

Gauging climate change effects at local scales: weather-based indices to monitor insect harassment in caribou

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Abstract. Climate change is occurring at an accelerated rate in the Arctic. Insect harassment may be an important link between increased summer temperature and reduced body condition in caribou and reindeer (both *Rangifer tarandus*). To examine the effects of climate change at a scale relevant to *Rangifer* herds, we developed monitoring indices using weather to predict activity of parasitic insects across the central Arctic. During 2007–2009, we recorded weather conditions and used carbon dioxide baited traps to monitor activity of mosquitoes (Culicidae), black flies (Simuliidae), and oestrid flies (Oestridae) on the post-calving and summer range of the Bathurst barren-ground caribou (*Rangifer tarandus groenlandicus*) herd in Northwest Territories and Nunavut, Canada. We developed statistical models representing hypotheses about effects of weather, habitat, location, and temporal variables on insect activity. We used multinomial logistic regression to model mosquito and black fly activity, and logistic regression to model oestrid fly presence. We used information theory to select models to predict activity levels of insects. Using historical weather data, we used hindcasting to develop a chronology of insect activity on the Bathurst range from 1957 to 2008. Oestrid presence and mosquito and black fly activity levels were explained by temperature. Wind speed, light intensity, barometric pressure, relative humidity, vegetation, topography, location, time of day, and growing degree-days also affected mosquito and black fly levels. High predictive ability of all models justified the use of weather to index insect activity. Retrospective analyses indicated conditions favoring mosquito activity declined since the late 1950s, while predicted black fly and oestrid activity increased. Our indices can be used as monitoring tools to gauge potential changes in insect harassment due to climate change at scales relevant to caribou herds.

Key words: black fly; caribou; climate change; index; mosquito; multinomial logistic regression; Northwest Territories and Nunavut, Canada; oestrid; *Rangifer tarandus groenlandicus*; retrospective.

INTRODUCTION

Arctic temperatures have risen at almost twice the global rate over the past century and predictions of continued warming for the near future are widely accepted (ACIA 2004, IPCC 2007, Post et al. 2009). 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). Clarification of effects on individuals, populations, communities, and ecosystems, as well as the mechanistic processes driving these responses will increase our understanding of climate change and facilitate development of appropriate mitigation measures (de Groot et al. 1995, Bale et al. 2002). Baseline knowledge of reference conditions and

natural variability can be used to develop ecological indices incorporating multiple sources of information to elucidate trends over time (Fore et al. 1996, Niemi and McDonald 2004, Hardman-Mountford et al. 2005). These tools facilitate cost-effective ecosystem monitoring and adaptive management in the face of global change (McGeoch 1998, Hopkins and Kennedy 2004, Hodkinson and Jackson 2005).

Developing 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 (Post et al. 2009) and logistical constraints add to research and monitoring expense (Boulanger et al. 2011). Caribou and reindeer (*Rangifer tarandus*) are fundamental 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 fluctuated

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in the past (Gunn 2003), 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, Boulanger et al. 2011).

One hypothesis of a contributing factor to declines in *Rangifer* populations is that warmer summer temperatures have increased harassment by parasitic insects (Brotton and Wall 1997, Mörchel and Klein 1997, Weladji et al. 2003, Callaghan et al. 2004). There is little information, however, on the types of parasitic insects on *Rangifer* post-calving and 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 behavioral interactions of *Rangifer*, 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 (Mörchel 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 1996).

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). Insect harassment experienced by *Rangifer* may begin earlier in the season, last longer, and intensify as summer conditions warm (Brotton and Wall 1997, Callaghan et al. 2004). The inclusion of local weather conditions within predictive indices provides a link between environmental conditions important at the scale of insects and *Rangifer* and larger-scale climatic processes (Forchhammer and Post 2004, Whitfield and Russell 2005, LaDeau et al. 2008). To understand the influence of a wide range of environmental variables on parasitic fly activity and to test hypotheses about the potential responses of mosquitoes, black flies, and oestrids to climate change, we systematically trapped insects and monitored local weather conditions on the post-calving and 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, time, and date on activity levels of mosquitoes, black flies, and oestrid flies; (2) develop indices to predict trends over time in the degree to which weather conditions favor insect activity; and (3) use hindcasting to create a chronology of predicted insect levels on the Bathurst range since the 1950s.

MATERIALS AND METHODS

Study area

The Bathurst caribou (*Rangifer tarandus groenlandicus*) herd numbered 31 900 (95% CI: 21 000–42 800)

animals as of 2009 (Adamczewski et al. 2009). Post-calving and summer range of the herd encompasses tundra habitat above tree line in Northwest Territories and Nunavut, Canada (Fig. 1). Within a few days of calving, caribou traveling in large groups leave the calving grounds near Bathurst Inlet, Nunavut to begin their post-calving migration. The migration generally follows a clockwise pattern of south/southwesterly movement paralleling tree line before heading northwest (Gunn et al. 2001). Caribou are continuously on the move during the post-calving and summer season (15 June–1 September) and the Bathurst herd ranges over an area of >30 000 km² at this time (Matthews et al. 2001).

Data collection

During 2007–2009, we collected insect trap catch and weather data in the central to southwestern portion of the Bathurst post-calving and summer range. We employed two sampling procedures: “intensive” and “baseline” monitoring. Intensive sampling was conducted periodically throughout the post-calving and summer season. This sampling procedure involved continuous data collection over the 24-h cycle at sites in the vicinity of caribou groups. In contrast, baseline monitoring was conducted every day from late June to mid-August at two sites near the Tundra Ecosystem Research Station at Daring Lake, Northwest Territories. Although baseline monitoring sites were within the Bathurst post-calving and summer range, caribou were infrequently nearby and data were collected at four randomly selected 2-h intervals throughout the 24-h cycle as opposed to continuously.

We used locations of 13–20 satellite-collared female caribou per year to choose sites for sampling during intensive monitoring sessions. Sites were accessed by helicopter, with new sites selected as caribou left the area. Sites were located 25 m to 2 km from caribou groups ranging in size from 1 to >500 caribou. The amount of time we spent collecting data at each site varied from 2 to 66 h depending on the size of caribou groups and speed of their movements. Intensive monitoring sessions occurred over a total of 33 days during 2007–2009; we sampled 13 sites in 2007, 27 in 2008, and 25 in 2009.

During both intensive and baseline monitoring, we collected weather data (barometric pressure, relative humidity, temperature, and wind speed) at 10-min intervals using a portable weather station mounted 1.0 m above the ground (Kestrel 4500 on Kestrel Portable Vane Mount; Nielsen Kellerman, Boothwyn, Pennsylvania, USA). We quantified cloud cover by measuring light intensity at 30-min intervals in 2007 (EA30 light meter; Extech, Waltham, Massachusetts, USA) and 10-min intervals in 2008–2009 (data-logging light meter; Sper Scientific, Scottsdale, Arizona, USA). We used Malaise traps baited with carbon dioxide (Anderson et al. 2001) to collect insects. Compressed gas cylinders equipped with Flowset1 valves (Clarke Mosquito

