

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to standing:

	Feeding			Lying			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Black fl.															
no	−0.003	−0.448	0.442	0.086	−0.585	0.757	−0.377	−0.915	0.161	−1.275	−2.712	0.162	−1.606	−2.188	−1.024
low	−0.024	−0.458	0.411	0.339	−0.357	1.034	−0.104	−0.685	0.477	0.065	−0.943	1.074	−0.470	−1.051	0.109
mod.	0.081	−0.441	0.602	0.036	−0.810	0.882	0.520	−0.005	1.044	0.470	−0.317	1.256	1.071	0.556	1.587
high	−0.054	−0.461	0.354	−0.461	−1.158	0.236	−0.039	−0.490	0.413	0.740	−0.265	1.744	1.005	0.268	1.743
Oestrid	−1.352	−1.984	−0.721	−2.429	−3.872	−0.985	−1.333	−2.171	−0.495	−1.350	−2.964	0.263	0.175	−0.912	1.262
Duration	>−0.001	−0.001	<0.001	0.002	0.001	0.002	−0.002	−0.003	−0.001	−0.002	−0.004	−0.001	<0.001	>−0.00	0.001

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to walking:

	Feeding			Lying			Standing			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Black fl.															
no	0.374	0.093	0.654	0.463	0.051	0.875	0.377	−0.161	0.915	−0.898	−2.274	0.478	−1.229	−2.079	−0.379
low	0.081	−0.406	0.567	0.443	−0.266	1.152	0.104	−0.477	0.685	0.170	−0.873	1.212	−0.367	−1.051	0.317
mod.	−0.439	−0.940	0.062	−0.484	−1.358	0.391	−0.520	−1.044	0.005	−0.050	−0.876	0.776	0.552	−0.009	1.113
high	−0.015	−0.408	0.378	−0.422	−1.058	0.214	0.039	−0.413	0.490	0.779	−0.153	1.710	1.044	0.319	1.770
Oestrid	−0.019	−0.779	0.741	−1.096	−2.761	0.570	1.333	0.495	2.171	−0.017	−1.177	1.142	1.508	0.671	2.344
Duration	0.002	0.001	0.002	0.004	0.003	0.004	0.002	0.001	0.003	<0.001	−0.002	0.002	0.002	0.002	0.003

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to running:

	Feeding			Lying			Standing			Walking			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Black fl.															
no	1.272	−0.123	2.666	1.361	−0.112	2.834	1.275	−0.162	2.712	0.898	−0.478	2.274	−0.331	−1.853	1.191
low	−0.089	−1.023	0.844	0.273	−0.819	1.366	−0.065	−1.074	0.943	−0.170	−1.212	0.873	−0.536	−1.536	0.463
mod.	−0.389	−1.220	0.442	−0.434	−1.636	0.769	−0.470	−1.256	0.317	0.050	−0.776	0.876	0.602	−0.284	1.488
high	−0.794	−1.891	0.304	−1.201	−2.468	0.067	−0.740	−1.744	0.265	−0.779	−1.710	0.153	0.266	−0.887	1.418
Oestrid	−0.002	−1.515	1.512	−1.078	−3.304	1.148	1.351	−0.263	2.964	0.018	−1.142	1.177	1.525	0.325	2.725
Duration	0.001	>−0.00	0.003	0.003	0.002	0.005	0.002	<0.001	0.004	>−0.001	−0.002	0.002	0.002	<0.001	0.004

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to insect avoidance:

	Feeding			Lying			Standing			Walking			Running		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Black fl.															
no	1.603	0.816	2.390	1.692	0.739	2.645	1.606	1.024	2.188	1.229	0.379	2.079	0.331	−1.191	1.853
low	0.447	−0.115	1.010	0.810	0.088	1.532	0.471	−0.109	1.051	0.367	−0.317	1.051	0.536	−0.463	1.536
mod.	−0.991	−1.568	−0.414	−1.035	−1.885	−0.185	−1.071	−1.587	−0.556	−0.552	−1.113	0.009	−0.602	−1.488	0.284
high	−1.059	−1.807	−0.312	−1.466	−2.472	−0.460	−1.005	−1.743	−0.268	−1.044	−1.770	−0.319	−0.266	−1.418	0.887
Oestrid	−1.527	−2.503	−0.550	−2.603	−4.286	−0.921	−0.175	−1.262	0.912	−1.508	−2.344	−0.671	−1.525	−2.725	−0.325
Duration	−0.001	−0.001	−0.001	0.001	0.001	0.002	>−0.001	−0.001	<0.001	−0.002	−0.003	−0.002	−0.002	−0.004	−0.001