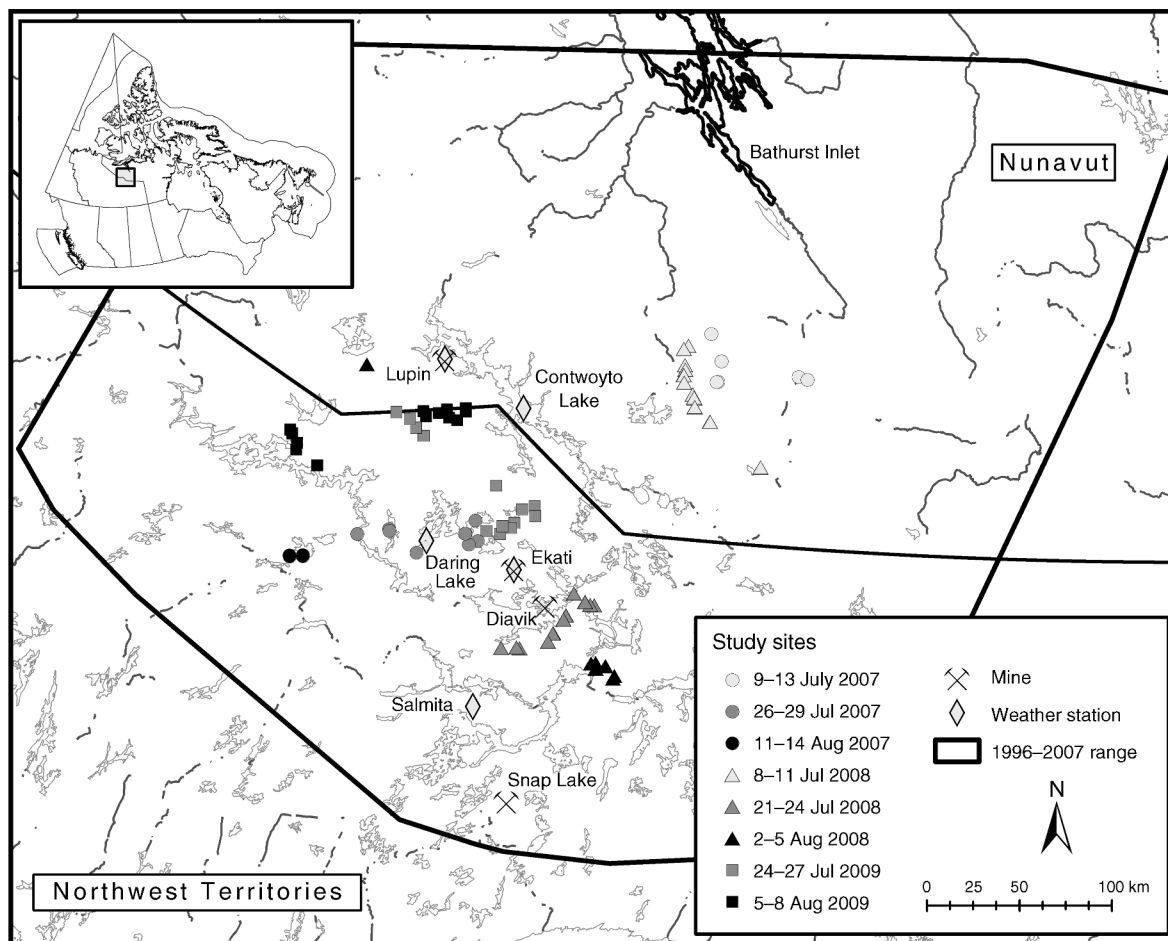


FIG. 1. Bathurst caribou post-calving and summer range based on locations of satellite-collared cows 1996–2007 in Northwest Territories and Nunavut, Canada. Point locations show mines, weather stations, Tundra Ecosystem Research Station at Daring Lake, and intensive session study sites from 2007 to 2009.

Control, Roselle, Illinois, USA) served as the carbon dioxide source. We 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 sampling sessions, we monitored traps over the 24-h period; with insects collected and counted at 2-h intervals. During baseline sessions, we divided the 24-h cycle into four periods; every day a 2-h interval for insect collection was randomly selected within each period. We averaged weather variables over each 2-h trapping session for use in insect models. We sorted insect catches into female mosquitoes, black flies, oestrid flies, and other. Subsamples of mosquito and black fly catch were identified to species (Poirier Laboratory, University of Northern British Columbia; D. Currie, Royal Ontario Museum). Identities of representative specimens of mosquito species were verified using DNA barcoding (Cywinska et al. 2006).

Model development

We developed predictive statistical models of insect activity levels based on weather, habitat, location, and temporal variables. For mosquitoes and black flies, we modeled four categories (no, low, moderate, and high) of relative activity based on hourly trap catch data collected during intensive and baseline sampling sessions (Table 1). Initially, we 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 assumption. Thus, we 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

levels of insect activity. Due to low trap catches, we modeled oestrid presence using logistic regression. For oestrid models, we used data from intensive sampling sessions, but not from baseline monitoring. Oestrid flies strongly track caribou movements (Nilssen and Anderson 1995). In contrast to mosquitoes and black flies, trap catches recorded when caribou are not in the vicinity are unlikely to adequately reflect oestrid activity around caribou. In all models, we used a robust clustering technique to account for potential autocorrelation among observations at a given trapping site (Nielsen et al. 2002). We withheld 20% of the data from each intensive sampling session for use in validation of the final models. We used Intercooled Stata 9.2 (Statacorp, College Station, Texas, USA) for statistical analyses.

Model parameters

We used a priori knowledge to develop model sets representing biologically plausible hypotheses. We classified models of mosquito and black fly activity, as well as models of oestrid presence, according to three explanatory themes: weather, habitat, and temporal. By organizing models within these themes, we were able to test if weather, habitat, or temporal variables were predominant drivers of insect activity as compared to the other themes. We also developed a fourth “combination” theme of models including explanatory variables from all other themes.

Weather-related variables included temperature, wind speed, light intensity, barometric pressure, and relative humidity (Table 2). Habitat-related variables included vegetation type, topography, and location on the Bathurst range. We modified Northern Land Cover/EOSD 30-m vegetation cover data (Wulder and Nelson 2003; Northern Land Cover of Canada circa-2000, *available online*)⁵ to create vegetation categories. We included easting and northing coordinates (Lambert Conformal Conic projection) of each site to determine whether insect activity varied depending on location within the Bathurst post-calving and summer range. Temporal variables included time of day, as well as variables representing seasonality. We used sunrise/set times (National Research Council Canada sunrise/sunset/sun angle calculator, *available online*)⁶ to create time of day categories. As a measure of season, we included variables specific to the emergence biology of insects. For mosquitoes and black flies, we 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 (Zalom et al. 1983). We used the ice-free date at Daring Lake (S. Matthews, *personal communication*) as the start date to begin accumulating gdd in order to capture the earliest

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

Category†	Mosquitoes (no./h)	Black flies (no./h)
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 66.67 percentile values.

potential activity of these insect families. Four weather stations record daily temperatures (Daring Lake, Ekati, Salmita, and Lupin) on the Bathurst post-calving and summer range (Fig. 1; Water Resources Division, Department of Indian Affairs and Northern Development, *unpublished data*; Environment Canada national climate data and information archive, *available online*).⁷ Data from the nearest station(s) were used to calculate gdd specific to each sampling location. For oestrid models, we calculated days since predicted eclosion (i.e., emergence of adult flies from the pupal case). To do so, we modified an equation developed by Nilssen (1997) to calculate daily pupal development rates and predicted eclosion date for oestrid flies based on day of year (1 January equals day 1), daily mean and maximum temperature, and cloud cover.

We screened independent variables for collinearity using multiple methods including examination of a correlation matrix and calculation of tolerance scores (Menard 2001). We removed models from the set if they included collinear variables. We parameterized categorical variables using deviation coding to contrast the effect of each level against the overall effect of the categorical variable (Menard 2001). While we made comparisons among models in each of the themes, this does not imply that we captured the full range of model possibilities.