Second-ranked fmlogit model

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to feeding:

	Lying			Standing			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Mosquito															
no	0.263	−0.347	0.873	0.032	−0.410	0.474	−0.411	−0.729	−0.093	0.236	−0.761	1.232	−0.327	−1.123	0.469
low	−0.248	−0.855	0.359	0.605	0.195	1.016	0.657	0.250	1.064	0.748	0.107	1.388	1.218	0.675	1.760
mod.	0.046	−0.562	0.655	−0.178	−0.659	0.303	−0.422	−0.806	−0.038	−0.788	−1.761	0.186	0.042	−0.636	0.719
high	−0.061	−0.814	0.691	−0.459	−1.127	0.209	0.177	−0.461	0.812	−0.196	−1.208	0.817	−0.932	−1.634	−0.230
Oestrid	−0.895	−2.341	0.550	1.208	0.634	1.783	0.128	−0.464	0.720	0.280	−0.883	1.444	1.675	0.745	2.605
Duration	0.002	0.002	0.003	<0.001	>−0.001	0.001	−0.002	−0.002	−0.001	−0.002	−0.004	−0.001	<0.001	>−0.001	0.001

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to lying:

	Feeding			Standing			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Mosquito															
no	−0.263	−0.873	0.347	−0.231	−1.130	0.668	−0.674	−1.288	−0.060	−0.028	−1.366	1.311	−0.590	−1.804	0.623
low	0.248	−0.359	0.855	.0.853	0.100	1.606	0.905	0.280	1.530	0.996	0.135	1.857	1.465	0.733	2.198
mod.	−0.046	−0.655	0.562	−0.225	−1.031	0.581	−0.468	−1.122	0.186	−0.834	−1.894	0.227	−0.005	−0.994	0.985
high	0.061	−0.691	0.814	−0.398	−1.366	0.571	0.237	−0.694	1.168	−0.134	−1.513	1.244	−0.871	−1.890	0.148
Oestrid	0.895	−0.550	2.341	2.104	0.779	3.429	1.024	−0.515	2.562	1.176	−0.899	3.250	2.571	0.921	4.220
Duration	−0.002	−0.003	−0.002	−0.002	−0.003	−0.001	−0.004	−0.005	−0.003	−0.004	−0.006	−0.002	−0.002	−0.002	−0.001

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to standing:

	Feeding			Lying			Walking			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Mosquito															
no	−0.032	−0.474	0.410	0.231	−0.668	1.130	−0.443	−0.989	0.103	0.203	−0.812	1.219	−0.359	−1.060	0.342
low	−0.605	−1.016	−0.195	−0.853	−1.606	−0.100	0.052	−0.497	0.601	0.142	−0.566	0.851	0.612	0.030	1.195
mod.	0.178	−0.303	0.659	0.225	−0.582	1.031	−0.244	−0.761	0.274	−0.609	−1.545	0.326	0.220	−0.558	0.997
high	0.459	−0.209	1.127	0.398	−0.571	1.366	0.635	−0.183	1.453	0.263	−0.997	1.524	−0.473	−1.316	0.370
Oestrid	−1.208	−1.783	−0.634	−2.104	−3.429	−0.779	−1.080	−1.872	−0.288	−0.928	−2.307	0.451	0.467	−0.604	1.538
Duration	>−0.001	−0.001	<0.001	0.002	0.001	0.003	−0.002	−0.003	−0.001	−0.002	−0.004	−0.001	<0.001	−0.001	0.001

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to walking:

	Feeding			Lying			Standing			Running			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Mosquito.															
no	0.411	0.093	0.729	0.674	0.060	1.288	0.443	−0.103	0.989	0.647	−0.336	1.630	0.084	−0.746	0.914
low	−0.657	−1.064	−0.250	−0.905	−1.530	−0.280	−0.052	−0.601	0.497	0.090	−0.553	0.733	0.560	0.049	1.071
mod.	0.422	0.038	0.806	0.468	−0.186	1.122	0.244	−0.274	0.761	−0.366	−1.197	0.466	0.464	−0.296	1.223
high	−0.176	−0.812	0.461	−0.237	−1.168	0.694	−0.635	−1.453	0.183	−0.371	−1.548	0.805	−1.108	−2.000	−0.215
Oestrid	−0.128	−0.720	0.464	−1.024	−2.562	0.515	1.080	0.288	1.872	0.152	−0.818	1.121	1.547	0.680	2.414
Duration	0.002	0.001	0.002	0.004	0.003	0.005	0.002	0.001	0.003	>−0.001	−0.002	0.002	0.002	0.001	0.003

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to running:

	Feeding			Lying			Standing			Walking			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Mosquito															
no	−0.236	−1.232	0.761	0.028	−1.311	1.366	−0.203	−1.219	0.812	−0.647	−1.630	0.336	−0.563	−1.509	0.384
low	−0.748	−1.388	−0.107	−0.996	−1.857	−0.135	−0.142	−0.851	0.566	−0.090	−0.733	0.553	0.470	−0.204	1.144
mod.	0.788	−0.186	1.761	0.834	−0.227	1.894	0.609	−0.326	1.544	0.366	−0.466	1.197	0.829	−0.319	1.977
high	0.196	−0.817	1.208	0.134	−1.244	1.513	−0.263	−1.524	0.997	0.371	−0.805	1.548	−0.736	1.931	0.459
Oestrid	−0.280	−1.444	0.883	−1.176	−3.250	0.899	0.928	−0.451	2.307	−0.152	−1.121	0.818	1.395	0.275	2.516
Duration	0.002	<0.001	0.003	0.004	0.002	0.006	0.002	<0.001	0.004	<0.001	−0.002	0.002	0.002	<0.001	0.004

Model coefficients for change in proportion of time individual caribou allocated to all other behaviours relative to insect avoidance:

	Feeding			Lying			Standing			Walking			Insect avoidance		
	β	95% CI		β	95% CI		β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper		Lower	Upper
Mosquito															
no	0.327	−0.468	1.123	0.590	−0.623	1.804	0.359	−0.342	1.060	−0.084	−0.914	0.746	0.563	−0.384	1.509
low	−1.218	−1.760	−0.675	1.466	−2.198	−0.733	−0.612	−1.195	−0.030	−0.560	−1.071	−0.049	−0.470	−1.144	0.204
mod.	−0.042	−0.719	0.636	0.005	−0.985	0.994	−0.220	−0.998	0.558	−0.463	−1.223	0.296	−0.829	−1.977	0.319
high	0.932	0.230	1.634	0.871	−0.148	1.890	0.473	−0.370	1.316	1.108	0.215	2.000	0.736	−0.459	1.932
Oestrid	−1.675	−2.605	−0.745	−2.571	−4.220	−0.921	−0.467	−1.538	0.604	−1.547	−2.414	−0.680	−1.395	−2.516	−0.275
Duration	>−0.001	−0.001	<0.001	0.002	0.001	0.002	>−0.001	−0.001	0.001	−0.001	−0.003	−0.001	−0.002	−0.004	−0.001

Appendix F. Bathurst caribou diet composition and nutrition as calculated from fecal matter collected during intensive sessions in 2008-2009 on the Bathurst post-calving/summer range, Northwest Territories and Nunavut, Canada.