Model selection and predictive ability

We based model selection on two complementary goals: (1) to increase understanding of parasitic fly ecology; and (2) to develop predictive models of insect activity that wildlife managers can use to examine past and monitor future conditions affecting insect activity across the range of Bathurst caribou. To meet the first goal, we considered more complex models that included covariates for habitat type, topography, and geographic location across the post-calving and summer range. This information is useful in understanding interactions between parasitic insects and their biotic and abiotic environments; however, from a management perspective

⁵ http://www.ccrs.nrcan.gc.ca/optical/landcover2000_e.php

⁶ <http://www.nrc-cnrc.gc.ca/eng/services/hia/sunrise-sunset/angle-calculator.html>

⁷ http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html

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

Variable	Description
Weather	
Temperature	mean air temperature over 2-h trapping period (°C)
Wind	mean wind speed over 2-h trapping period (m/s)
Light	mean light intensity over 2-h trapping period (lux)
BP	mean barometric pressure over 2-h trapping period (in Hg)
RH	mean relative humidity over 2-h trapping period (%)
Habitat, vegetation†	
Tussock tundra/sedge	tussock graminoid tundra and sedge
Non-tussock tundra	moist to dry non-tussock graminoid/dwarf shrub tundra
Shrub	low to tall shrub
Prostrate shrub	prostrate dwarf shrub
Habitat, topography	
Lowland	topographic depressions and lower slopes
Mid-slope/flats	flat plains and mid-slopes
Upland	ridge or esker tops and upper slopes
Habitat, location	
Easting	Cartesian coordinates for eastward-measured distance (m)
Northing	Cartesian coordinates for northward-measured distance (m)
Temporal, time‡	
Dawn	1 h before to 2 h after sunrise
Morning	2 h after sunrise to local/solar noon
Afternoon	local/solar noon to 2 h before sunset
Dusk	2 h before sunset to 1 h after sunset
Night	1 h after sunset to 1 h before sunrise
Temporal, seasonality	
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 (1997) equation
Eclosion ²	quadratic term for days since predicted oestrid eclosion

† In oestrid models, vegetation type was collapsed into a binary variable: "shrub" included prostrate dwarf shrub, low shrub, and tall shrub and "tundra" included tussock tundra, non-tussock tundra, and sedge.

‡ In oestrid models, time was collapsed into a binary variable: dusk/night/dawn/morning and afternoon.

it is necessary to develop predictions that are applicable range-wide. Thus, when identifying the best model for retrospective and prospective applications, we restricted the set to models without habitat or location covariates.

For both modeling objectives, we 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). We interpreted w as approximating the probability that a given model was the best within a model set. When two or more top models had a difference in $AIC_c < 2$, we considered these models to be of near equal parsimony (Burnham and Anderson 1998). The top two black fly models and top six models within the oestrid set had similar AIC_c scores. In the ITMC framework, model averaging is recommended when a single model is not clearly superior (Burnham and Anderson 1998). We did not apply model averaging, however, due to the unwieldy nature of this method in a multivariate model framework. For black flies, we chose to discuss

covariates from the second-ranked model. This model contained all the covariates that would be included if we adopted a model averaging approach, but did not account for additional weighing of the covariates present in both the first- and second-ranked models. For oestrid flies we used the top model as the index of activity, but examined the effects of coefficients from all six of the top models to gain a better understanding of oestrid fly biology.

For the best models, we estimated β coefficients and 95% confidence intervals for each parameter. We calculated Pearson's standardized residuals to assess model fit; cases where a residual exceeded two in absolute value were considered to have a poor fit. Using the 20% of the data withheld during model development, we calculated 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). For multinomial models, we calculated AUC for each possible binary comparison between categorical outcomes. Models were interpreted

as predicting activity level or presence relative to trap catch.

Retrospective analysis

To demonstrate the use of our mosquito, black fly, and oestrid models as tools for retrospective or prospective prediction of insect activity levels, we performed a hindcasting exercise using Bathurst range weather station records dating from 1957 to 2008. We calculated correlation coefficients between meteorological variables recorded at our study sites and at four permanent weather stations currently in operation on the Bathurst range (Fig. 1) to understand the degree of spatial variation in weather conditions. Strong correlations suggested that measures of a given weather variable at a few monitoring locations were representative of range-wide conditions. Additionally, we compared the range of values for each meteorological variable in the historical data set with values used in model fitting to ensure extrapolations were not being made well beyond the range of the training data.

Contwoyto Lake weather station had records from 1957 to 1981 and Lupin from 1982 to 2008 (Environment Canada national climate data and information archive, see footnote 7). These stations are located on opposite ends of Contwoyto Lake, within 50 km of each other. We compiled records into a single data set of hourly weather data for 06:00–18:00 for the 1957–2008 post-calving and summer seasons. Stations did not record barometric pressure, so we used the average value from our 2007–2009 field measurements for all predictions. Weather records did not contain data on light intensity, so we substituted lux measurements corresponding to average values by time category from our field data. For all years, we used mean ice-free date from Daring Lake 1996–2009 records (day of year 169) as the start date to begin accumulating gdd.

We used insect activity models to make predictions about mosquitoes, black flies, and oestrids for each hour where weather data were available between 15 June and 1 September. For mosquitoes and black flies, we calculated the predicted probability of the four insect activity levels (no, low, moderate, high) for each hourly weather record. We considered insect activity to be the level with the highest predicted probability for the hour. We totaled 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 from the 15 June–1 September interval. We used this ratio to compare intensity of insect activity across years. We treated oestrid predictions in a similar manner. We considered the probability of oestrid presence to be high if the predicted probability exceeded 0.13, the 95th percentile value of predicted probabilities from our 2007–2009 data set. We 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.

We used Spearman's rank correlation to examine potential trends in insect activity over time. The late 1970s and early 1980s were the beginning of a period of increased global temperatures (Jones and Moberg 2003). Based on this, the years from 1957 to 2008 were split into intervals: 1957–1981 and 1982–2008. We used *t* tests to compare mean index values between the two time periods.

RESULTS

Insect trap catch

We trapped at least five species of mosquitoes, including *Ochlerotatus excrucians*, *O. punctor/abserratus*, and *O. hexodontus* (A. Cywinska and L. Poirier, *personal communications*). The two remaining species were identified to the genus level (*Ochlerotatus* and *Aedes*). Black flies included *Simulium vittatum*, *S. rostratum*, the *S. venustum* complex, and the *S. arcticum* complex (D. Currie, *personal communication*). Oestrid flies were positively identified in 2008–2009 trap catches. We trapped 16 female warble flies (*Hypoderma tarandi*) and four female nose bot flies (*Cephenemyia trompe*) in 2008. One additional oestrid fly was trapped in 2008, but it escaped before we could identify it to species. Seven female warble flies were trapped in 2009.

Mosquito models

The activity 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 3; Appendix A). 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. Using independent data, AUC scores for the set of binary logistic regressions that represented the four levels of mosquito activity ranged from 0.86 to 1.00.

Several coefficients from the top-ranked mosquito activity model were statistically significant (Table 4; Appendix D). 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

TABLE 3. Multinomial logistic regression (mlogit) models of mosquito activity on the Bathurst caribou post-calving and summer range, 2007–2009.