Relatively little is known about the diet composition of Bathurst caribou during the post-calving/summer season. During 1998-1999, calving and early post-calving (late May – late June) diets were dominated by lichens (Griffith et al. 2001). Nitrogen signatures in antlers, however, suggested a potential increase in the importance of graminoids later in the post-calving/summer season (Griffith et al. 2001). I did not have the resources to conduct a rigorous study of post-calving/summer diet or forage conditions. Instead, I collected caribou fecal samples on an ad hoc basis during intensive sessions in 2008-2009 in order to obtain a rough estimate of Bathurst post-calving/summer diet composition. I collected composite fecal samples at 14 of the 28 sites visited during intensive sessions in 2008, and at 13 of 26 sites in 2009. Composite samples consisted of fecal pellets from 2-20 ($\bar{x} = 6.6 \pm 0.8$ SE) separate pellet groups. I used color and consistency to identify fresh fecal pellet groups for collection. Samples were frozen for transport and later oven-dried at 50° C for 24-48 hr. The Wildlife Habitat and Nutrition Laboratory (Washington State University, Pullman, WA) analyzed samples for diet composition and nutrition indices. Percent diet composition was determined using epidermal fragment cover as the sampling criteria, based on 4 slides and 25 views per slide. Forage class (moss, lichen, *Equisetum* spp., sedge/rush, grass, shrub, forbs) and 28 major forage species were identified. A portion of each composite sample was ground for nutritional analyses on an oven-dry basis. The tables below present a summary, followed by complete reporting of raw results from the diet composition and nutrition analyses. Due to small sample size and the opportunistic nature of data collection, I refrained from performing statistical analyses on these data.

Diet Analysis Summary[*]:

	Moss % ($\bar{x}$ ± SE)	Lichen % ($\bar{x}$ ± SE)	Equisetum % ($\bar{x}$ ± SE)	Sedge/rushes % ($\bar{x}$ ± SE)	Grasses % ($\bar{x}$ ± SE)	Shrubs % ($\bar{x}$ ± SE)	Forbs % ($\bar{x}$ ± SE)
Jul 8-11, 2008 (n=3)	21.6 ± 2.8	32.2 ± 0.6	0 ± 0	10.3 ± 3.5	0.9 ± 0.3	34.9 ± 4.2	0.1 ± 0.1
Jul 21-24, 2008 (n=7)	9.6 ± 1.7	42.6 ± 4.7	0.6 ± 0.3	3.7 ± 1.4	0.6 ± 0.3	36.8 ± 2.0	6.1 ± 2.0
Aug 2-5, 2008 (n=4)	6.0 ± 1.0	50.5 ± 1.7	0.6 ± 0.4	3.4 ± 1.0	0.3 ± 0.3	38.3 ± 1.0	1.0 ± 0.7
Jul 24-27, 2009 (n=7)	11.2 ± 1.5	25.8 ± 3.6	0 ± 0	3.1 ± 0.4	0.3 ± 0.2	57.1 ± 2.6	2.4 ± 1.0
Aug 5-8, 2009 (n=6)	11.3 ± 2.4	34.8 ± 2.9	0.8 ± 0.7	1.4 ± 0.7	0.3 ± 0.1	49.6 ± 1.6	1.8 ± 0.6
2008 (n=14)	11.1 ± 1.9	42.6 ± 2.9	0.5 ± 0.2	5.1 ± 1.2	0.6 ± 0.2	36.8 ± 1.3	3.4 ± 1.3
2009 (n=13)	11.4 ± 1.3	30.0 ± 2.6	0.4 ± 0.3	2.1 ± 0.4	0.3 ± 0.1	53.7 ± 1.9	2.1 ± 0.6
Averaged diets (n=28)[**]	11.0 ± 1.1	37.0 ± 2.3	0.5 ± 0.2	3.8 ± 0.7	0.5 ± 0.1	44.6 ± 1.9	2.7 ± 0.7

[*] n is number of composite samples.

[**] Includes an additional composite sample collected from Daring Lake area on Aug 28, 2009.

Nutrition Analysis Summary[*]:

	% Oven dry matter (ODM) ($\bar{x}$ ± SE)	% Total ash (T. Ash) ($\bar{x}$ ± SE)	% Fecal neutral detergent fibre (FNDF) ($\bar{x}$ ± SE)	% Fecal nitrogen (FN) ($\bar{x}$ ± SE)
Jul 8-11, 2008 (n=3)	90.64 ± 0.04	7.54 ± 0.23	48.19 ± 1.53	1.96 ± 0.22
Jul 21-24, 2008 (n=7)	91.00 ± 0.16	8.58 ± 0.97	47.84 ± 1.59	2.53 ± 0.19
Aug 2-5, 2008 (n=4)	91.02 ± 1.94	6.86 ± 0.14	40.70 ± 1.71	2.85 ± 0.06
Jul 24-27, 2009 (n=7)	89.52 ± 0.05	7.01 ± 0.33	40.50 ± 0.83	2.73 ± 0.07
Aug 5-8, 2009 (n=6)	89.50 ± 0.05	7.05 ± 0.64	37.33 ± 2.03	2.91 ± 0.09
2008 (n=14)	90.93 ± 0.50	7.87 ± 0.51	45.75 ± 1.28	2.50 ± 0.13
2009 (n=13)	89.51 ± 0.03	7.03 ± 0.33	39.04 ± 1.09	2.81 ± 0.06
Averaged nutrition (n=28)[**]	90.30 ± 0.29	7.94 ± 0.57	43.03 ± 1.14	2.65 ± 0.08

[*] n is number of composite samples.

[**] Includes an additional composite sample collected from Daring Lake area on Aug 28, 2009.

Detailed Diet Analysis

2008 diet composition (%) by site/date:

	Mara II (Jul 9)	Small Lake (Jul 9)	Mara V (Jul 10)	Thonokied Lake (Jul 21)	Thonokied Lake II (Jul 21)	Diavik View II (Jul 22)	Lac de Gras II (Jul 22)	Snake Lake (Jul 23)	Bay of de Gras (Jul 23)	Courageous/de Gras/MacKay (Jul 23)	MacKay Lake (Aug 3)	MacKay Lake II (Aug 3)	Thonokied/ MacKay (Aug 4)	Thonokied/Afridi (Aug 5)	N. Esker Daring Lake (Aug 25)
Aulacomnium	4.2	14.6	6.7	4.4	—	*	*	*	*	1.8	*	*	*	—	1.3
Dicranum	7.4	5.4	4.7	*	—	*	—	*	*	3.0	*	5.9	—	*	—
Polytrichum	2.8	2.3	2.0	*	1.2	*	—	*	—	—	*	—	—	*	—
Sphagnum	6.0	4.6	4.0	9.5	8.2	5.9	*	*	4.3	5.8	*	*	*	5.6	4.4
Mosses (sum *)	—	—	—	3.4	—	6.6	4.8	5.4	2.6	—	4.3	2.4	4.2	1.4	—
Total Moss:	20.4	26.9	17.4	17.3	9.4	12.5	4.8	5.4	6.9	10.6	4.3	8.3	4.2	7.0	5.7
Alectoria	2.5	1.1	*	3.4	13.6	3.9	5.1	3.3	6.5	4.0	3.7	5.0	5.0	2.2	10.8
Cetraria/Dactylina	8.1	5.0	7.5	*	1.6	8.6	3.2	6.9	11.9	8.9	3.4	—	9.5	4.8	10.4
Cladina/Cladonia	11.6	12.7	13.4	10.2	13.6	13.7	21.0	30.7	18.3	34.7	30.2	25.8	19.4	29.1	14.9
Peltigera	5.7	7.7	6.3	6.3	3.9	5.9	9.5	10.9	7.6	6.6	12.0	12.6	16.5	10.4	10.1
Stereocaulon	4.2	6.7	*	*	3.1	3.5	2.8	4.5	5.0	2.5	0.9	3.2	4.6	3.6	2.8
Lichens (sum *)	—	—	4.0	3.0	—	—	—	—	—	—	—	—	—	—	—
Total Lichen:	32.1	33.2	31.2	22.9	35.8	35.6	41.6	56.3	49.3	56.7	50.2	46.6	55.0	50.1	49.0
Equisetum:	0.0	0.0	0.0	1.9	0.0	1.6	0.8	0.0	0.0	0.0	1.8	0.6	0.0	0.0	1.6
Carex	11.3	3.1	6.3	9.7	6.2	2.7	3.6	0.6	—	1.3	3.7	*	0.8	5.0	3.5
Eleocharis	—	—	—	—	—	—	—	—	—	—	—	*	—	—	—
Eriophorum	1.8	2.7	*	—	0.4	—	—	—	0.7	—	—	—	—	0.6	1.3
Luzula	4.2	—	*	1.0	—	—	—	—	—	—	—	—	—	—	—
Sedge/Rush (sum *)	—	—	1.6	—	—	—	—	—	—	—	—	3.5	—	—	—
Total Sedge/Rush:	17.3	5.8	7.9	10.7	6.6	2.7	3.6	0.6	0.7	1.3	3.7	3.5	0.8	5.6	4.8
Poa	0.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unknown grass	—	1.5	0.4	—	1.9	—	1.6	—	—	0.5	—	—	1.2	—	1.6
Total Grass:	0.7	1.5	0.4	0.0	1.9	0.0	1.6	0.0	0.0	0.5	0.0	0.0	1.2	0.0	1.6