Model	<i>K</i>	Log-likelihood	AIC _c	ΔAIC _c	<i>w</i>
Temporal					
Gdd + gdd ² + time	18	−762.04	1561.06	292.92	<0.001
Gdd + gdd ²	6	−780.10	1572.33	304.19	<0.001
Weather					
Temp + wind	6	−823.36	1658.84	390.69	<0.001
Temp + wind + light + BP + RH	15	−814.71	1660.11	391.97	<0.001
Habitat					
Vegetation + topography + easting + northing	21	−874.66	1792.66	524.51	<0.001
Topography	6	−958.54	1929.20	661.06	<0.001
Combination					
Gdd + gdd ² + time + temp + wind + light + BP + RH + vegetation + topography + easting + northing	54	−575.54	1268.14	0†	0.99
Gdd + gdd ² + time + temp + wind + light + BP + RH	33	−619.18	1307.69	39.54‡	<0.001

Note: 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 the two best models per theme (temporal, weather, habitat, and combination) are given.

† To meet the goal of increasing understanding of mosquito ecology, we used the top-ranked model to explore the effects of covariates on mosquito activity.

‡ We 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. We did not consider models including habitat and location covariates for use in retrospective analysis due to the need for an index that could be generalized across the Bathurst range.

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

TABLE 4. Coefficients (β) and 95% confidence intervals (CI) from top multinomial logistic regression (mlogit) models comparing high relative to no mosquito and black fly activity and the top oestrid fly logistic regression (logit) model for comparison of presence relative to absence.

Variable	Mosquito model			Black fly model			Oestrid model		
	β	95% CI		β	95% CI		β	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
Gdd	0.026	−0.007	0.059	0.035	0.028	0.042			
Gdd ²	− 0.124	−0.221	−0.028	− 0.061	−0.074	−0.049			
Temp	0.523	0.253	0.793	0.785	0.575	0.996	0.327	0.173	0.481
Wind	− 2.083	−2.376	−1.790	− 1.522	−1.999	−1.050			
Light	−0.016	−0.040	0.009	−0.002	−0.033	0.029			
BP	6.865	2.328	11.401	−0.797	−3.449	1.855			
RH	0.035	0.009	0.061	−0.002	−0.032	0.027			
Time									
Dawn	−0.566	−1.319	0.186	−0.928	−2.009	0.153			
Morning	−0.578	−1.200	0.043	1.086	0.542	1.630			
Afternoon	−0.234	−0.952	0.485	0.842	−0.438	2.123			
Dusk	0.782	0.210	1.353	0.852	−0.033	1.737			
Night	0.596	−0.584	1.777	− 1.852	−3.461	−0.244			
Vegetation									
Tussock	0.268	−1.024	1.560	0.598	−0.263	1.459			
Non-tussock	−0.199	−1.641	1.242	0.627	−0.614	1.869			
Shrub	0.330	−0.651	1.310	0.092	−0.754	0.938			
Prostrate shrub	−0.398	−1.737	0.940	− 1.317	−2.158	−0.475			
Topography									
Lowland	1.066	0.066	2.066	0.622	−0.119	1.364			
Mid-slope	−0.723	−1.845	0.398	0.072	−0.762	0.906			
Upland	−0.342	−1.137	0.452	− 0.695	−1.342	−0.047			
Easting	0.032	0.010	0.055	− 0.013	−0.022	−0.005			
Northing	0.054	0.029	0.078	−0.013	−0.026	<0.001			

Notes: Coefficients for growing degree-days (gdd), gdd², light, easting, and northing are scaled by a factor of 1000. Significant coefficients are in bold (*P* < 0.05).

TABLE 5. Multinomial logistic regression (mlogit) models of black fly activity on the Bathurst caribou post-calving and summer range, 2007–2009.

Model	<i>K</i>	Log-likelihood	AIC _c	ΔAIC _c	<i>w</i>
Temporal					
Gdd + gdd ² + time	18	−777.12	1591.24	320.51	<0.001
Gdd + gdd ²	6	−831.03	1674.18	403.45	<0.001
Weather					
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
Habitat					
Vegetation + topography + easting + northing	21	−855.14	1753.61	482.89	<0.001
Topography	6	−879.03	1770.17	499.44	<0.001
Combination					
Gdd + gdd ² + time + temp + wind + light + BP + RH	33	−600.71	1270.73	0†	0.53
Gdd + gdd ² + time + temp + wind + light + BP + RH + vegetation + topography + easting + northing	54	−576.94	1270.94	0.21‡	0.47

Note: 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 the two best models per theme (temporal, weather, habitat, and combination) are given.

† We 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. We did not consider models including habitat and location covariates for use in retrospective analysis due to the need for an index that could be generalized across the Bathurst range.

‡ We used the second-ranked model to explore the effects of covariates on black fly activity to meet the goal of increasing understanding of black fly ecology.

activity was not strongly related to vegetation type. Topography, however, influenced activity levels with increased probability of high activity in lowlands. Many of the relationships between mosquito levels and location were also strong, with higher activity levels to the north and east within the Bathurst post-calving and summer range.

Black fly models

Two models of black fly activity had nearly identical AIC_c scores; the second-ranked model scored 0.21 higher than the first (Table 5; Appendix B). The top-ranked model contained covariates related to weather, time, and date (*K* = 33). The second-ranked model contained the same covariates as the first, as well as additional habitat variables (*K* = 54). We selected the second-ranked model for use as our “best” model. This model had reasonable to very good ability to distinguish between different levels of black fly activity. Using independent data, ROC scores for the set of binary logistic regressions representing the four levels of black fly activity ranged from 0.84 to 1.00.

Temperature had a positive effect on black fly activity, and the majority of coefficients were statistically significant (Table 4; Appendix D). Wind speed had a consistent negative effect on black fly levels. Coefficients for barometric pressure suggested a negative association with black fly activity. 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.

Oestrid models

There was substantial model selection uncertainty in determining the best of the set of oestrid models (Table 6; Appendix C). The six top-ranked models differed in AIC_c score by <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 other top-ranked models contained covariates related to other weather and habitat parameters.

Temperature was the covariate with the strongest influence on the presence of oestrids (Table 4; Appendix D). The probability of oestrid presence increased significantly as temperature rose. Relative humidity and light had weak positive effects on oestrids, while wind speed and barometric pressure had slightly 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.

TABLE 6. Logistic regression models of oestrid fly presence on the Bathurst caribou post-calving and summer range, 2007–2009.

Model	K	Log-likelihood	AIC _c	Δ AIC _c	w	AUC
Temporal						
Eclasion + time	2	–41.15	86.33	7.60	0.005	0.75
Eclasion + eclasion 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
Temp + wind + light + BP + RH	5	–34.65	79.49	0.75	0.16	0.87
Habitat						
Vegetation + topography + easting + northing	5	–38.58	87.35	8.61	0.003	0.79
Topography	2	–42.45	88.93	10.20	0.001	0.69
Combination						
Temp + wind + light + BP + RH + vegetation + topography + easting + northing	10	–29.24	79.18	0.45	0.19	0.91
Eclasion + eclasion ² + time + temp + wind + light + BP + RH	8	–31.92	80.30	1.56	0.11	0.88

Note: Number of parameters (K), log-likelihood, Akaike's Information Criterion (AIC_c) scores, differences in AIC_c scores (Δ AIC_c), AIC_c weights (w), and area under the receiver operating characteristic curve (AUC) calculated using the training data set for the two best models per theme (temporal, weather, habitat, and combination) are given.

Retrospective analysis

We found strong correlations among temperature, light, and relative humidity for the four weather stations across the Bathurst post-calving and summer range; however, wind speed was quite variable among stations. Correlation coefficients for temperature ranged from 0.82 to 0.97, light from 0.75 to 0.94, and relative humidity from 0.67 to 0.95. Wind speed correlation coefficients varied from 0.37 to 0.74. Historical weather data had a similar range of values as those observed at our field sites in 2007–2009. We examined 52 310 hourly weather records from 1957 to 2008; of these, the only instances of extrapolation outside of our range of values included 4.6% of historical cases where temperatures fell below the minimum of those we observed and 7.7% of historical records of wind speed values greater than our maximum observed wind speed.

Oestrid flies ($t = -6.39$, $df = 50$, $P < 0.001$) and black flies ($t = -2.49$, $df = 50$, $P = 0.008$) had higher mean index values 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, we examined correlations between year and index levels (Fig. 2). There was a positive correlation between oestrid index and year ($r_s = 0.73$, $P < 0.001$) and black fly predictions and year ($r_s = 0.29$, $P = 0.039$). Mosquito index and year were negatively correlated ($r_s = -0.56$, $P < 0.001$), indicative of a trend toward declining mosquito activity over time.

DISCUSSION

Temperature is consistently cited as a key driver of insect activity (Sommerman et al. 1955, Haufe and Burgess 1956, Danks 2004, Quinlan et al. 2005), and we found it important in predicting mosquito, black fly, and oestrid levels. Oestrid flies were least tolerant of low temperatures. Other weather variables mediate the

effects of temperature on insect activity. In particular, wind negatively affected activity of mosquitoes, black flies, and oestrids, but this effect was strongest for mosquitoes. Time of day also affected insect activity. The probability of higher mosquito activity increased at dusk/night. In contrast, we observed higher black fly activity at morning, afternoon, and dusk and greater probability of oestrid presence during afternoon. Additionally, activity levels varied at the larger temporal scale of the post-calving and summer season. Both mosquito and black fly activity showed a seasonal peak and decline as growing degree-days (gdd) accumulated over the summer. Peak mosquito activity occurred shortly after lakes became free of ice in early to mid-July. Black fly activity peaked between late July and early August after ~ 300 gdd had accumulated. Although not statistically significant, we trapped more oestrids later in the season. The lack of a clear relationship may be an artifact of low oestrid sample size. Topography played a role in moderating activity with the highest insect levels observed in lowlands. Understanding how these factors drive variations in insect activity is important as such changes have implications for how caribou use the landscape and allocate their time throughout the post-calving and summer season (Downes et al. 1986, Skarin et al. 2008, Witter et al. 2012).

Insect indices that were calculated retrospectively indicated conditions conducive to mosquito activity on the Bathurst range declined since the late 1950s, while conditions became increasingly favorable for black flies and oestrids. Black fly and oestrid predictions were driven by a trend of increasing summer temperatures. 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 percentage of the post-calving and summer season with relative humidity values $>80\%$ declined while the amount of time winds exceeded

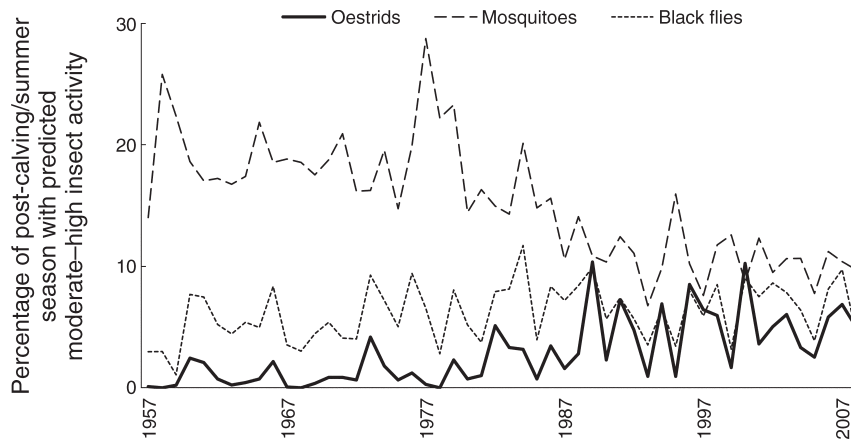


FIG. 2. Retrospective indices of insect activity at Lupin/Contwoyto weather station on the Bathurst caribou post-calving and summer range, Northwest Territories and Nunavut, Canada, from 1957 to 2008.

4 m/s increased. These measures are consistent with a declining trend in mosquito index values. Retrospective predictions should be compared with independent historical data to gauge their accuracy, but data on insect activity on the Bathurst range in the past are lacking. In the absence of this, results of the hindcasting exercise must be interpreted with caution. The exercise, however, is useful in demonstrating the use of indices as monitoring tools and provides our best estimate of past conditions in the absence of historical insect data.

Caribou and reindeer have evolved with parasitic flies, and it is unlikely that insect harassment is a sole driver of *Rangifer* population declines. While causal mechanisms behind the recent decline of the Bathurst herd have not been firmly established, this fluctuation was likely driven by a suite of factors including changes in hunting technology and access, habitat changes resulting from greater human presence including mines and other developments, and changes in range condition caused by climatic fluctuations (Johnson et al. 2005, Boulanger et al. 2011). The direct costs of blood loss and parasitic loading combined with indirect costs of behavioral modification due to insect harassment (Dieterich and Haas 1981, Russell et al. 2005, Colwell et al. 2006, Witter et al. 2012), however, are stressors that could accelerate 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 trade-offs 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 *Rangifer* 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 (Asbakk et al. 2005, Hawlena et al. 2006).

Increased winter mortality rates in *Rangifer* calves may be associated with high oestrid infestation following warm summers (Klein 1991). In addition to reduced recruitment rates, cohorts experiencing high parasitism as calves may experience fitness consequences that continue into adulthood (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 unfavorable 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 useful tools to increase understanding of Bathurst caribou population dynamics when used in conjunction with ongoing caribou demographic and body condition monitoring. Indices must be grounded in understanding of the ecology of the species they seek to represent (Fore et al. 1996, Linton and Warner 2003). We attempted to provide this by intensively monitoring insect levels in conjunction with a wide range of biotic and abiotic factors, by continuing this monitoring across the majority of the insect season, over multiple years, and at varied locations across the Bathurst range. We modeled weather conditions at hourly time steps to address changes at temporal scales relevant to insects and caribou. By including fine-scale measures, the indices can also capture unusual weather conditions. The frequency of these extreme weather events is expected to increase as climate change occurs with potentially large regulatory effects on insect activity and abundance (Harrington et al. 2007). This was one of the most spatially and temporally intensive samplings of the relationships between parasitic insects, weather,

habitat, and time conducted to date across the circum-Arctic region inhabited by *Rangifer*. It should be noted, however, that the parasitic insect fauna of the central Arctic is relatively understudied and our work represents an attempt to gain baseline information regarding these species.

Indices are inherently simplifications of reality. One limitation of our short-term study was the inability to observe the full range of natural variability that occurs over longer timescales. Any extrapolations made using the indices implicitly assume that current or future climatic changes have not and will not fundamentally alter the structure of the system. Nonetheless, the use of data on daily weather variations to make inferences regarding long-term trends is not without precedent and can provide useful information (Roy et al. 2001, Goulson et al. 2005, Harrington et al. 2007). There are also some important aspects of insect ecology not accounted for in our models. Data on a number of mosquito and black fly species were lumped together, potentially masking species-specific differences in response to weather variables. Our indices provide a qualitative assessment of the conditions that caribou may experience relative to insect harassment, but do not distinguish changes in insect abundance from variations in activity levels.