Alnus stem	—	—	—	—	—	—	—	—	*	*	—	—	—	—	—
Arctostaphylos stem	—	*	—	—	*	*	—	—	—	*	—	—	*	—	—
Betula leaf	1.8	*	*	*	*	2.4	4.0	*	—	*	*	*	*	2.2	*
Betula stem	6.0	*	—	*	—	0.8	—	—	—	*	—	—	—	4.2	—
Cassiope/*Andromeda* leaf	5.3	6.1	4.3	*	*	5.1	*	3.0	4.0	*	4.0	*	4.6	5.1	*
Dryas leaf	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dryas stem	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Empetrum/*Kalmia* leaf	3.5	*	7.1	9.2	3.5	*	*	*	4.3	5.3	*	*	4.6	4.8	*
Ledum leaf	*	*	3.2	5.3	*	*	4.3	4.8	4.3	3.5	6.5	5.6	6.6	10.7	3.5
Loiseleuria leaf	—	—	*	—	—	—	*	—	—	—	—	*	—	—	—
Potentilla	—	—	—	—	—	—	—	—	—	—	*	—	—	—	—
Salix leaf	8.5	12.7	15.8	6.1	22.6	17.7	22.6	15.7	19.8	7.1	12.3	16.4	12.8	5.6	19.3
Salix stem	2.1	2.3	6.3	4.9	5.5	5.9	5.1	5.4	5.0	3.8	9.2	7.0	2.1	2.2	—
Vaccinium leaf	*	*	*	—	—	—	—	*	—	—	—	*	—	—	3.2
Vaccinium stem	—	*	*	—	—	—	—	*	*	—	*	—	*	—	2.2
Ericaceous leaf	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ericaceous stem	—	*	*	*	—	*	*	3.0	*	4.0	*	*	*	*	*
Unknown shrub leaf	—	—	—	—	—	—	0.8	—	—	—	0.6	—	—	—	—
Unknown shrub stem	0.7	0.8	0.8	—	—	—	—	0.6	1.1	—	—	—	—	—	1.3
Shrub (sum *)	1.6	10.3	5.6	4.9	7.1	8.0	6.0	2.7	2.8	5.9	7.4	10.8	5.3	2.5	6.2
Total Shrub:	29.5	32.2	43.1	30.4	38.7	39.9	42.8	35.2	41.3	29.6	40.0	39.8	36.0	37.3	35.7
Astragalus	—	0.4	—	3.2	2.1	1.8	*	*	—	*	—	*	*	—	—
Hedysarum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lupinus/*Oxytropis*	—	—	—	11.7	5.5	5.9	*	*	—	*	—	*	*	—	—
Unknown forbs	—	—	—	1.9	—	—	1.2	—	1.8	—	—	0.6	1.2	—	1.6
Forbs (sum *)	—	—	—	—	—	—	3.6	2.5	—	1.3	—	0.6	1.6	—	—
Total Forbs:	0.0	0.4	0.0	16.8	7.6	7.7	4.8	2.5	1.8	1.3	0.0	1.2	2.8	0.0	1.6

* indicates trace amounts
— indicates absence

2009 diet composition (%) by site/date:

	N. Yamba (Jul 24)	NE. Yamba (Jul 24)	Ajax Lake (Jul 24)	S. Ajax (Jul 25)	E. Achilles (Jul 25)	N. Border (Jul 26)	Border III (Jul 27)	Itchen/Point II (Aug 5)	Itchen/Point III (Aug 5)	Itchen/Point IV (Aug 5-6)	Border Crossing (Aug 6-7)	Windy I (Aug 7)	Calm I (Aug 7)
Aulacomnium	4.4	*	4.9	*	*	*	3.9	*	1.6	*	2.4	6.0	5.8
Dicranum	3.2	6.7	5.7	6.3	6.2	*	5.7	3.6	3.6	*	3.3	10.5	2.4
Polytrichum	—	*	1.1	—	*	*	*	*	—	—	—	—	—
Sphagnum	3.5	4.5	4.9	*	4.1	*	*	*	4.8	*	3.3	6.0	3.4
Mosses (sum *)	—	2.5	—	1.0	3.0	4.5	2.5	6.5	—	4.7	—	—	—
Total Moss:	11.1	13.7	16.6	7.3	13.3	4.5	12.1	10.1	10.0	4.7	9.0	22.5	11.6
Alectoria	*	5.4	1.8	9.5	4.4	*	4.0	6.2	5.2	7.0	*	*	4.8
Cetraria/*Dactylina*	6.5	4.8	3.5	5.3	*	*	4.7	7.3	3.2	7.8	9.9	11.6	9.6
Cladina/*Cladonia*	8.9	9.9	6.7	21.1	8.0	13.5	8.3	9.8	16.5	22.3	11.1	5.6	15.4
Peltigera	5.6	*	6.7	9.1	12.7	3.0	3.6	5.4	7.2	4.7	11.3	6.3	6.1
Stereocaulon	*	*	—	1.4	*	*	1.1	0.4	1.2	3.1	*	*	5.1
Lichens (sum *)	1.2	2.8	—	—	3.0	4.0	—	—	—	—	2.7	2.1	—
Total Lichen:	22.2	22.9	18.7	46.4	28.1	20.5	21.7	29.1	33.3	44.9	35.0	25.6	41.0
Equisetum:	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	4.4	0.0	0.0	0.0	0.0
Carex	4.7	3.2	*	*	*	3.0	3.6	4.7	—	0.8	0.6	1.4	1.0
Eleocharis	—	—	—	—	—	—	—	—	—	—	—	—	—
Eriophorum	—	1.0	*	*	*	—	—	—	—	—	—	—	—
Luzula	—	—	—	—	—	—	—	—	—	—	—	—	—
Sedge/Rush (sum *)	—	—	2.8	1.7	1.8	—	—	—	—	—	—	—	—
Total Sedge/Rush:	4.7	4.2	2.8	1.7	1.8	3.0	3.6	4.7	0.0	0.8	0.6	2.8	2.0
Poa	—	—	—	—	—	—	—	—	—	—	—	—	—
Unknown grass	—	—	—	0.3	0.6	—	1.4	—	0.4	0.8	—	—	0.3
Total Grass:	0.0	0.0	0.0	0.3	0.6	0.0	1.4	0.0	0.4	0.8	0.0	0.0	0.3
Alnus stem	—	—	—	—	—	—	—	—	—	—	—	—	—
Arctostaphylos stem	*	—	—	—	—	—	—	—	—	—	—	—	—