Insect abundance in any given year is affected by the previous season's population size, weather conditions, and host abundance, as well as by conditions affecting larval development in the current year. Many mosquito and black fly species in the Arctic are facultatively autogenous, and the number of eggs developed varies depending on whether a female has access to a blood meal (Corbet 1967, Currie 1997, Danks 2004). Water temperature and food availability are also important factors in mosquito and black fly larval development (Sommerman et al. 1955, Haufe and Burgess 1956, Corbet and Danks 1973, Merritt et al. 1982). Oestrids are highly fecund and populations can rebound quickly following favorable summers (Anderson and Nilssen 1996, Nilssen 1997). During summers with unfavorable weather conditions, however, oestrid flight may be limited to 25% of the season, restricting reproductive potential and affecting population levels the following year (Anderson et al. 1994). Developmental rates of oestrid larvae within *Rangifer* 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 are also vulnerable to predation and fungal infection at this time (Nilssen 1997, 2006).

Effects of climatic change may include alterations in both the physiology and phenology of insect species (de Groot et al. 1995, Baker et al. 2000, Harrington et al. 2001, Teklehaimanot et al. 2004). For example, the time required for mosquito larvae and pupae to develop

decreases as temperature rises (Teklehaimanot et al. 2004, Laaksonen et al. 2009). Favorable conditions might lead to an increased number of black fly or mosquito generations in a season (Harrington et al. 2001), whereas the oestrid life cycle is more constrained due to the obligatory development of larvae within the *Rangifer* host. Altered species interactions, including changes in the incidence of parasitoids, pathogens, and predators might also be expected (Jenkinson et al. 1996, Schneider and Root 1996, Stenseth et al. 2002, Goulson et al. 2005). Long-term monitoring and further research into the effects of climate on life cycles and life history parameters of parasitic insects in *Rangifer* habitats will be crucial for increasing our ability to anticipate outcomes under climate change scenarios.

Insect indices can be used as simple cost-effective tools to translate meteorological data collected on a regular basis on the Bathurst range into predictions about the potential for mosquito, black fly, and oestrid activity over time. In the absence of historical data on insect activity, retrospective indices allow us to infer reference 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 barren-ground caribou. 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). Although consideration of large-scale climatic variability is critical, indices can help translate these changes into an understanding of potential responses at the levels of individuals and populations (Whitfield and Russell 2005, LaDeau et al. 2008). 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.

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LITERATURE CITED

- ACIA. 2004. Impacts of a warming arctic: Arctic climate impact assessment. Cambridge University Press, Cambridge, UK.
- Adamczewski, J., J. Boulanger, B. Croft, D. Cluff, B. Elkin, J. Nishi, A. Kelly, A. D'Hont, and C. Nicolson. 2009. Decline in the Bathurst caribou herd 2006–2009: a technical evaluation of field data and modeling. Draft Technical Report. Environment and Natural Resources, Government of the Northwest Territories, Yellowknife, Northwest Territories, Canada.
- Albon, S. D., A. Stien, R. J. Irvine, R. Langvatn, E. Ropstad, and O. Halvorsen. 2002. The role of parasites in the dynamics of a reindeer population. *Proceedings of the Royal Society B* 269:1625–1632.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence and an alternative. *Journal of Wildlife Management* 64:912–923.
- Anderson, J. R., and A. C. Nilssen. 1996. Trapping oestrid parasites of reindeer: the response of *Cephenemyia trompe* and *Hypoderma tarandi* to baited traps. *Medical and Veterinary Entomology* 10:337–346.
- Anderson, J. R., and A. C. Nilssen. 1998. Do reindeer aggregate on snow patches to reduce harassment by parasitic flies or to thermoregulate? *Rangifer* 18:3–17.
- Anderson, J. R., A. C. Nilssen, and I. Folstad. 1994. Mating behaviour and thermoregulation of the reindeer warble fly, *Hypoderma tarandi* L. (Diptera: Oestridae). *Journal of Insect Behavior* 7:679–706.
- Anderson, J. R., A. C. Nilssen, and W. Hemmingsen. 2001. Use of host-mimicking trap catches to determine which parasitic flies attack reindeer, *Rangifer tarandus*, under different climatic conditions. *Canadian Field-Naturalist* 115:274–286.
- Asbakk, K., A. Oksanen, M. Nieminen, R. E. Haugerud, and A. C. Nilssen. 2005. Dynamics of antibodies against hypodermin C in reindeer infested with the reindeer warble fly, *Hypoderma tarandi*. *Veterinary Parasitology* 129:323–332.
- Bader, D. C., C. Covey, W. J. Gutowski, I. M. Held, K. E. Kunkel, R. I. Miller, R. T. Tokmakian, and M. H. Zhang. 2008. Climate models: an assessment of strengths and limitations. A report by the U.S. Climate Change Science Program, U.S. Department of Energy, Washington, D.C., USA.
- Baker, R. H. A., C. E. Sansford, C. H. Jarvis, R. J. C. Cannon, A. MacLeod, and K. F. A. Walters. 2000. The role of climatic mapping in predicting the potential geographic distribution of non-indigenous pests under current and future climates. *Agriculture, Ecosystems and Environment* 82:57–71.
- Bale, J. S., et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8:1–16.
- Boulanger, J., A. Gunn, J. Adamczewski, and B. Croft. 2011. A data-driven demographic model to explore the decline of the Bathurst caribou herd. *Journal of Wildlife Management* 75:883–896.
- Brant, R. 1990. Assessing proportionality in the proportional odds model for ordinal logistic regression. *Biometrics* 46:1171–1178.
- Brotton, J., and G. Wall. 1997. Climate change and the Bathurst caribou herd in the Northwest Territories, Canada. *Climate Change* 35:35–52.
- Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Burns, C. E., B. J. Goodwin, and R. S. Ostfeld. 2005. A prescription for longer life? Bot fly parasitism of the white-footed mouse. *Ecology* 86:753–761.
- Callaghan, T. V., L. O. Bjorn, Y. Chernov, T. Chapin, T. R. Christensen, and B. Huntley. 2004. Effects on the structure of Arctic ecosystems in the short- and long-term perspectives. *Ambio* 33:436–447.
- Careau, V., D. W. Thomas, and M. M. Humphries. 2010. Energetic cost of bot fly parasitism in free-ranging eastern chipmunks. *Oecologia* 162:303–312.
- Colwell, D. D., M. J. R. Hall, and P. J. Scholl. 2006. A synopsis of the biology, hosts, distribution, disease significance and management of the genera. Pages 220–305 in D. D. Colwell, M. J. R. Hall, and P. J. Scholl, editors. *The oestrid flies: biology, host–parasite relationships, impact and management*. CABI Publishing, Oxfordshire, UK.
- Corbet, P. S. 1967. Facultative autogeny in Arctic mosquitoes. *Nature* 215:662–663.
- Corbet, P. S., and H. V. Danks. 1973. Seasonal emergence and activity of mosquitoes (Diptera: Culicidae) in a high-arctic locality. *Canadian Entomologist* 105:837–872.
- Coulson, T., P. Rohani, and M. Pascual. 2004. Skeletons, noise and population growth: the end of an old debate? *Trends in Ecology and Evolution* 19:359–364.
- Currie, D. C. 1997. Black flies (Diptera: Simuliidae) of the Yukon, with reference to the black-fly fauna of northwestern North America. Pages 563–614 in H. V. Danks and J. A. Downes, editors. *Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods)*, Ottawa, Ontario, Canada.
- Cywinska, A., F. F. Hunter, and P. D. N. Hebert. 2006. Identifying Canadian mosquito species through DNA barcodes. *Medical and Veterinary Entomology* 20:413–424.
- Danks, H. V. 2004. Seasonal adaptations in arctic insects. *Integrative and Comparative Biology* 44:85–94.
- Dau, J. 1986. Distribution and behaviour of barren-ground caribou in relation to weather and parasitic insects. Thesis. University of Alaska, Fairbanks, Alaska, USA.
- de Groot, R. S., P. Ketner, and A. H. Ova. 1995. Selection and use of bio-indicators to assess the possible effects of climate change in Europe. *Journal of Biogeography* 22:935–943.
- Dieterich, R. A., and G. E. Haas. 1981. Warbles. Pages 179–182 in R. A. Dieterich, editor. *Alaskan wildlife diseases*. University of Alaska, Fairbanks, Alaska, USA.
- Doherty, S. J., et al. 2009. Lessons learned from IPCC AR4: scientific developments needed to understand, predict, and respond to climate change. *Bulletin of the American Meteorological Society* 90:497–513.
- Downes, C. M., J. B. Theberge, and S. M. Smith. 1986. The influence of insects on the distribution, microhabitat choice, and behaviour of the Burwash caribou herd. *Canadian Journal of Zoology* 64:622–629.
- Dye, D. G. 2002. Variability and trends in the annual snow-cover cycle in Northern Hemisphere land areas, 1972–2000. *Hydrological Processes* 16:3065–3077.
- Eberhardt, L. L., and K. W. Pitcher. 1992. A further analysis of the Nelchina caribou and wolf data. *Wildlife Society Bulletin* 20:385–395.
- Forchhammer, M. C., and E. Post. 2004. Using large-scale climate indices in climate change ecology studies. *Population Ecology* 4:1–12.
- Forchhammer, M. C., E. Post, N. C. Stenseth, and D. M. Boertmann. 2002. Long-term responses in arctic ungulate dynamics to changes in climatic and trophic processes. *Population Ecology* 44:113–120.
- Fore, L. S., J. R. Karr, and R. W. Wisseman. 1996. Assessing invertebrate responses to human activities: evaluating alternative approaches. *Journal of the North American Benthological Society* 15:212–231.

- Goulson, D., L. C. Derwent, M. E. Hanley, D. W. Dunn, and S. A. Abolins. 2005. Predicting calyptrate fly populations from the weather, and probable consequences of climate change. *Journal of Applied Ecology* 42:795–804.
- Gunn, A. 2003. Voles, lemmings and caribou—population cycles revisited? *Rangifer Special Issue* 14:105–111.
- Gunn, A., J. Dragon, and J. Boulanger. 2001. Seasonal movements of satellite-collared caribou from the Bathurst herd. Final report. West Kitikmeot Slave Study Society, Yellowknife, Northwest Territories, Canada.
- Hagemoen, R. I. M., and E. Reimers. 2002. Reindeer summer activity pattern in relation to weather and insect harassment. *Journal of Animal Ecology* 71:883–892.
- Hardman-Mountford, N. J., J. I. Allen, M. T. Frost, S. J. Hawkins, M. A. Kendall, N. Mieszkowska, K. A. Richardson, and P. J. Somerfield. 2005. Diagnostic monitoring of a changing environment: an alternative UK perspective. *Marine Pollution Bulletin* 50:1463–1471.
- Harrington, R., S. J. Clark, S. J. Welham, P. J. Verrier, C. H. Denholm, M. Hullé, D. Maurice, M. D. Rounsevell, and N. Cocu. 2007. Environmental change and the phenology of European aphids. *Global Change Biology* 13:1550–1564.
- Harrington, R., R. A. Fleming, and I. P. Woiwod. 2001. Climate change impacts on insect management and conservation in temperate regions: can they be predicted? *Agricultural and Forest Entomology* 3:233–240.
- Haufe, W. O., and L. Burgess. 1956. Development of *Aedes* (Diptera: Culicidae) at Fort Churchill, Manitoba, and prediction of dates of emergence. *Ecology* 37:500–519.
- Hawlena, H., B. R. Krasnov, Z. Abramsky, I. S. Khokhlova, D. Saltz, M. Kam, A. Tamir, and A. A. Degen. 2006. Flea infestation and energy requirements of rodent hosts: are there general rules? *Functional Ecology* 20:1028–1036.
- Helle, T., and L. Tarvainen. 1984. Effects of insect harassment on weight gain and survival in reindeer calves. *Rangifer* 4:24–27.
- Hodkinson, I. A., and J. K. Jackson. 2005. Terrestrial and aquatic invertebrates as bioindicators for environmental monitoring, with particular reference to mountain ecosystems. *Environmental Management* 35:649–666.
- Hopkins, H. L., and M. L. Kennedy. 2004. An assessment of indices of relative and absolute abundance for monitoring populations of small mammals. *Wildlife Society Bulletin* 32:1289–1296.
- IPCC (Intergovernmental Panel on Climate Change). 2007. Climate change 2007: synthesis report. IPCC, Geneva, Switzerland.
- Jenkinson, L., A. Davis, S. Wood, B. Shorrocks, and J. Lawton. 1996. Not that simple: global warming and predictions of insect ranges and abundances: results from a model insect assemblage in replicated laboratory conditions. *Aspects of Applied Biology* 45:343–348.
- Johnson, C. J., M. S. Boyce, R. L. Case, H. D. Cluff, R. J. Gau, and A. Gunn. 2005. Cumulative effects of human developments on arctic wildlife. *Wildlife Monographs* 160:1–36.
- Jones, P. D., and A. Moberg. 2003. Hemispheric and large scale surface air temperature variations: an extensive revision and update to 2001. *Journal of Climate* 16:206–223.
- Klein, D. R. 1991. Comparative ecological and behavioural adaptations of *Ovibus moschatus* and *Rangifer tarandus*. *Rangifer* 12:47–55.
- Laaksonen, S., M. Solismaa, R. Kortet, J. Kuusela, and A. Oksanen. 2009. Vectors and transmission dynamics for *Setaria tundra* (Filarioidea; Onchocercidae), a parasite of reindeer in Finland. *Parasites and Vectors* 2:3.
- LaDeau, S. L., P. P. Marra, A. M. Kilpatrick, and C. A. Calder. 2008. West Nile virus revisited: consequences for North American ecology. *BioScience* 58:937–946.
- Lee, S. E., M. C. Press, J. A. Lee, T. Ingold, and T. Kurttila. 2000. Regional effects of climate change on reindeer: a case study of the muotkatunturi region in Finnish Lapland. *Polar Research* 19:99–105.
- Linton, D. M., and G. F. Warner. 2003. Biological indicators in the Caribbean coastal zone and their role in integrated coastal management. *Ocean and Coastal Management* 46:261–276.
- Long, J. S. 1997. Regression models for categorical and limited dependent variables. Sage, Thousand Oaks, California, USA.
- Long, J. S., and J. Freese. 2001. Regression models for categorical dependent variables using Stata. Stata Press, College Station, Texas, USA.
- Matthews, S., H. Epp, and G. Smith. 2001. Vegetation classification for the West Kitikmeot/Slave study region. Final report. West Kitikmeot/Slave Study, Yellowknife, Northwest Territories, Canada.
- McGeoch, M. A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* 73:181–201.
- McKelvey, K. S., and D. E. Pearson. 2001. Population estimation with sparse data: the role of estimators versus indices revisited. *Canadian Journal of Zoology* 79:1754–1765.
- Menard, S. 2001. Applied logistic regression analysis. Sage University Paper Series on Quantitative Applications in the Social Sciences, 07-106. Sage, Thousand Oaks, California, USA.
- Merritt, R. W., D. H. Ross, and G. H. Larson. 1982. Influence of stream temperatures and seston on the growth and production of overwintering larval black flies (Diptera: Simuliidae). *Ecology* 63:1322–1331.
- Mörschel, F. M. 1999. Use of climatic data to model the presence of oestrid flies in caribou herds. *Journal of Wildlife Management* 63:588–593.
- Mörschel, F. M., and D. R. Klein. 1997. Effects of weather and parasitic insects on the behavior and group dynamics of caribou of the Delta herd, Alaska. *Canadian Journal of Zoology* 75:1659–1670.
- Nielsen, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. *Ursus* 13:45–56.
- Niemi, G. J., and M. E. McDonald. 2004. Application of ecological indicators. *Annual Review of Ecology, Evolution, and Systematics* 35:89–111.
- Nilssen, A. C. 1997. Effect of temperature on pupal development and eclosion dates in the reindeer oestrids *Hypoderma tarandi* and *Cephenemyia trompe* (Diptera: Oestridae). *Environmental Entomology* 26:296–306.
- Nilssen, A. C. 2006. Pupal biology and metamorphosis behaviour. Pages 124–139 in D. D. Colwell, M. J. R. Hall, and P. J. Scholl, editors. The oestrid flies: biology, host-parasite relationships, impact and management. CABI, Oxfordshire, UK.
- Nilssen, A. C., and J. R. Anderson. 1995. Flight capacity of the reindeer warble fly, *Hypoderma tarandi* (L.), and the reindeer nose bot fly, *Cephenemyia trompe* (Modeer) (Diptera: Oestridae). *Canadian Journal of Zoology* 73:1228–1238.
- Nilssen, A. C., and R. E. Haugerud. 1994. The timing and departure rate of larvae of the reindeer warble fly *Hypoderma* (= *Oedemagena*) *tarandi* (L.) and the reindeer nose bot fly *Cephenemyia trompe* (Modeer) (Diptera: Oestridae) from the reindeer. *Rangifer* 14:113–122.
- Post, E., et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325:1355–1358.
- Quinlan, R., M. S. V. Douglas, and J. P. Smol. 2005. Food web changes in arctic ecosystems related to climate warming. *Global Change Biology* 11:1381–1386.
- Roy, D. B., P. Rothery, D. Moss, E. Pollard, and J. A. Thomas. 2001. Butterfly numbers and weather: predicting historical