Betula leaf	*	4.5	*	*	1.2	*	*	0.7	0.8	5.9	*	1.4	2.7
Betula stem	—	1.9	—	*	2.4	*	*	3.3	3.2	1.2	*	2.5	2.4
Cassiope/Andromeda leaf	8.9	*	6.0	5.6	5.6	5.4	3.6	4.4	12.9	3.1	6.3	*	*
Dryas leaf	—	—	—	—	*	—	4.3	*	*	—	—	0.3	*
Dryas stem	—	—	—	—	—	—	—	—	—	*	4.2	4.9	—
Empetrum/Kalmia leaf	4.4	*	*	*	3.2	*	*	*	—	—	—	*	—
Ledum leaf	6.5	*	*	6.7	3.8	*	—	*	3.2	*	*	*	*
Loiseleuria leaf	—	—	—	—	*	—	—	—	—	*	—	—	—
Potentilla	—	—	—	—	—	—	—	—	—	*	*	—	—
Salix leaf	21.0	28.7	32.9	19.6	32.5	46.0	31.2	20.3	16.9	16.4	30.8	23.2	28.3
Salix stem	7.4	11.5	8.5	4.9	2.4	3.4	13.3	13.1	7.7	9.0	3.6	4.9	5.1
Vaccinium leaf	4.7	—	*	—	—	*	*	*	—	—	—	2.5	—
Vaccinium stem	0.6	*	—	—	—	—	—	*	—	—	*	1.4	—
Ericaceous leaf	—	—	—	—	—	—	—	1.8	—	1.2	*	—	—
Ericaceous stem	*	*	*	*	*	*	*	3.3	*	1.9	*	*	*
Unknown shrub leaf	—	0.6	0.7	1.1	0.6	—	0.7	—	—	0.8	1.2	1.0	—
Unknown shrub stem	—	—	0.7	—	—	—	—	0.7	1.6	—	—	0.7	0.7
Shrub (sum *)	5.1	10.8	11.6	5.3	3.0	9.2	7.9	5.8	2.0	5.8	8.4	7.7	6.2
Total Shrub:	58.6	58.0	60.4	43.2	54.7	64.0	61.0	53.4	48.3	45.3	54.5	50.5	45.4
Astragalus	*	*	*	*	*	2.2	—	—	0.4	*	—	—	—
Hedysarum	—	—	—	—	—	—	—	—	—	*	—	—	—
Lupinus/Oxytropis	*	*	*	—	*	5.1	0.2	0.9	3.2	*	—	—	—
Unknown forbs	0.9	0.6	—	0.7	0.3	0.7	—	1.4	—	—	0.9	—	0.7
Forbs (sum *)	2.5	0.6	1.5	0.4	1.2	—	—	—	—	3.5	—	—	—
Total Forbs:	3.4	1.2	1.5	1.1	1.5	8.0	0.2	2.3	3.6	3.5	0.9	0.0	0.7

* indicates trace amounts
— indicates absence

Detailed Nutrition Analysis:

Site	Date	% ODM	% T. Ash	% FNDF	% FN
Mara II	Jul 9, 2008	90.57	7.33	51.26	1.80
Small Lake	Jul 9, 2008	90.71	7.30	46.75	1.69
Mara V	Jul 10, 2008	90.65	8.00	46.57	2.39
Thonokied Lake	Jul 21, 2008	90.89	7.19	43.23	2.09
Thonokied Lake II	Jul 21, 2008	90.68	6.83	52.48	2.62
Diavik View II	Jul 22, 2008	91.07	6.75	52.14	2.69
Lac de Gras II	Jul 22, 2008	90.71	7.12	47.29	2.03
Snake Lake	Jul 23, 2008	90.52	7.57	41.26	2.68
Bay of de Gras	Jul 23, 2008	91.39	12.31	48.89	3.48
Courageous/deGras/MacKay	Jul 23, 2008	91.73	12.29	47.84	2.11
MacKay Lake	Aug 3, 2008	95.81	6.73	36.46	2.99
MacKay Lake II	Aug 3, 2008	86.34	6.51	39.64	2.93
Thonokied/Mackay	Aug 4, 2008	91.21	7.11	44.30	2.78
Thonokied/Afridi	Aug 5, 2008	90.72	7.08	42.41	2.71
N. Esker Daring Lake	Aug 25, 2008	91.70	20.97	56.92	2.79
N of Yamba I	Jul 24, 2009	89.58	6.51	37.16	2.78
NE Yamba	Jul 24, 2009	89.63	6.28	43.56	2.82
Ajax Lake	Jul 24, 2009	89.46	5.86	38.39	2.94
South Ajax	Jul 25, 2009	89.56	7.91	40.76	2.44
E Achilles	Jul 25, 2009	89.53	7.06	41.21	2.51
North Border	Jul 26, 2009	89.62	8.32	42.36	2.84
Border III	Jul 27, 2009	89.26	7.13	40.07	2.77
Itchen/Point II	Aug 5, 2009	89.57	6.15	36.59	2.88
Itchen/Point III	Aug 5, 2009	89.34	6.42	43.39	2.85
Itchen/Point IV	Aug 5-6, 2009	89.44	5.4	41.91	2.82
Border Crossing	Aug 6-7, 2009	89.52	7.73	36.24	3.05
Windy I	Aug 7, 2009	89.44	9.82	36.48	2.58
Calm I	Aug 7, 2009	89.67	6.75	29.38	3.26