- trends in abundance and the future effects of climate change. *Journal of Animal Ecology* 70:201–217.
- Russell, D. E., A. M. Martell, and W. A. C. Nixon. 1993. Range ecology of the Porcupine caribou herd in Canada. *Rangifer Special Issue* 8:1–168.
- Russell, D. E., R. G. White, and C. J. Daniel. 2005. Energetics of the Porcupine caribou herd: a computer simulation model. Technical Report Series Number 431. Canadian Wildlife Service, Ottawa, Ontario, Canada.
- Scheer, N. A. A. 2008. The effect of Oestridae fly parasites on the body condition of female Porcupine caribou. Thesis. University of Maryland, College Park, Maryland, USA.
- Schneider, S. H., and T. L. Root. 1996. Ecological implications of climate change will include surprises. *Biodiversity and Conservation* 5:1109–1119.
- Skarin, A., Ö. Danell, R. Bergström, and J. Moen. 2008. Summer habitat preferences of GPS-collared reindeer *Rangifer tarandus tarandus*. *Wildlife Biology* 14:1–15.
- Slansky, F. 2007. Insect/mammal associations: effects of cuterebrid bot fly parasites on their hosts. *Annual Review of Entomology* 52:17–36.
- Sommerman, K. M., R. I. Sailer, and C. O. Esselbough. 1955. Biology of Alaskan black flies (Simuliidae, Diptera). *Ecological Monographs* 25:345–385.
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297:1292–1296.
- Swets, J. A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240:1285–1293.
- Teklehaimanot, H. D., J. Schwartz, A. Teklehaimanot, and M. Lipsitch. 2004. Weather-based prediction of *Plasmodium falciparum* malaria in epidemic-prone regions of Ethiopia II. Weather-based prediction systems perform comparably to early detection systems in identifying times for interventions. *Malaria Journal* 3:44.
- Vincente, J., Y. Fierro, M. Martínez, and C. Gortázar. 2004. Long-term epidemiology, effect on body condition and interspecific interactions of concomitant infection by nasopharyngeal bot fly larvae (*Cephenemyia auribarbis* and *Pharyngomyia picta*, Oestridae) in a population of Iberian red deer (*Cervus elaphus hispanicus*). *Parasitology* 129:349–361.
- Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. *Global Change Biology* 15:2626–2633.
- Weladji, R. B., O. Holand, and T. Almoy. 2003. Use of climatic data to assess the effect of insect harassment on the autumn weight of reindeer (*Rangifer tarandus*) calves. *Journal of Zoology* 260:79–85.
- Weladji, R. B., D. R. Klein, O. Holand, and A. Mysterud. 2002. Comparative response of *Rangifer tarandus* and other northern ungulates to climatic variability. *Rangifer* 22:33–50.
- Whitfield, P. H., and D. Russell. 2005. Recent changes in seasonal variations of climate within the range of northern caribou populations. *Rangifer Special Issue* 16:11–18.
- Witter, L. A., C. J. Johnson, B. Croft, A. Gunn, and M. P. Gillingham. 2012. Behavioural trade-offs in response to external stimuli: time allocation of an Arctic ungulate during varying intensities of harassment by parasitic flies. *Journal of Animal Ecology* 81:284–295.
- Wulder, M., and T. Nelson. 2003. EOSD land cover classification legend report. Canadian Forest Service, Natural Resources Canada, Victoria, British Columbia, Canada.
- Zalom, F. G., P. B. Goodell, L. T. Wilson, W. W. Barnett, and W. J. Bentley. 1983. Degree-days: the calculation and use of heat units in pest management. University of California Division of Agriculture and Natural Resources Leaflet 21373, Berkeley, California, USA.

SUPPLEMENTAL MATERIAL

Appendix A

Candidate multinomial logistic regression (mlogit) models of mosquito activity on the Bathurst caribou post-calving and summer range, 2007–2009. We also report 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 models within the temporal, weather, habitat, and combination themes (*Ecological Archives* A022-099-A1).

Appendix B

Candidate multinomial logistic regression (mlogit) models of black fly activity on the Bathurst caribou post-calving and summer range, 2007–2009. We also report 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 models within the temporal, weather, habitat, and combination themes (*Ecological Archives* A022-099-A2).

Appendix C

Candidate logistic regression models of oestrid fly presence on the Bathurst caribou post-calving and summer range, 2007–2009. We also report number of parameters (K), 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 models within the temporal, weather, habitat, and combination themes (*Ecological Archives* A022-099-A3).

Appendix D

Coefficients (β) and 95% confidence intervals (CI) from multinomial logistic regression (mlogit) models of mosquito and black fly activity and from logistic regression model of oestrid presence on the Bathurst caribou post-calving and 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 are scaled by a factor of 1000 (*Ecological Archives* A022-099-A4).